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Ecological Dynamics Across the Arctic Associated with Recent Climate Change

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At the close of the Fourth International Polar Year, we take stock of the ecological consequences of recent climate change in the Arctic, focusing on effects at population, community, and ecosystem scales. Despite the buffering effect of landscape heterogeneity, Arctic ecosystems and the trophic relationships that structure them have been severely perturbed. These rapid changes may be a bellwether of changes to come at lower latitudes and have the potential to affect ecosystem services related to natural resources, food production, climate regulation, and cultural integrity. We highlight areas of ecological research that deserve priority as the Arctic continues to warm.

While the global mean surface temperature has increased by 0.4°C over the past 150 years, Arctic warming has been two to three times that amount (*1*), a rate exceeding the century-scale warming at the Pleistocene-Holocene transition (*2*) that coincided with widespread vegetation shifts (*3*) and faunal extinctions across the Arctic (*4*). Over the past two to three decades, seasonal minimal sea ice extent throughout the Arctic has declined by 45,000 km^2/year (*5*, *6*), besides breaking up earlier and freezing later (*7*), and annual extent of terrestrial snow cover in the Northern Hemisphere has declined, with further reductions expected (*8*) (Fig. 1). Changes in ecological systems consistent with expected effects of anthropogenic warming have been reported for all biomes on Earth (*9*, *10*). The ecological consequences of climate change in the Arctic remain, however, comparatively underreported despite the magnitude of abiotic changes in the Arctic exceeding those in temperate, tropical, and montane biomes (*11*). Here we review ecological responses to recent Arctic warming and associated changes and highlight priorities for research and policy.

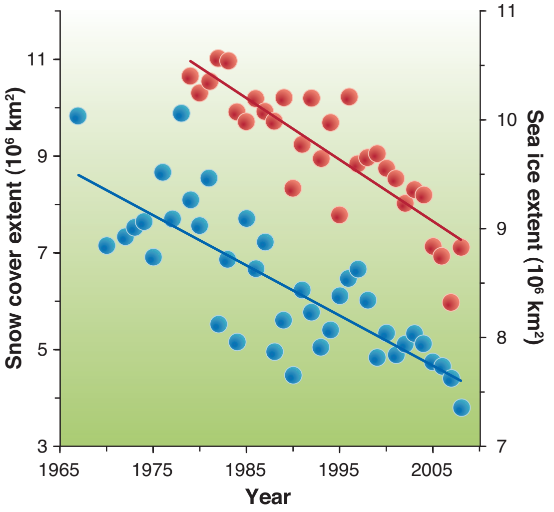

Fig. 1. Reductions in terrestrial snow cover (blue) and sea ice (red) extent during June to August over the Northern Hemisphere since the late 1960s and 1970s, respectively. Data are from the Global Snow Lab, Rutgers University, New Jersey, and the U.S. National Snow and Ice Data Center, University of Colorado, Boulder.

Sudden Direct, Indirect, and Reciprocal Changes Across the Arctic

Changes in temperature, snow, ice-cover, and nutrient availability exert major influences on biological dynamics in the Arctic, and extensive ecological consequences of recent warming-related trends in these abiotic parameters are highlighted briefly here (*12*). For example, earlier onset of the spring melt associated with rapid warming has been linked to lengthening of the growing season in aquatic (*13*) and terrestrial systems (*14*): Plant flowering and invertebrate appearance have advanced by up to 20 days over the past decade in some areas (*14*) (Fig. 2A). Recent episodes of unusually early spring rain in the Canadian Arctic have led to melting, collapse, and washout of subnivean birth lairs of ringed seals (*Pusa hispida*), leaving newborn pups exposed on bare ice, increasing their vulnerability to hypothermia and predation (*15*). Episodic melting may, however, also benefit some animal populations, depending on the degree of melting (ablation). For example, substantial ablation associated with winter warming resulted in reduced mortality, increased fecundity, and increased abundance of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (*16*) (Fig. 2B). Some of the most rapid ecological changes associated with warming have occurred in marine and freshwater environments, associated with changes in sea ice dynamics and external nutrient loading. Species most affected are those with limited distributions and specialized feeding habits that depend on ice for foraging, reproduction, and predator avoidance, including the ivory gull (*Pagophila eburnean*), Pacific walrus (*Odobenus rosmarus divergens*), ringed seal, hooded seal (*Cystophora cristata*), narwhal (*Monodon monoceros*), and polar bear (*Ursus maritimus*) (*12*, *17*). Polar bears, in particular, are experiencing rapid declines in birth rates and survival due to loss of sea ice habitat. In contrast to reduced stratification of Antarctic lakes (*18*), warming in the Arctic has enhanced lake stratification, changed the migration pattern of some fish species (*19*), and increased the likelihood of their colonizing fishless lakes and altering lake ecosystem structure and function (*20*, *21*).

