

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

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

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

*Keywords:* cryosphere, ecosystem response, environmental observatories

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

## The cryosphere

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

Permafrost (figure 2a) is widespread in the Arctic and boreal regions of the Northern Hemisphere, with the permafrost zone occupying about 24% of the exposed land area. Most of this (78%) occurs in lowlands below 1000 meters (m) of elevation, whereas deposits of alpine permafrost are widely distributed. Changes in permafrost are typically documented by two metrics: temperature and the *depth to the permafrost*, which is defined as the *active layer*, which in turn is the surface layer that thaws seasonally. Since the 1980s, permafrost temperatures have generally increased between 0.5° and 2°C when measured at about 10 m, a depth at which seasonal variations cancel each other out and thus yield a seasonally constant value (Romanovsky et al. 2007). At some Russian sites, where many data are available, the active layer increased by 1.7–5.5 centimeters (cm) per year over the 10-year period between 1997 and 2007

(Mazhitova et al. 2008), whereas other sites have shown little change (Zamolodchikov et al. 2008). However, recent data have shown that active-layer depth measurements alone may obscure the degradation of permafrost, because the ground

surface subsides as permafrost thaws and internal ice melts. This subsidence process (called *thermokarst*) can radically restructure surface hydrology by altering the dynamics of water bodies, initiating or expanding surface channel

incision, and drying surface soil layers. Observations near Toolik Lake, Alaska, have shown rapid mass wasting of surface soils undergoing thaw, which resulted in an increased loading of suspended sediment in streams, with direct and indirect effects on stream biota (Bowden et al. 2008). In the McMurdo Dry Valleys of Antarctica, enhanced incision of stream water into massive subsurface ice has caused one river to flow underground for some distance. At Niwot Ridge in Colorado, increasing water flow and solute concentrations in early autumn have been attributed to the melting of alpine permafrost (Caine 2010).

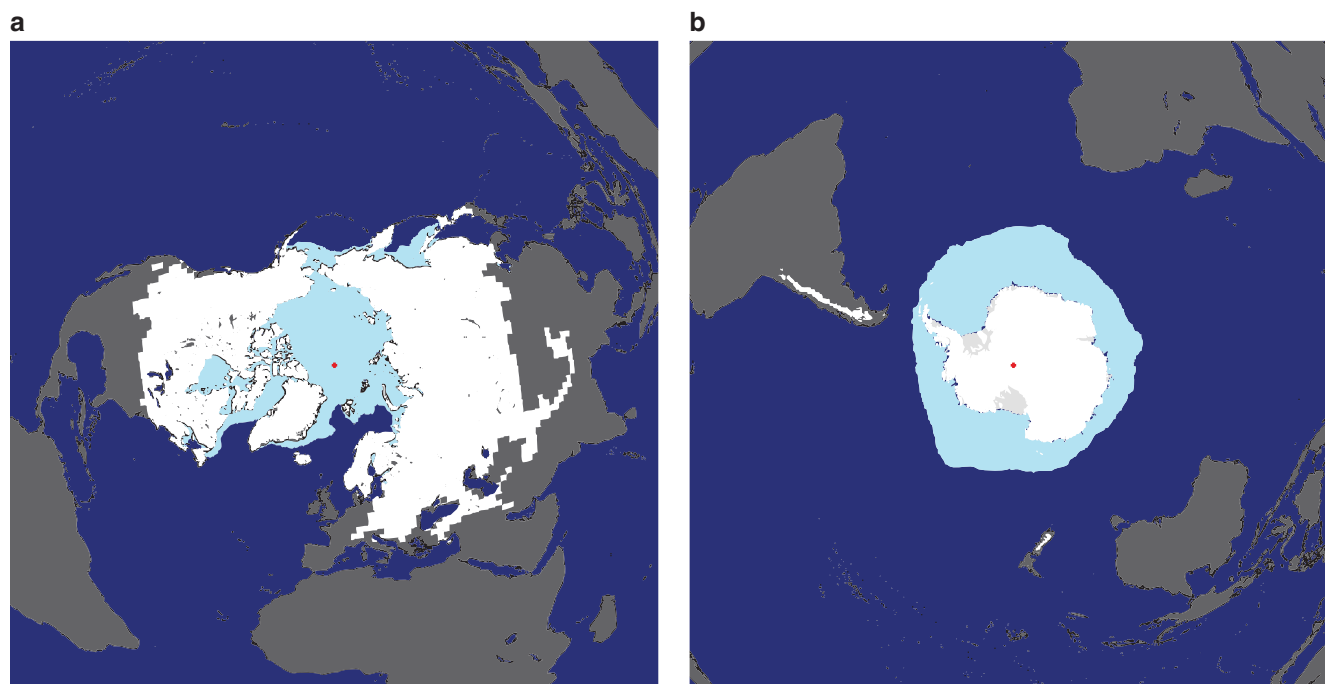
One iconic and highly conspicuous feature of global warming is glacier recession (figure 2b).

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

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

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

<sup>a</sup>See table 2 for the site abbreviations.



