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Acknowledgments: This work was supported in part by an NSF grant (DEB-0643831) to S.A., a Fellowship from the David and Lucile Packard Foundation and NSF grant (IOS-1121529) to P.T.J.J., an NSF Research Coordination Network grant on the Ecology of Infectious Marine Diseases, NSF Ecology and Evolution of Infectious Diseases grant (OCE-1215977) to C.D.H., and by the Atkinson Center for a Sustainable Future at Cornell University. S.K. thanks the Natural Sciences and Engineering Council of Canada, the Nasivvik Centre for Inuit Health; the governments of the Northwest Territories, Nunavut, and Yukon; and the government of Canada International Polar Year Program.

Supplementary Materials
www.sciencemag.org/cgi/content/full/341/6145/514/DC1
Materials and Methods
Supplementary Text
Fig. S1
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10.1126/science.1239401

REVIEW

Ecological Consequences of Sea-Ice Decline

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After a decade with nine of the lowest arctic sea-ice minima on record, including the historically low minimum in 2012, we synthesize recent developments in the study of ecological responses to sea-ice decline. Sea-ice loss emerges as an important driver of marine and terrestrial ecological dynamics, influencing productivity, species interactions, population mixing, gene flow, and pathogen and disease transmission. Major challenges in the near future include assigning clearer attribution to sea ice as a primary driver of such dynamics, especially in terrestrial systems, and addressing pressures arising from human use of arctic coastal and near-shore areas as sea ice diminishes.

As one of Earth's major biomes, sea ice not only comprises unique ecosystems in, on, and under the ice itself but also strongly influences patterns and processes in adjacent terrestrial ecosystems (*1*, *2*) (Fig. 1). Sea ice harbors an array of microorganisms, provides critical habitat for vertebrates, and influences terrestrial productivity and diversity in the Arctic, where 80% of low-lying tundra lies within 100 km of seasonally ice-covered ocean (*3*–*5*). Ice-loss-driven amplification of arctic warming is a potentially important driver of ecological dynamics in the region, where seasonal temperature limitation is an important constraint on productivity (*6*). Here, we synthesize recent developments in the study of ecological responses to arctic sea-ice decline and highlight the importance of sea-ice loss as a driver of ecological dynamics in both marine and terrestrial systems.

Record of Recent Sea-Ice Loss

One of the most conspicuous consequences of recent anthropogenic warming has been declining annual minimum extent of arctic sea ice (*7*). Over the past several decades, the Arctic has warmed at twice the global rate, with sea-ice loss accelerating (*8*) (Fig. 2A), especially along the coasts of Russia, Alaska, and the Canadian Archipelago (Fig. 2B). The sea ice's annual minimum reached a record low in 2012. Arctic sea-ice loss has exceeded most model projections (*9*) and is unprecedented in the past 1.5 millennia (*10*).

Sea-ice loss is most commonly discussed as an indicator of arctic warming (*11*), but it is also a major factor in amplification of warming in the Arctic through feedback deriving from declining surface albedo (*6*). In 2007, the year of second-lowest arctic sea-ice extent on record, sea ice loss accounted for a large portion of warming over land north of 60° (*12*). Further, much of arctic near-surface warming over the past three decades is attributable to declining sea ice concentration (*13*), and land-surface warming is linked to summer sea-ice loss in global climate models (*14*).

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Direct Effects of Sea-Ice Loss

Primary producers dependent upon sea ice as their habitat underpin the entire marine food web of the Arctic (Fig. 1A). The loss of over 2 million km^2 of arctic sea ice since the end of the last century (Fig. 2A) (*10*) represents a stunning loss of habitat for sea-ice algae and sub-ice phytoplankton, which together account for 57% of the total annual primary production in the Arctic Ocean (*15*). The seasonal timing of the ice algae bloom, driven by light penetration through thinning sea ice, is critical to the successful reproduction of zooplanktonic copepod grazers, and the timing of the subsequent phytoplankton bloom as the ice edge retreats is critical to the growth and survival of copepod offspring (*15*). These two annual pulses of productivity, including the release of organic material from seasonally melting ice, fuel the arctic marine food web (*2*).