The northward and altitudinal expansion of species' distributions already reported for temperate and north-temperate ecosystems (*22*) are also occurring in the Arctic. Range expansions of Low Arctic trees (*23*) and shrubs (*24*) are a prom-

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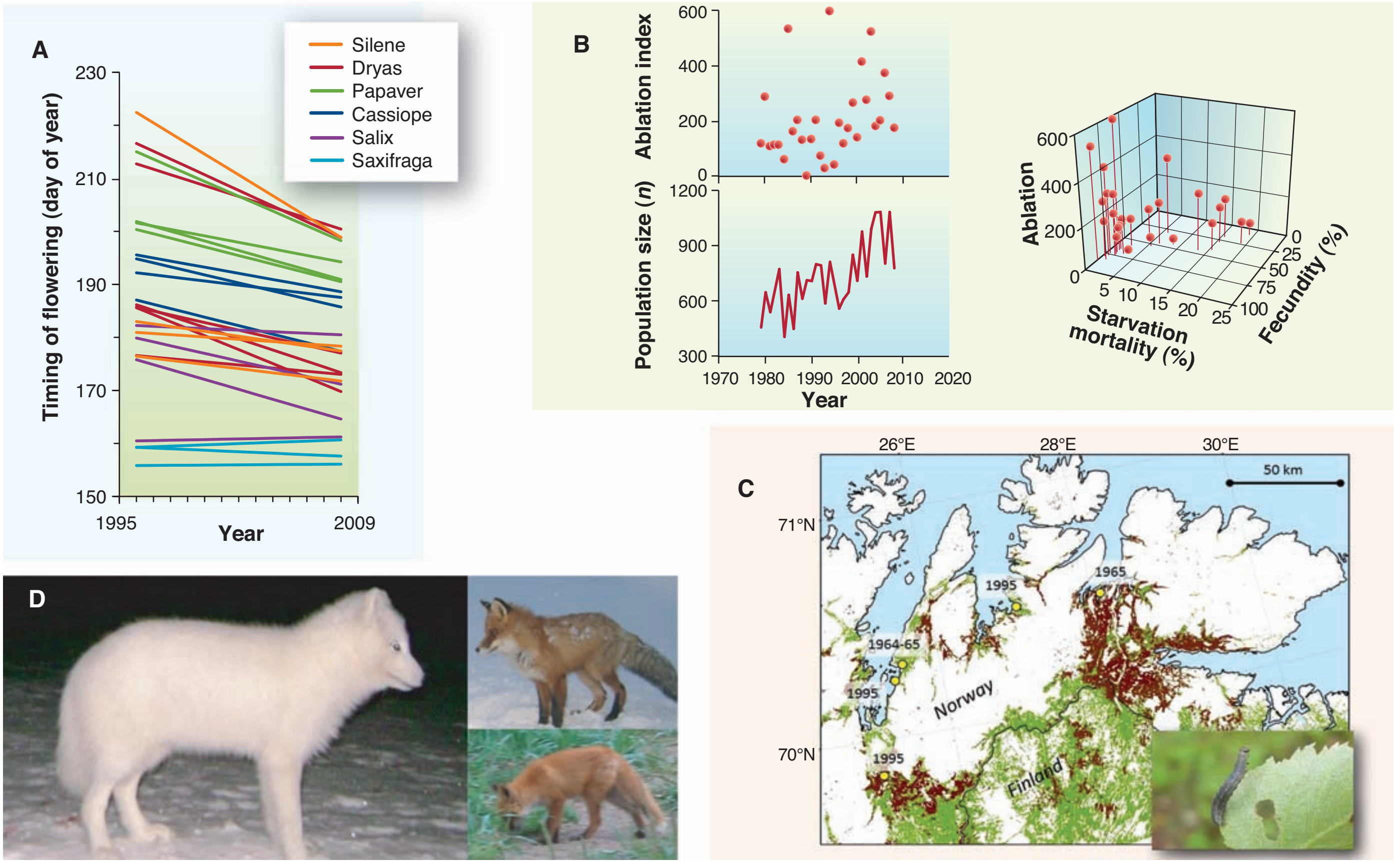