**Figure 1. Approximate geographic limits of the cryosphere. (a) January climatology of Northern Hemisphere sea ice (measured between 1979 and 2005) and snow extent (measured between 1967 and 2005) with the North Pole referenced (the red dot). (b) September climatology of Southern Hemisphere sea ice (measured between 1979 and 2003) and snow extent (measured between 1987 and 2002) with the South Pole referenced (the red dot). Source: Reprinted from John Maurer, Atlas of the Cryosphere. National Snow and Ice Data Center (2007; <http://nsidc.org/data/atlas>).**



**Figure 2.** Examples of the cryosphere. (a) Winter eastern forest, Mount Washington, New Hampshire (Photograph: Jerry and Marcy Monkman, [www.ecophotography.com](http://www.ecophotography.com)); (b) Melting sea ice and an iceberg, Charcot Island, Antarctic Peninsula (Photograph: Grace K. Saba, Rutgers University); (c) Massive ice exposed by degrading permafrost, Noatak National Preserve, Arkansas (Photograph: Edward A. G. Schuur); (d) Dana Glacier, Sierra Nevada, California. The top panel is the glacier in 1883 (Photograph: I. C. Russell, US Geological Survey); the bottom panel is from 2004 (Photograph: Hassan Basagic).

Glaciers have been receding worldwide since the end of the Little Ice Age in the late 1800s, although regional and temporal variations in recession have occurred (Dyurgerov and Meier 2000). In recent decades, glacier-mass loss has accelerated, with the increased rate ascribed to increased temperatures. Glacier change in the United States reflects these global trends through area losses over the past century of 34%–56% in the Sierra Nevada and the Cascades of Oregon and Washington and about 40% at Niwot Ridge, in the Colorado Front Range. In contrast to these observations and to those elsewhere in the alpine Southern Hemisphere, glaciers in the McMurdo Dry Valleys of Antarctica appear to be in equilibrium, since their positions have not changed

since their observation began in 1993 (Fountain et al. 2006). The removal of water from long-term storage in glacial ice increases summer streamflow and global sea level. However, as the mass of glaciers declines, their ability to support summer streamflow declines, and they decrease in their ability to buffer the watersheds against drought.

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

1970s, widespread decreases in sea ice have been recorded throughout most of the Arctic at an average rate of 3% loss per decade (Comiso and Nishio 2008). In contrast, decreases in Antarctic sea ice have been regionally confined and juxtaposed against regions of increasing sea ice, such that the average rate of change overall is a slight increase of 1% per decade. Changes in sea ice alter the extent and distribution of foraging platforms for larger mammals and refuge habitat for smaller species. At the Palmer Peninsula, seasonal sea-ice cover has been shrinking at astonishing rates because of increases in onshore winds driven by hemispheric changes in atmospheric circulation. The duration of sea-ice cover has declined by 85 days since 1978 (Stammerjohn et al. 2008).

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

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

by 21 days over the past 53 years (Campbell et al. 2010), which has led to major changes in terrestrial and aquatic ecosystems.

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

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

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

Prolonged, systematic studies of this type are a key contribution of LTER. The LTER Network of sites facilitates long-term observations, experiments, and comparative studies that enable us to identify common processes and mechanisms across diverse ecosystems. The highly interdisciplinary nature of LTER helps to quickly reveal interpretations of

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

Site	Abbreviation	Record	Continental glacier	Alpine glacier	Sea ice	Lake ice	Continuous permafrost	Discontinuous permafrost	Seasonal snow	Transient snow
McMurdo	MCM <sup>1</sup>	1988–2009	X		X		X		X	
Arctic Tundra	ARC <sup>1</sup>	1988–2008				X	X		X	
Niwot Ridge	NWT <sup>1</sup>	1952–2006		X		X		X	X	
Bonanza Creek	BNZ <sup>1</sup>	1988–2009						X	X	
Palmer	PAL <sup>1</sup>	1989–2010	X		X		X		X	
Loch Vale	LWV <sup>2</sup>	1993–2008		X		X		X	X	
Marcell	MAR	1961–2010							X	
North Temperate Lakes	NTL <sup>1</sup>	1978–2010				X			X	
Hubbard Brook	HBR <sup>1,3</sup>	1964–2007							X	
Harvard Forest	HFR <sup>1</sup>	1964–2002							X	
Kellogg	KBS <sup>1</sup>	1988–2010							X	
Shortgrass Steppe	SGS <sup>1</sup>	1969–2010							X	
Sevilleta	SEV <sup>1,4</sup>	1991–2010							X	
Fernow	FER <sup>3</sup>	1951–2007								X
Konza	KNZ <sup>1</sup>	1982–2011								X
Plum Island	PIE <sup>1</sup>	1950–2004							X	X
Coweeta	CWT <sup>1,3</sup>	1950–2009								X
Baltimore	BES <sup>1</sup>	2000–2009								X
Andrews Forest	AND <sup>1,3</sup>	1957–2007							X	X
Jornada	JRN <sup>1,3</sup>	1983–2009								X
Olympic	OLY <sup>5</sup>	1962–2009								X