Disruption of the seasonality of the ice algal and phytoplankton blooms by ice thinning, accelerated melt timing, and an increase in the length of the annual melt season by 20 days over the past three decades (*16*) has created mismatches for the timing of zooplankton production, with consequences for higher consumers (*17*, *18*). Earlier seasonal sea-ice melt and earlier phytoplankton blooms may shorten the length of the annual window of arctic marine primary productivity (*19*), affecting zooplankton production and that of the arctic cod that feed on them (*20*) as well as their seabird and marine mammalian predators (*2*, *21*) (Fig. 1B).

Warming-related reductions in sea-ice thickness and snow cover on sea ice in the Arctic Ocean have also been associated with increased sub-ice primary production. A midsummer phytoplankton bloom below the sea ice in 2011 was attributed to enhanced light transmission through a thin layer of first-year ice (*22*). Hence, replacement of thick, multiyear ice by thin, first-year ice as the Arctic warms may contribute to increases in the frequency and magnitude of algae and phytoplankton blooms. However, the roles of sea-ice loss and ocean freshening in the tradeoffs between light versus nutrient limitation of arctic marine primary productivity remain poorly understood (*1*). Freshening of the euphotic layer associated with sea-ice melt may ultimately reduce nutrient availability for phytoplankton, limiting their productivity despite increased solar input with sea-ice retreat (*23*). Also, increased solar irradiance of sea-ice algae through thinning ice reduces their fatty acid content and quality as forage for marine copepod grazers (*24*). Furthermore, freshening of the Arctic Ocean due to increased meltwater from sea ice and runoff from coastal rivers is associated with the replacement of larger nanoplankton by smaller picoplankton, reducing the efficiency of seasonal energy transfer in marine food webs (*25*).

Vertebrate species dependent upon sea ice for foraging, reproduction, and resting are also directly affected by sea-ice loss and thinning (*3*). Examples of marine vertebrates adversely affected by sea-ice decline and longer ice-free seasons include declines in body condition and abundance of polar bears (*26*) and loss of critical habitat for reproduction and offspring provisioning by ringed seals (*27*). Pacific walrus have recently displayed greater use of shoreline haul-out areas and declining abundance in portions of their range, as retreating near-coastal sea ice has reduced their access to critical shallow water foraging from the ice edge (*28*). Mass mortality among Pacific walrus along the coast of the Chukchi Sea in Alaska has been attributed to loss of sea ice over the continental shelf (*29*).

Indirect Effects of Sea-Ice Loss

Sea-ice loss may also influence ecological dynamics indirectly through effects on movement, population mixing, and pathogen transmission. For populations and species currently isolated only during the summer ice-free season in the