Fig. 2. Direct and rapid responses to recent Arctic climate change have included (**A**) earlier flowering of plants in Greenland [replicate slopes for each genus are based on annual estimates from 1996 to 2008 in Zackenberg; adapted from (*14*)]. (**B**) increased periodic ablation—melting of winter snow—on Svalbard that has promoted a rapid increase in a population of reindeer there through increased fecundity and reduced starvation mortality [adapted from (*16*)]. (**C**) Northward expansion of insect herbivores such as the winter moth in northernmost Fennoscandia (intact mountain birch forest is shown in green, severely defoliated forest during the most recent outbreak in 2005 to 2008 is in dark brown, and tundra beyond the tree line is in white; reports of local winter moth outbreaks before the last extensive outbreak period are indicated by yellow dots and years of observation [modified from (*28*)]. (**D**) Displacement of Arctic foxes (left) by invading red foxes, shown here in Finnmark, Norway (upper right), and on St. Matthew Island, Alaska, USA (lower right), where they have recently established a permanent presence (photos by R. A. Ims and D. R. Klein).

inent example of climate change–induced shifts in distributions. These have broader ecological consequences as well (*25*), including alteration of trace gas exchange (*26*). Hence, shifts in species composition may affect land-atmosphere greenhouse gas balances (*27*). Animal invasions due to range shifts in the Arctic will also alter the dynamics of simple Arctic systems. For example, two species of geometrid moths are rapidly expanding in northern Fennoscandian birch forests (Fig. 2C), consistent with warmer winters and earlier springs (*28*), and their outbreaks are already altering the atmospheric carbon budgets of parts of the Arctic (*29*). Numbers of Arctic fox (*Alopex lagopus*) are declining in parts of the Arctic in conjunction with northward expansion of the range of red foxes (*Vulpes vulpes*), which may itself be a response to warming (*30*) (Fig. 2D).

Not all biological responses to climate change in the Arctic have been direct or as readily apparent. Responses to climate change may be masked by species interactions (*31*), risking that responses are overlooked or misinterpreted as evidence that climate change has no effect on a particular species, or that the strength of species interactions outweighs the effects of abiotic factors on persistence of populations. For instance, in aquatic systems, increases in the proportion of rain in precipitation may enhance nutrient loading of lakes and increase cross-lake fish colonization due to enhanced connectedness, with important cascading effects in lake food webs (*20*, *32*). In Low Arctic Greenland, onset of the plant growing season has advanced in response to warming, whereas the timing of caribou (*R. tarandus*) calving has not (*33*) (Fig. 3A). Consequently, a trophic mismatch has developed, and the peak demand for resources by reproductive females now falls significantly later than the seasonal peak of resource availability, apparently contributing to reduced production and survival of caribou calves (*33*). Similar warming-induced disruptions may have a role in the current Arctic-wide decline of nearly all caribou populations (*34*). Temporal changes in plant-herbivore relationships may also have consequences throughout food webs. The recent, climate-driven collapse of small-rodent cycles (Fig. 3B), for example, threatens to alter trophic interactions and ecosystem processes of which these species are key determinants (*35*, *36*).