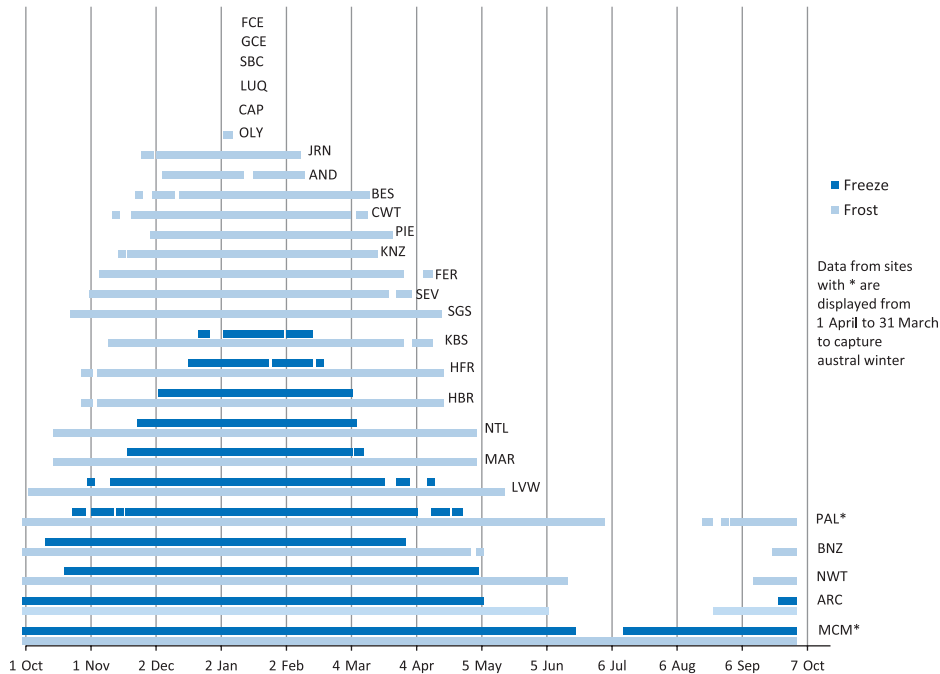
Note: The superscript number next to the abbreviation refers to the sponsoring agency for that site: 1, US LTER Network site; 2, US Geological Survey Water, Energy, and Biochemical Budgets site; 3, US Department of Agriculture Experimental Forest and Range site; 4, National Wildlife Refuge; 5, State Experimental Forest. Record refers to the length of the air-temperature record used to estimate frost and freezing duration at each location.

causes and consequences and needed adjustments of monitoring approaches to catch signals of previously unmonitored or unanticipated system behaviors. Here, we present some notable examples of ecological and biogeochemical changes in response to cryosphere loss.

**Changes in populations and trophodynamic implications.** Decadal-scale declines or distributional shifts in snow- and ice-dependent species are now extensive and well documented (Chapin et al. 2005). When ice-dependent species suffer habitat loss, the changes in frozen habitats (glaciers, sea ice, snowpacks, and permafrost) impose both bottom-up and top-down forcings on terrestrial and aquatic ecosystems. Ice loss affects ecosystems directly through the loss of physical habitat and through alterations in thermal conditions and indirectly by altering light and nutrient supply to primary producers. Both Arctic and Antarctic sea ice harbor a resident microbial community of diatoms, other phytoplankton, bacteria, and protozoan grazers that contributes to the total primary production of polar seas. Like sea ice, ice and rock glaciers are habitats for specially adapted species that may disappear as glaciers retreat and their cold, glacier-fed streams disappear. The American pika

(*Ochotona princeps*)—although it is not as well known or charismatic as penguins or polar bears—is attaining new status as a poster child for glacier loss and climate change. Pikas do not hibernate and use subsurface microclimates in rocky debris to persist where surface conditions would preclude their survival. Despite this adaptation, some local pika extinctions in the Northwest have been linked to cold exposure caused by a loss of insulating snow cover (Ray et al. 2012). Permafrost thaw also results in habitat disappearance for its resident species. Because permafrost occurs in so many different habitats in different stages of development, its loss may trigger primary or secondary successions.

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

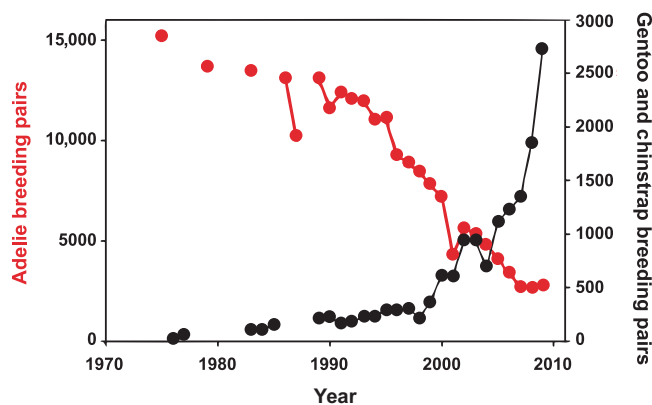


**Figure 3.** Duration of frost and freezing periods at LTER and related long-term research sites, from climate records. See table 2 for the site abbreviations. Frost days are those with long-term mean daily minimum temperatures below 0 degrees Celsius ( $^{\circ}\text{C}$ ); freeze days are those with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