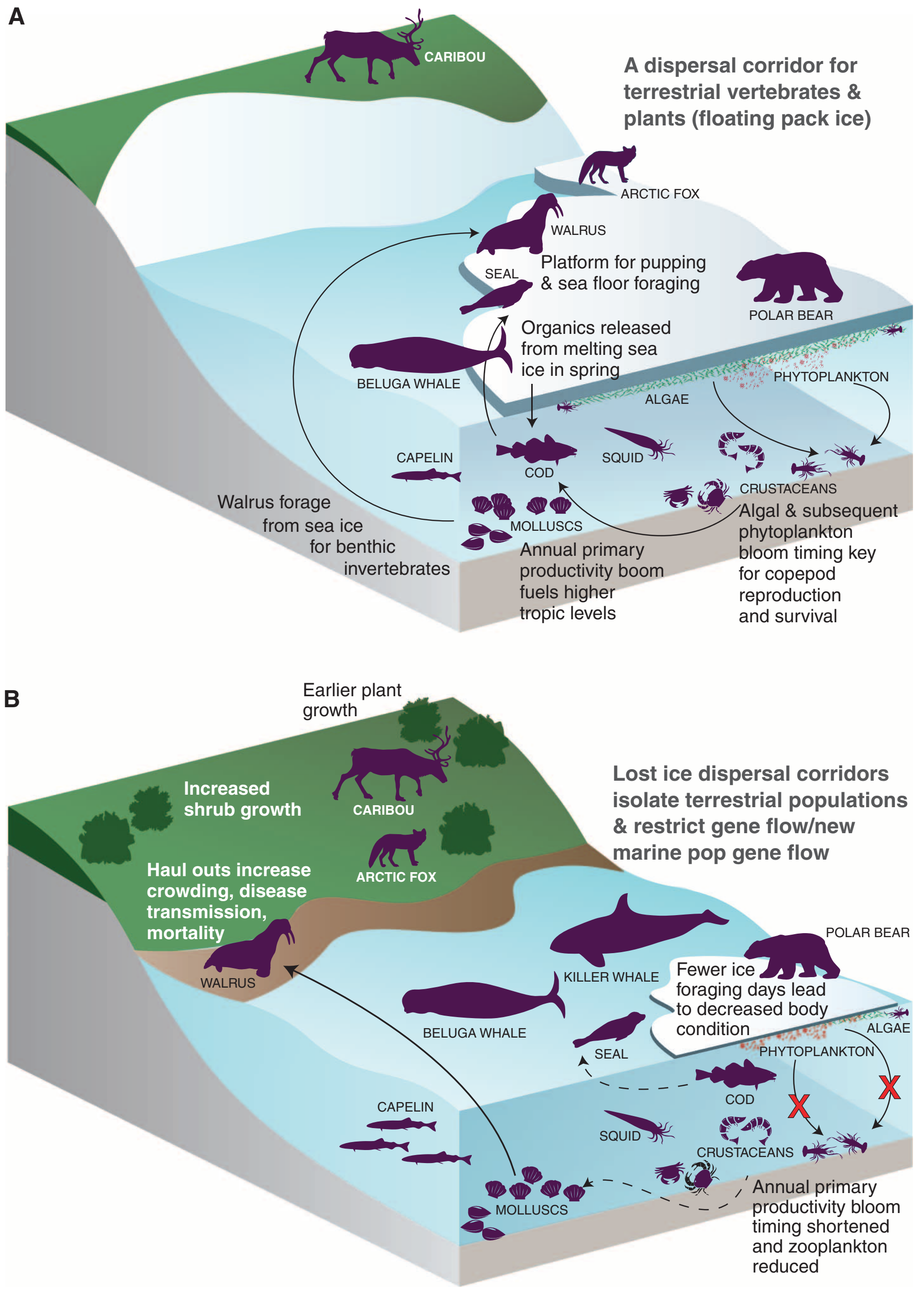

Fig. 1. Ecological interactions influenced by sea ice. The sea-ice biome influences the abundance, distribution, seasonality, and interactions of marine and terrestrial species by its presence (**A**). It is unique for its complete seasonal disappearance in portions of its distribution. Lengthening of this annual period of absence and an overall decline in ice extent, thickness, and stability will have considerable consequences for these species and interactions (**B**).

Arctic, declining annual presence of sea ice will reduce trans-ice and interisland migrations outside of the summer season. Sea-ice loss and a lengthening of the ice-free season will thus increase genetic isolation among populations of such species. Sea ice is the strongest predictor of genetic differentiation among arctic fox populations (*30*). In the Canadian Arctic Archipelago, interisland and island-mainland migration can promote genetic rescue of isolated wolf populations (*31*). The loss of sea ice that seasonally connects these populations will render such genetic rescue increasingly unlikely.

In species for which sea ice acts as a barrier to dispersal, its loss and a lengthening of the ice-free season will increase population mixing, reducing genetic differentiation. Perennial sea ice likely maintains genetic divergence between North Pacific and North Atlantic populations of walrus (*32*) and some whales (*33*). Loss of sea ice will also increase contact among closely related species for which it currently acts as a barrier to mixing, increasing the likelihood of hybridization. For instance, at least seven pairs of arctic and subarctic marine mammals hybridize, and many more hybridizations are expected with sea-ice loss (*34*). Observed hybridization between polar bears and grizzly bears may be the result of increasing inland presence of polar bears as a result of prolonged ice-free seasons (*34*). Loss of sea ice may reduce arctic faunal diversity if it promotes hybridization among populations, species, and genera currently isolated by ice (*34*).