Vegetation responses to abiotic changes in the Arctic are not confined to individual growth responses or changes in plant community composition (*37*). Rather, they also influence the dynamics of trace gas exchange between the biosphere and atmosphere, which may ultimately feed back onto climate itself (*37*, *38*). For instance, the aforementioned expansion of shrubs and trees has promoted snow accumulation, increased winter soil temperatures, and enhanced soil microbial activity and nutrient mineralization rates, which collectively may further promote shrub growth (*39*). Experimental studies also indicate potential atmospheric feedback consequences of vegetation response to warming. In the Canadian High Arctic, experimental warming increased by 2 weeks the period during the plant growing season when the tundra acts as a CO_2 sink (*40*). Recent warming has also altered biogeochemical cycles and hydrological cycles across the Arctic, leading to feedbacks to the atmosphere, further complicating prediction of the magnitude of future climate change in the region (*12*, *41*).

Improving Our Understanding of Ecological Complexity in the Arctic

The Arctic is often regarded as a relatively simple system in which species interactions and environment-organism dynamics are straightforward and easily understood. Recent research on the effects of climate change in the Arctic has, however, revealed far greater ecological interconnectedness in this region (*42*, *43*).

The Arctic's structural complexity is evident in nutrient cycling between terrestrial, freshwater, and marine components, which may be subject to rapid modification with future warming. For example, transport of terrestrial carbon into the fjords of northeast Greenland is expected to increase as the ice-free period doubles following the expected 6°C warming over the next century, with implications for increased nutrient input and productivity of fjords and lakes (*44*). Such changes at the interface between terrestrial and aquatic systems have key implications for the dynamics of species whose existence is dependent on aquatic productivity.

Species interactions are also a key component of the complexity of ecological responses to climate change in the Arctic. Increasing summer temperatures may increase insect harassment and parasitism of caribou, potentially reducing the annual caribou harvest by local communities, threatening cultural integrity and subsistence traditions already compromised by encroachment and landscape alteration due to exploitation of northern oil and gas reserves (*42*). Warming may also alter food-web structure in aquatic communities in the Arctic. Studies of 10 first-order streams in Iceland differing in geothermal influence and temperature showed that macro-invertebrate evenness and species overlap decreased with increasing temperature, whereas density of other organisms, notably of filter feeders, increased (*45*). Moreover, food-web complexity increased markedly along this natural temperature gradient, with implications for the sole fish species present (*45*).

Vegetation responses to warming may likewise be more complex than warming experiments suggest. One consistent finding has been that warming results in the expansion of shrubs, in turn leading to a short-term decline in vascular plant diversity (*46*, *47*). Herbivory by caribou and muskoxen (*Ovibos moschatus*), however, constrains the positive effects of warming on the growth of shrubs, but promotes the growth of graminoids (*48*). Although warming is currently insufficient to promote shrub expansion in the High Arctic, graminoids are also promoted there by herbivores. Both reindeer and geese trample and compact the moss layer, resulting in elevation of soil temperature that, together with grazing and fecal deposition, promotes the productivity and expansion of graminoids (*49*), and also productivity in lakes where geese rest (*50*, *51*). Collectively, these findings indicate the need for understanding plant-herbivore interactions in a warming Arctic and their further consequences for below-ground biodiversity, community composition, and ecological processes.