are those that overwinter below ground, since snow insulates the subsurface and moderates its temperature. The shortgrass steppe in the western United States receives little snowfall and therefore presents an endpoint in the spectrum of snow cover. At this semiarid, high-elevation site, snowfall from November to late February has little effect on ecological processes; however, large snowfalls in March and April (after the ground has thawed) strongly influence the subsequent productivity by controlling the availability of water and nutrients (Cayan et al. 2001). Some plants are photosynthetically active in shallow spring snowpacks, giving them a competitive advantage in regions with short growing seasons (Starr and Oberbauer 2003). As the climate warms, the disappearance of snow cover and the increased length of the growing season may benefit some plants, provided that other requirements for growth are not limiting. Many plants in alpine and tundra regions are reliant on snow for water and nutrients and therefore are found in the greatest abundance where the range of snow depths is optimal (Walker et al. 1993). Although the snow-free period will lengthen in a warmer climate, the lack of snow cover during colder months will increase soil temperature variation, making roots susceptible to winter injury. Soil freezing can directly and adversely affect roots by causing cellular damage and can also sever fine roots through frost heaving. Reduced nutrient uptake as a result of root injury has been shown to lower nutrient retention and to increase hydrologic fluxes from soils during the growing season (Fitzhugh et al. 2001).

Changes in habitat and productivity regimes can ripple up the trophic ladder, as is demonstrated extensively in marine food webs. Changing snow and ice conditions alter habitat suitability for many bird species (e.g., petrels, Adeline penguins [*Pygoscelis adeliae*]) and limit the physical space available for habitation (Micol and Jouventin 2001, Weimerskirch et al. 2003). The huge populations of krill in Antarctic marginal sea-ice zones serve in turn as a major food resource for a suite of large predators, including seabirds, seals, and whales. Sea-ice microbial communities serve as a principal food source for juvenile krill, which also hide from predators in under-ice cryptic spaces. Therefore, the regional decline in the duration and extent of sea-ice cover in the Bellingshausen and Amundsen Seas has resulted in declining

abundance and ranges of Antarctic krill (*Euphausia superba*), possibly the most numerous metazoan species on Earth. Atkinson and colleagues (2004) documented large-scale, order-of-magnitude declines in krill populations over 50 years in the South Atlantic sector of the Antarctic seas. Meanwhile, the number of salps—pelagic, gelatinous, ice-avoiding tunicates with few predators—has increased; they have, in effect, replaced krill as an intermediate species in Antarctic marine food chains. One of the best-studied examples of the response of predator populations to sea-ice loss is the Adeline penguin, a true Antarctic penguin with strong fidelity to sea ice as a platform for foraging activity (Ducklow et al. 2007). Since 1975, Adeline penguins nesting near Palmer Station have declined by about 80% in response to a host of environmental changes, including habitat loss and altered food availability (figure 4). Fraser and Hofmann (2003) demonstrated that penguin chicks weighing less than 300 grams at fledging had a reduced probability of surviving past the first year. They suggested that changes in the sea-ice season shifted the period of maximum krill stocks away from the penguins' peak foraging season. Over the same period, two subpolar species—chinstrap (*Pygoscelis antarcticus*) and gentoo penguins (*Pygoscelis papua*)—have successfully immigrated to the region and now constitute half of the total penguin population in the region. The mechanisms behind these shifts and their long-term outcome are unclear (Trivelpiece et al. 2011). The recent loss of sea ice could boost primary productivity in the Arctic Ocean by a factor of two or three. In the northern Bering Sea, primary-productivity changes caused by warming



**Figure 4.** Populations of ice-dependent (*Adelie*) and ice-tolerant (*chinstrap* and *gentoo*) penguins near Palmer Station, Antarctica, measured between 1976 and 2009. Source: Adapted from Ducklow and colleagues (2007).

and sea-ice loss have resulted in a dramatic reorganization of the ecosystem (Grebmeier et al. 2006). This shallow marine ecosystem was formerly characterized by high primary productivity and efficient export to the bottom, which supports a high stock of benthic prey for diving ducks and walrus. With the loss of sea ice and the warming of the water column, the export of surface productivity into the benthos has declined, which has caused a switch from a system with top predators sustained by benthic prey to one dominated by pelagic fish.

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

preferred food for Antarctic krill (see above)—are being replaced by less-palatable cryptophytes. Glacial inputs change light availability by stabilizing the surface-water column and possibly stimulate growth selectively by adding limiting micronutrients (Dierssen et al. 2002). Melting glaciers and sea ice also transfer airborne pollutants stored in the snow and ice to the marine environment.