Arctic warming and sea-ice loss will also facilitate invasions by new hosts, pathogens, and disease vectors. The projected decrease in sea-ice cover in arctic Canada will increase contact between eastern and western arctic species, promoting mixing of pathogen communities previously isolated. Phocine distemper virus, currently endemic to pinnipeds of the eastern Arctic, may spill over to western arctic species where it is currently absent. Mixing of Atlantic and Pacific pathogen communities that have been ecologically and evolutionarily isolated may be expected across a range of marine species, with important implications for the health of populations previously not exposed to them. For walrus, reduced sea-ice cover forces increased use of shoreline haul-outs (Fig. 1B), increasing the local density of animals. This promotes transmission of environmentally and density-dependent pathogens. Additionally, increased time spent on land by marine species may enhance transmission of pathogens between them and terrestrial species (*35*).

Changes in animal behavior as a result of sea-ice loss may also alter patterns of pathogen exposure. In the Canadian Arctic, later freeze-ups and increased shipping traffic could shift or prevent the annual migration of the Dolphin and Union caribou herd. Because migration poses benefits for reducing parasitism, such a change may increase parasite loads in this herd. Conversely, sea-ice loss may be beneficial in preventing pathogen introduction and disease epidemics to island ecosystems in cases where sea ice provides a corridor for pathogen transmission. Sporadic outbreaks of rabies on Svalbard are attributed to introduction by arctic foxes traversing sea ice from the Russian mainland (*36*). Reduction in sea ice would likely minimize or eliminate this movement.

Shifts in feeding ecology mediated by sea-ice loss may also alter the community of parasites within a host, particularly in the case of parasites with complex life cycles (*37*). For example, the diet of thick-billed murres in Hudson Bay has shifted from arctic cod to capelin (*38*), potentially affecting the occurrence of parasites transmitted through the food web. Similarly, sea-ice alteration of exposure of wildlife to environmental toxicants will have important impacts on the immune function of animal species and their ability to cope with existing and new pathogens (*35*).

Effects on Terrestrial Systems

Contributions of sea-ice loss to near-surface warming over land across the Arctic (*13*) indicate that earlier annual sea-ice melt and ice loss will influence seasonality in terrestrial systems. Local warming over land adjacent to areas of sea-ice loss is expected to increase terrestrial primary production for two reasons: Surface warming advances arctic soil thaw dates and delays soil freeze dates (*39*), and sea-ice loss is expected to promote permafrost warming up to 1500 km inland from the coastline (*40*).

In West Greenland, long-term monitoring of plant phenology at an inland site indicates a close association between the annual timing of the plant growing season and sea-ice extent (Fig. 3A) (*41*). Here, springs with low sea-ice extent are characterized by early green-up of vegetation. Advancement of the timing of the spring pulse of primary production, in turn, exacerbates trophic mismatch for caribou at the site (*41*), as it does for copepod grazers in the marine food web (*17*). At the same inland site, abundance of dwarf shrubs has