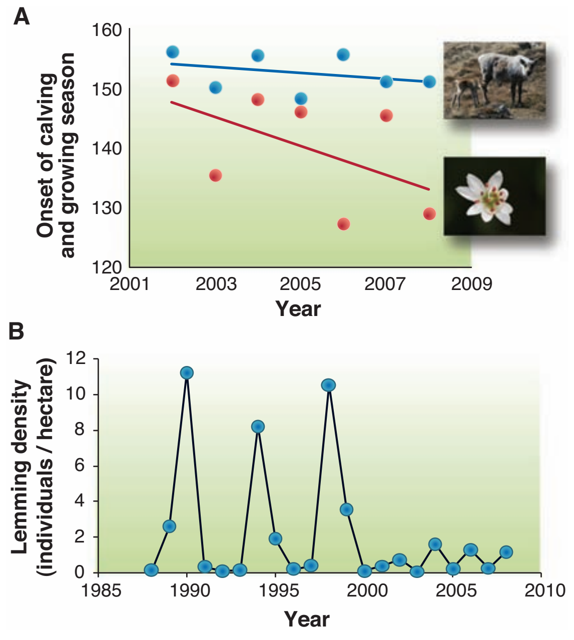

Fig. 3. Complex responses to Arctic climate change that may have broader community and ecosystem consequences. (**A**) A developing trophic mismatch between the timing of caribou calving (blue), which has not changed, and the timing of plant growth (red), which is advancing with warming in Greenland [updated from (*33*)]. (**B**) The recent observed collapse in the population cycles of small rodents, shown here for lemmings in northeast Greenland, as a result of diminished snow cover in the Arctic [from (*36*)].

Priorities for Future Research

Here we focus on areas of research we believe are in need of immediate emphasis.

Conservation. The assumption that the Arctic is species-poor has resulted in little focus on conserving its biodiversity. However, when considering the importance of individual species for supporting ecosystem function or providing key ecosystem services to both traditional culture and emerging Arctic interests such as tourism, low-diversity ecosystems like the Arctic warrant greater conservation attention. There is little functional redundancy among species in Arctic ecosystems, especially on island complexes. Therefore, extirpation or range shifts in the Arctic may precipitate larger and more fundamental changes in ecosystem dynamics compared to those within more speciose ecosystems where loss of individual species may have less immediate consequence for ecosystem processes.

Dynamics outside the growing season. Winter conditions are likely of key importance to the annual Arctic cycle and may exert cascading effects throughout the growing season. Despite long-standing assumptions that winter is a period of inactivity, recent research has demonstrated the importance of winter snow cover to nutrient cycles (*26*) and carbon budgets in the Arctic (*52*). Moreover, one sub-Arctic winter warming episode led to vegetation damage so extensive that plant productivity based on NDVI measurements the following summer was reduced by 26% over at least 1400 km^2 (*53*). As well, a recent study in Greenland reported an unexpectedly large release of methane into the atmosphere at the onset of autumn soil freezing (*54*). Such observations indicate that important components of ecosystem dynamics occur after the growing season has terminated, and that warming events in winter may have disproportionately long-term effects.

Trophic interactions. Trophic interactions modulate ecosystem responses to climate change in the Arctic. Herbivory shapes plant productivity and community responses to warming, which may, in turn, be mediated by changes in decomposer communities and mycorrhizal associations. Such interactions are the basis of complex feedbacks between consumers and resources not easily captured by studies of dynamics at single trophic levels. We urge more studies of the role of climate warming in trophic dynamics, and of species interactions in response to climate change at different trophic levels, especially in aquatic systems, soils, and sediments (Fig. 4A).

Heterogeneity as a buffer against climate change in the Arctic. Although some components of the Arctic respond synchronously to climate forcing, there remains a high degree of heterogeneity in ecological responses to climate change (*55*). Moreover, in contrast to some of the examples given above, there are large areas of the Arctic where little or no change in ecosystems seems to have occurred. In contrast to Antarctica, where numerous invasions of diverse taxonomic groups have been documented (*56*), examples of species invasions in the Arctic are still exceptional (*28*); in the Arctic, most community changes are merely shifts in species' abundances (*47*). To date, little effort has been devoted to understanding the degree, causes, and consequences of heterogeneity in ecological responses to changing climate, some of which are a function of the heterogeneity in Arctic climate conditions (*55*). However, we should also expect considerable response diversity within climatically homogeneous regions (*55*), which may contribute to compensatory dynamics and species persistence (*57*). Such response diversity, both within and among species, will be key to understanding how the Arctic as a whole responds to future climate changes.