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

In cold regions, nutrient cycling is closely coupled with snowpack dynamics, with much of the annual export of stream nutrients occurring in winter, when biological uptake is low. Changes in the snowpack alter hydrology, which affects the amount, timing, and magnitude of spring snowmelt. The resulting changes in streamflow not only affect nutrient transport but, when they are combined with changes in temperature, also affect aquatic habitats, causing potential shifts in species assemblages. Nutrients accumulate in the snowpack over winter and are released in an ionic pulse during the first portion of snowmelt (Johannessen and Henriksen 1978). Although snowmelt can be an important source of nutrients and water early in the growing season, it can also cause episodic acidification in areas with high atmospheric deposition and poorly buffered soils (e.g., Schaefer et al. 1990). The soils beneath the snowpack are also an important source of nutrients during winter and early spring. The snowpack regulates soil temperatures, keeping them warm enough for many biologically mediated reactions. Snow fence experiments, which enhance winter snow accumulation, have shown that higher rates of soil microbial respiration and nitrogen mineralization occur under deeper snowpacks in subalpine forest and Arctic tundra environments because of warmer soil temperatures that result from the thermally insulating effects of the snow (Schimel et al. 2004). In contrast, in boreal spruce and temperate hardwood forests, thin winter snowpacks increase the frequency and depth of soil freezing, which results in elevated summer nitrogen emissions that are probably a result of reduced nitrate uptake by damaged roots and by root decomposition (Fitzhugh et al. 2001, Maljanen et al. 2010). Fluxes of carbon dioxide ( $\text{CO}_2$ ) mirror those of nitrogen, and the timing and magnitude of the nitrogen and  $\text{CO}_2$  fluxes in all cases

depends on plant species. Elevated nitrogen mineralization contributes significantly to fluxes of greenhouse gases and to the cycling of nitrogen and carbon. In the mixed-grass prairie of North America, greater snowpack increased soil moisture by midsummer, which resulted in increased soil respiration (Chimner and Welker 2005) and increased plant invasions (Blumenthal et al. 2008).

But most of the attention to the biogeochemical consequences of cryosphere loss has been focused on the potential for changes in carbon storage and release. Arctic permafrost contains twice the  $\text{CO}_2$  found in the atmosphere, which dramatically demonstrates the potential for altering the climate as further warming occurs. Site-specific information can provide some indication as to the future release rate of carbon from thawing permafrost. A recent group of studies was focused on an upland thermokarst site near Denali National Park in Alaska, where changes in plant and soil processes were studied as a function of time since the thermokarst disturbance was initiated. The studies showed that increased permafrost thaw and ground-surface subsidence increased net and gross primary productivity as plant growth was stimulated by a thaw (Vogel et al. 2010). Plant species composition changed along with changes in plant growth rates as graminoid-dominated moist acidic tundra shifted to shrub-dominated tundra with increased rates of thawing. The increased carbon uptake by plants initially offset the greater ecosystem respiration, such that this thermokarst was a net sink of carbon 15 years after the initiation of the thaw, even though decomposition of older carbon deep in the soil was already taking place (Schuur et al. 2009). Over more decades of thaw, plant growth rates remained high, but increased old soil carbon losses eventually offset the greater carbon uptake, and this thermokarst became a net source of carbon to the atmosphere.

In a contrasting study of lowland thermokarst in three Canadian peatlands, the carbon accumulation in surface soil organic matter was higher in unfrozen bogs and in areas where permafrost had degraded than in areas where permafrost was intact (Turetsky et al. 2007). This growth in surface soil carbon accumulation was consistent with the Alaskan upland study, but the equivalent net ecosystem carbon exchange measurements were not available to determine whether the thawed permafrost peat ecosystems were overall net sources or sinks of carbon. Permafrost thaw in this lowland system promoted the release of methane ( $\text{CH}_4$ ) because waterlogged conditions predominated in *Sphagnum* moss lawns that replaced the feather moss (*Hylocomium splendens*) and black spruce (*Picea mariana*) forest in locations where permafrost degraded. This  $\text{CH}_4$  release was hypothesized to potentially offset the observed surface soil carbon accumulation for at least for 70 years, until plant and ecosystem succession in the moss lawn created conditions more like those in the unfrozen bogs, which stored surface soil carbon but released only small amounts of  $\text{CH}_4$ . The release of  $\text{CH}_4$  is a common pathway of carbon loss in lowland thermokarst, where drainage is restricted

(Myers-Smith et al. 2007), and  $\text{CH}_4$  has 25 times greater heat-trapping capacity than  $\text{CO}_2$  on a century timescale. However, decreased total carbon emissions in anaerobic systems can partially offset the increased radiative forcing of  $\text{CH}_4$  release, which possibly makes the net radiative forcing of increased carbon losses in lowland and upland thermokarst more similar than what the difference in heat-trapping capacity between  $\text{CO}_2$  and  $\text{CH}_4$  would initially suggest.

The oceanic sink for anthropogenic  $\text{CO}_2$  is large and lessens the potential greenhouse effect by limiting  $\text{CO}_2$  accumulation in the atmosphere. The current (2009) net annual carbon uptake by the ocean is  $2.3 \pm 0.4$  petagrams (Pg) of carbon per year, compared to 2.4 Pg of carbon per year for land, but the land uptake is partially offset by the  $1.1 \pm 0.7$  Pg of carbon per year in releases caused by deforestation (Le Quéré et al. 2009). As the ocean warms and its inventory of  $\text{CO}_2$  increases, the oceanic sink is expected to weaken. Oceanic  $\text{CO}_2$  uptake is governed by gas exchange across the air–sea interface, so the regional allocation of  $\text{CO}_2$  uptake is primarily a function of the area of sea surface involved. This fraction has been predicted to increase as ice melts and productivity increases, which will expose new ocean areas to solar irradiance (Peck et al. 2010). The Arctic Ocean constitutes just 3% of the total ocean area and is mostly covered by sea ice, which blocks gas exchange, but it accounts for 5%–14% of the total ocean  $\text{CO}_2$  uptake. New observations suggest, however, that the recent dramatic loss of sea ice has been accompanied by decreased rather than increased  $\text{CO}_2$  uptake (Cai et al. 2010), which is counter to current understanding and predictions. The rapid, diverse, and complex changes wrought by cryosphere loss constitute a major scientific challenge that demands new large-scale observing systems on land and in the ocean to provide new observational infrastructure as a resource for coordinated experimental studies performed by the LTER Network and other scientists.