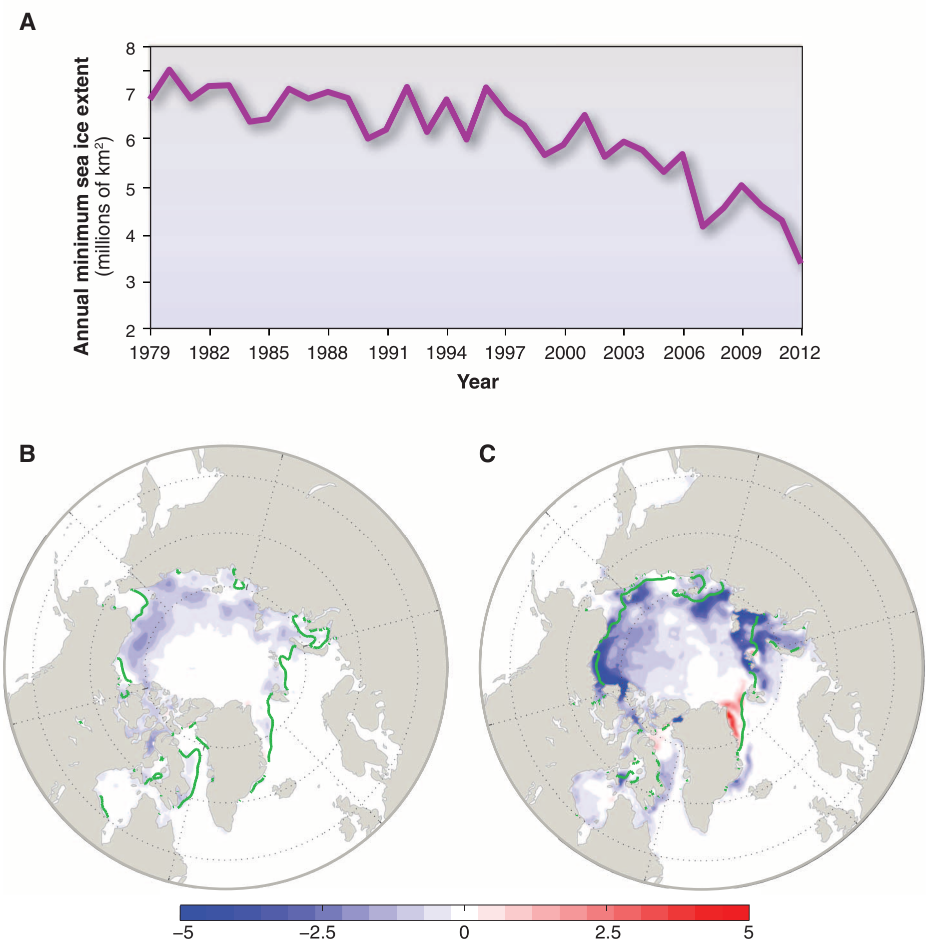

Fig. 2. Trends in arctic sea ice through time and space. Annual minimum sea-ice extent (**A**) has declined dramatically from 1979 to 2012. The percentage concentration loss per year in seasonal sea-ice minimum extent (July to September) has increased most between 1979 and 1999 (**B**) and between 2000 and 2011 (**C**) along the coasts of Russia, Alaska, and the Canadian Archipelago. The color bar indicates the direction of the sea-ice trend in percentage change per year; in the panels, the mean 15% concentration contour is shown in green. All data is from NASA Distributed Active Archive Center at the National Snow and Ice Data Center.