The scale dependence of climate responses. Experimental and observational studies have in

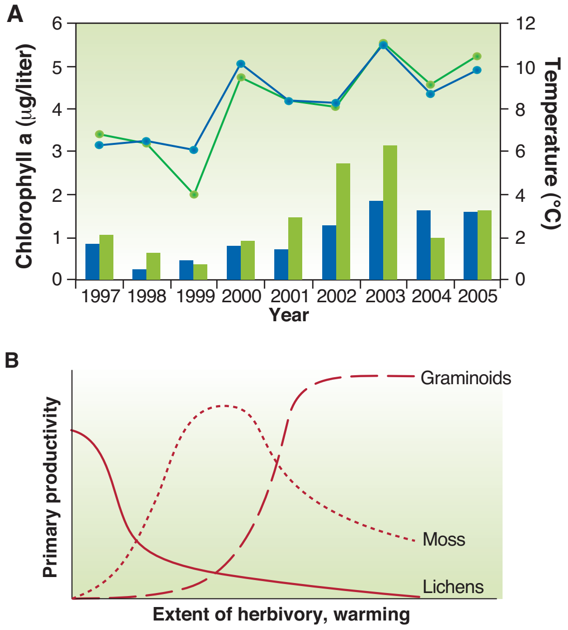

Fig. 4. Priorities for future research on ecological responses to Arctic climate change include (**A**) the role of trophic interactions in primary productivity response to warming (shown are temperature trends as lines and chlorophyll concentrations as bars in lakes with fish (green) and without fish (blue) in Greenland [modified from (*32*)]. (**B**) The potential for development of alternate vegetation states in Arctic communities as a result of interactions between herbivory and warming [modified from (*60*)].

some cases resulted in contrasting conclusions concerning the direction and magnitude of ecological responses to warming. This may be a consequence of the disparity of scales at which such studies have been conducted. Whereas observation is performed at both large and small scales, experimentation is conducted almost exclusively at small scales. There is similar disparity regarding the temporal scales of observation and experimentation. As with ecological studies in general (*58*), we urge greater consideration of the consequences posed by scale of study on the interpretation of data gathered in studies of ecological response to Arctic climate change.

Extreme events, tipping points, and resilience. Insect outbreaks, sudden and transient temperature changes, rapid retreat of sea- and lake ice, bouts of abnormally high precipitation or extended droughts, wildfires, the sudden release of water from melting glaciers, and slumping of permafrost are examples of stochastic events that may have disproportionately large effects on ecological dynamics. Such processes, and ecological responses to them, may be nonlinear and difficult to predict (*59*). We urge research aimed specifically at understanding the role of extreme events in ecological dynamics in the Arctic, in particular with regard to the build-up of tipping points in ecological systems. An important consideration for conservation and management in the Arctic, for example, is whether alteration of species composition of plant and animal communities due to climate change will lead to alternate ecosystem states or persistent instability (*60*) (Fig. 4B), or whether system states can rebound from abiotic perturbations due to species resilience.

Baseline studies in anticipation of predicted changes. The most informative studies for assessing the consequences of climate warming are those undertaken systematically for long enough to quantify changes from earlier baselines (*31*, *61*). To increase our ability to make quantitative assessments of how ecological changes may develop in areas where the impact appears to be minimal to date, we suggest establishing integrated baseline and monitoring studies in a pan-Arctic network, including physical conditions and the distribution and abundance of species, for long enough to address questions of interest. Such networks will substantially aid in developing meaningful responses and goals for future conservation and management adaptations, and we support recent efforts to accomplish this (*62*).

The extensive changes in living components of the Arctic associated with recent climate change documented here have been rapid and widespread across terrestrial, freshwater, and marine systems. Foreseeing and mitigating the ecological consequences of future climate change will require more intensive, multidisciplinary monitoring of both the physical drivers of these systems and biological responses to them. The Fourth International Polar Year has facilitated a short-term boost for such internationally concerted actions, and the products and collaborative precedent established by this effort should set a standard for future, critical research on ecological effects of climate change in the Arctic and other regions.

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