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

Cryosphere loss will result in far-reaching social, economic, and geopolitical impacts, but a detailed treatment is beyond the scope of this synthesis. Most attention has been devoted to the impacts associated with a loss of snow cover, glacier melting, and sea-level rise, which are treated elsewhere (Kundzewicz et al. 2007). Thawing permafrost will also have important social consequences, because it can destabilize engineered structures and can cause destructive slides, flows, and slumps. Changes in snow cover can have important consequences for humans and may affect many diverse activities, including agriculture, recreation, tourism, engineering, commerce, and energy production. For example, the New Hampshire ski industry has abandoned low-elevation ski areas in the southern part of the state since the 1970s, in part because of climate warming, in favor of ski areas at higher elevations in the north (Hamilton et al. 2003). Skiing contributes about \$1 billion annually to the economy of Utah, but recent climate change



evaluations of the ski industry there suggest that it is at risk in the next several decades (Lazar and Williams 2008). A similar impact is anticipated for the Pacific Northwest. The most important effect is the influence on streamflow. In many semiarid regions of the world, such as the southwestern United States, snowmelt from mountain snowpacks is the dominant source of water for human consumption and irrigation. Therefore, changes in the amount and timing of snowmelt in mountainous areas could affect stream ecosystem services, such as drinking-water supply, wastewater assimilation, and hydropower. Lesser amounts of snow could also have an impact on agriculture and the ability to produce food, both through an increased occurrence of drought and through an inadequate supply of water for irrigation. Some evidence suggests that changes in snowmelt may also increase the risk of forest fires. In the western United States, earlier snowmelt dates correspond to increased wildfire frequency, because soils and vegetation are becoming drier and the period of potential ignition is lengthening (Westerling et al. 2006). Estimates of sea-level rise to 2100 have been continually revised upward since the 2007 report of the Intergovernmental Panel on Climate Change (Solomon et al. 2007) as new data and modeling have been developed. At the time of this writing, the rise in sea level by the end of the century is projected to be about 1 m (Pfeffer et al. 2008). The economic cost of a 1-m rise in sea level is estimated to exceed \$1 trillion (Anthoff et al. 2010), with enormous social and political dislocations as residents of low-lying regions are forced to move to higher ground.

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

## Conclusions

Earth is distinguished in the solar system by the coexistence of water in its three phases: solid (frozen), liquid (melted), and gas (evaporated). The solid phase—the global cryosphere in all its components: glaciers; snow; permafrost; sea, lake, and river ice—is arguably the most rapidly changing element of the Earth system. Cryosphere loss can be viewed

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

## Acknowledgments

The authors wish to thank the funding provided by the National Science Foundation's (NSF) Long Term Ecological Research (LTER) Network for supporting our long-term studies, in which we track the ecosystem response to the disappearing cryosphere. The LTER Network office supported the workshop from which this article is derived. Table 2 and figure 3 were kindly contributed by Julia A. Jones, Kendra L. Hatcher, and Evan S. Miles. Valuable contributions were made by Mike Antolin, Anne Giblin, John Hobbie, John Magnusson, Anne Nolin, Bruce Peterson, Bill Sobczak, and Will Wolheim. We greatly appreciate all who participated. Fred Swanson offered many helpful suggestions, and David Foster carefully edited the manuscript (and it is much improved). NSF LTER Site Grants OPP 0823101, OPP 1115245, DEB 1114804, DEB-1026415, DEB-0620579, and DEB-1027341 supported the authors during the preparation of this article.

## References cited

- Anthoff D, Nicholls R, Tol RSJ. 2010. The economic impact of substantial sea-level rise. *Mitigation and Adaptation Strategies for Global Change* 15: 321–335.
- Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100–103.
- Baron JS, Schmidt TM, Hartman MD. 2009. Climate-induced changes in high elevation stream nitrate dynamics. *Global Change Biology* 15: 1777–1789.
- Blumenthal D, Chimner RA, Welker KM, Morgan JA. 2008. Increased snow facilitates plant invasion in mixedgrass prairie. *New Phytologist* 179: 440–448.

- Bowden WB, Gooseff MN, Balsler A, Green A, Peterson BJ, Bradford J. 2008. Sediment and nutrient delivery from thermokarst features in the foothills of the North Slope, Alaska: Potential impacts on headwater stream ecosystems. *Journal of Geophysical Research* 113 (Art. G02026). doi:10.1029/2007JG000470.
- Cai W-J, et al. 2010. Decrease in the CO<sub>2</sub> uptake capacity in an ice-free Arctic Ocean basin. *Science* 329: 556–559.
- Caine N. 2002. Declining ice thickness on an alpine lake is generated by increased winter precipitation. *Climatic Change* 54: 463–470.
- . 2010. Recent hydrologic change in a Colorado alpine basin: An indicator of permafrost thaw? *Annals of Glaciology* 51: 130–134.
- Campbell JL, Ollinger SV, Flerchinger GN, Wicklein H, Hayhoe K, Bailey AS. 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Hydrological Processes* 24: 2465–2480.
- Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH. 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* 82: 399–415.
- Chapin FS III, et al. 2005. Polar systems. Pages 717–743 in Hassan R, Scholes R, Ash N, eds. *Ecosystems and Human Well-being: Current State and Trends*. Island Press.
- Chimner RA, Welker JM. 2005. Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA. *Biogeochemistry* 73: 257–270.
- Comiso JC, Nishio F. 2008. Trends in the sea ice cover using enhanced and compatible AMSR-E, SSM/I, and SMMR data. *Journal of Geophysical Research* 113 (Art. C02S07). doi:10.1029/2007JC004257.
- Déry SJ, Brown RD. 2007. Recent Northern Hemisphere snow cover extent trends and implications for the snow-albedo feedback. *Geophysical Research Letters* 34 (Art. L22504). doi:22510.21029/22007GL031474.
- Dierssen HM, Smith RC, Vernet M. 2002. Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula. *Proceedings of the National Academy of Sciences* 99: 1790–1795.
- Driscoll CT, Lambert KF, Chapin FS III, Nowak DJ, Spies TA, Swanson FJ, Kitteridge DB Jr, Hart CM. 2012. Science and society: The role of long-term studies in environmental stewardship. *BioScience* 62: 354–366.
- Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W. 2007. Marine pelagic ecosystems: The west Antarctic peninsula. *Philosophical Transactions of the Royal Society of London B* 362: 67–94.
- Dyurgerov MB, Meier MF. 2000. Twentieth century climate change: Evidence from small glaciers. *Proceedings of the National Academy of Sciences* 97: 1406–1411.
- Fitzhugh RD, Driscoll CT [Jr], Groffman PM, Tierney GL, Fahey TJ, Hardy JP. 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. *Biogeochemistry* 56: 215–238.
- Fountain AG, Nylén TH, MacClune KL, Dana GL. 2006. Glacier mass balances (1993–2001), Taylor Valley, McMurdo Dry Valleys, Antarctica. *Journal of Glaciology* 52: 451–462.
- Fraser WR, Hofmann EE. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* 265: 1–15.
- Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL. 2006. A major ecosystem shift in the northern Bering Sea. *Science* 311: 1461–1464.
- Hamilton LC, Rohall DE, Brown BC, Hayward GF, Keim BD. 2003. Warming winters and New Hampshire's lost ski areas: An integrated case study. *International Journal of Sociology and Social Policy* 23: 52–73.
- Johannessen M, Henriksen A. 1978. Chemistry of snow meltwater: Changes in concentration during melting. *Water Resources Research* 14: 615–619.
- Knapp AK, et al. 2012. Past, present, and future roles of long-term experiments in the LTER network. *BioScience* 62: 377–389.
- Kofinas GP, Chapin FS III, BurnSilver S, Schmidt JI, Fresco NL, Kielland K, Martin S, Springsteen A, Rupp TS. 2010. Resilience of Athabaskan subsistence systems to interior Alaska's changing climate. *Canadian Journal of Forest Research* 40: 1347–1359.
- Kundzewicz ZW, Mata LJ, Arnell NW, Döll P, Kabat P, Jiménez B, Miller K, Oki T, Sen Z, Shiklomanov IA. 2007. Freshwater resources and their management. Pages 173–210 in Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, eds. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Lazar B, Williams M. 2008. Climate change in western ski areas: Potential changes in the timing of wet avalanches and snow quality for the Aspen ski area in the years 2030 and 2100. *Cold Regions Science and Technology* 51: 219–228.
- Le Quéré C, et al. 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geoscience* 2: 831–836.
- Magnuson JJ, et al. 2000. Historical trends in lake and river cover in the Northern Hemisphere. *Science* 289: 1743–1746.
- Maljanen M, Alm J, Martikainen PJ, Repo T. 2010. Prolongation of soil frost resulting from reduced snow cover increases nitrous oxide emissions from boreal forest soil. *Boreal Environment Research* 15: 34–42.
- Maurer J. 2007. Atlas of the Cryosphere. National Snow and Ice Data Center. (26 January 2012; <http://nsidc.org/data/atlas>).
- Mazhitova G, Malkova G, Chestnykh O, Zamolodchikov D. 2008. Recent decade thaw depth dynamics in the European Russian Arctic based on the Circumpolar Active Layer Monitoring (CALM) data. Pages 433–438 in Kane DL, Hinkel KM, eds. *Proceedings of the Ninth International Conference on Permafrost*. Institute of Northern Engineering, University of Alaska, Fairbanks.
- Micol T, Jouventin P. 2001. Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie): Human impact compared with environmental change. *Polar Biology* 24: 175–185.
- Myers-Smith IH, McGuire AD, Harden JW, Chapin FS III. 2007. Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest. *Journal of Geophysical Research* 112: 11.
- Nemergut DR, Anderson SP, Cleveland CC, Martin AP, Miller AE, Seimon A, Schmidt SK. 2007. Microbial community succession in unvegetated, recently-deglaciated soils. *Microbial Ecology* 53: 110–122.
- Nolin AW, Daly C. 2006. Mapping “at risk” snow in the Pacific Northwest. *Journal of Hydrometeorology* 7: 1164–1171.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.
- Peck LS, Barnes DKA, Cook AJ, Fleming AH, Clarke A. 2010. Negative feedback in the cold: Ice retreat produces new carbon sinks in Antarctica. *Global Change Biology* 16: 2614–2623.
- Pfeffer WT, Harper JT, O'Neil S. 2008. Kinematic constraints on glacier contributions to 21st-century sea-level rise. *Science* 321: 1340–1343.
- Prowse TD, Wrona FJ, Reist JD, Gibson JJ, Hobbie JE, Lévesque LMJ, Vincent WF. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. *Ambio: A Journal of the Human Environment* 35: 347–358.
- Ray C, Beever E, Loarie S. 2012. Retreat of the American pika: Up the mountain or into the void? In Brodie JF, Post E, Doak D, eds. *Conserving Wildlife Populations in a Changing Climate*. University of Chicago Press. Forthcoming.
- Robertson GP, et al. 2012. Long-term ecological research in a human-dominated world. *BioScience* 62: 342–353.
- Romanovsky VE, Gruber S, Instanes A, Jin H, Marchenko SS, Smith SL, Trombotto D, Walter KM. 2007. Frozen ground. Pages 181–200 in United Nations Environment Programme (UNEP). *Global Outlook for Ice and Snow*. UNEP.
- Schaefer DA, Driscoll CT Jr, van Dreason R, Yatsko CP. 1990. The episodic acidification of Adirondack lakes during snowmelt. *Water Resources Research* 26: 1639–1647.
- Schimel JP, Bilbrough C, Welker JM. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biogeochemistry* 36: 217–227.

- Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459: 556–559.
- Solomon SD, Qin M, Manning Z, Chen M, Marquis KB, Avery T, Tignor M, Miller HL, eds. 2007. *Climate Change 2007: The Physical Science Basis*. Cambridge University Press.
- Stammerjohn SE, Martinson DG, Smith RC, Iannuzzi RA. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research* 55: 2041–2058.
- Starr G, Oberbauer SF. 2003. Photosynthesis of Arctic evergreens under snow: Implications for tundra ecosystem carbon balance. *Ecology* 84: 1415–1420.
- Thompson JR, Wiek A, Swanson FJ, Carpenter SR, Fresco N, Hollingsworth T, Spies TA, Foster DR. 2012. Scenario studies as a synthetic and integrative research activity for long-term ecological research. *BioScience* 62: 367–376.
- Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.
- Turetsky MR, Wieder RK, Vitt DH, Evans RJ, Scott KD. 2007. The disappearance of relict permafrost in boreal north America: Effects on peatland carbon storage and fluxes. *Global Change Biology* 13: 1922–1934.
- Vogel JG, Schuur EAG, Trucco C, Lee H. 2010. The carbon cycling response of arctic tundra to permafrost thaw and thermokarst development. *Journal of Geophysical Research* 114 (Art. G4). doi:10.1029/2008JG000901
- Walker DA, Halfpenny JC, Walker MD, Wessman CA. 1993. Long-term studies of snow–vegetation interactions. *BioScience* 43: 287–301.
- Weimerskirch H, Inchausti B, Guinet C, Barbraud C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* 15: 249–256.
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313: 940–943.
- Williams MW, Losleben M, Caine N, Greenland D. 1996. Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. *Limnology and Oceanography* 41: 939–946.
- Williams MW, Knauf M, Cory R, Caine N, Liu F. 2007. Nitrate content and potential microbial signature of rock glacier outflow. *Earth Surface Processes and Landforms* 32: 1032–1047.
- Wood ME, Kelley JT, Belknap DF. 1989. Patterns of sediment accumulation in the tidal marshes of Maine. *Estuaries* 12: 237–246.
- Zamolodchikov D, Kotov A, Karelin D, Razzhivin V. 2008. Recent climate and active layer changes in northeast Russia: Regional output of Circumpolar Active Layer Monitoring (CALM). Pages 2021–2026 in Kane DL, Hinkel KM, eds. *Proceedings of the Ninth International Conference on Permafrost*. Institute of Northern Engineering, University of Alaska, Fairbanks.

---

*Andrew G. Fountain (andrew@pdx.edu) is a professor in the Department of Geology at Portland State University in Portland, Oregon. John L. Campbell is an ecologist at the US Department of Agriculture Forest Service in Durham, New Hampshire. Edward A. G. Schuur is an associate professor in the Department of Biology at the University of Florida, Gainesville. Sharon E. Stammerjohn is an assistant professor in the Department of Ocean Sciences at the University of California, Santa Cruz. Mark W. Williams is a professor in the Department of Geography at the University of Colorado, Boulder. Hugh W. Ducklow is a senior scientist and director of The Ecosystems Center at the Marine Biological Laboratory in Woods Hole, Massachusetts.*