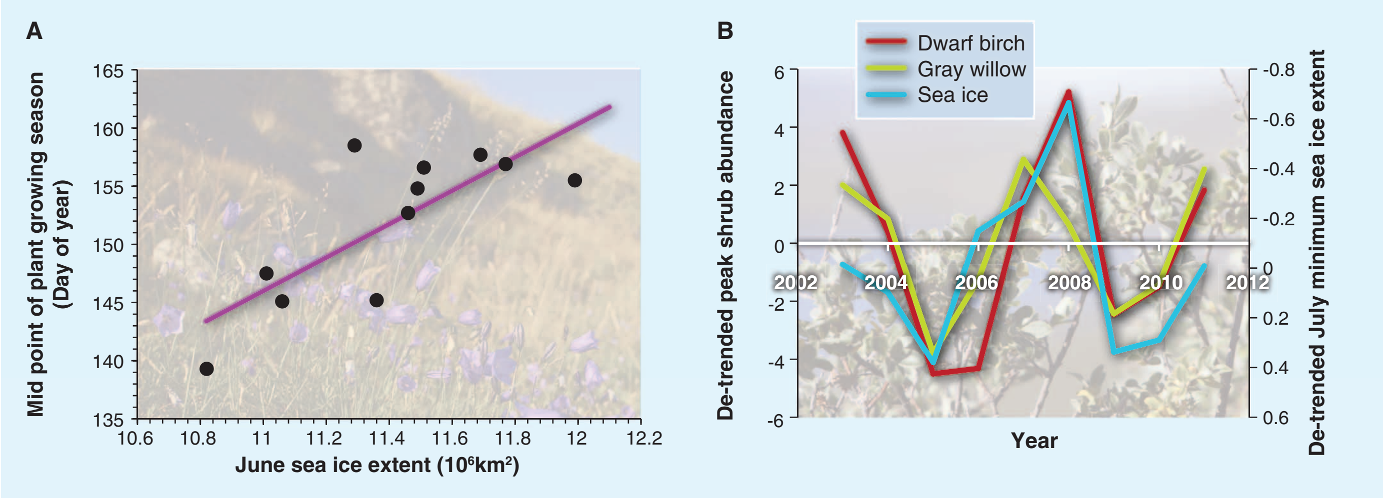

Fig. 3. Relations between sea ice and timing and abundance of terrestrial plant growth. (**A**) The annual midpoint of the plant growing season at an inland site in Greenland, when 50% of species have emerged on plots monitored between 1993 and 2011, is closely associated with Arctic-wide sea-ice extent in June [data from (*41*)]. (**B**) Detrended annual peak aboveground abundance of dwarf shrubs [data from (*42*)], which have been increasing at the same site (*42*), displays a close association with July sea-ice extent in the previous year.

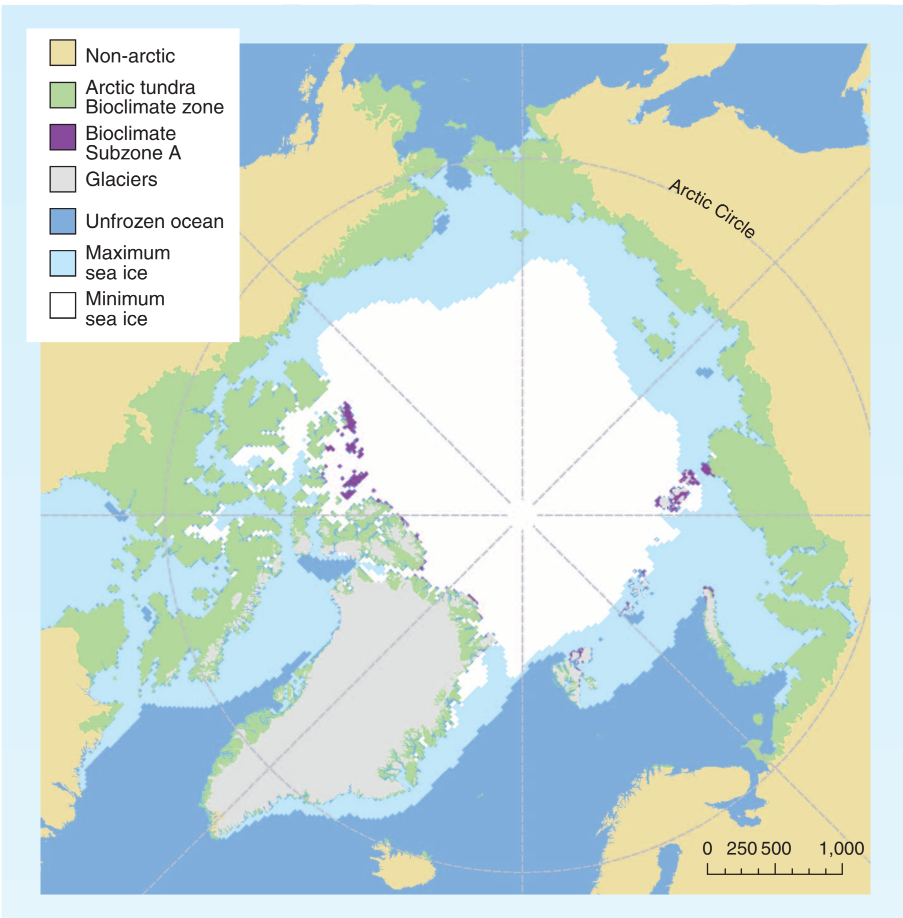

Fig. 4. Arctic terrestrial vegetation zones in relation to sea ice. The extent and locations of the arctic tundra bioclimate zone and bioclimate subzone A [boundaries of both from (*44*)] are closely related to the climatological maximum and minimum spatial extent of sea ice. The mean (1982 to 2010) maximum ice boundary (50% ice cover) is shown for week 22 (1 June), and the minimum ice boundary (50% ice cover) is shown for week 35 (1 September). The tundra extent generally corresponds to the extensive presence of sea ice during the late winter and spring. Bioclimate subzone A relates to the presence of extensive ice cover during all of the summer and early autumn (*45*). Ice boundaries were determined from passive microwave data averaged for 1982 to 2012.

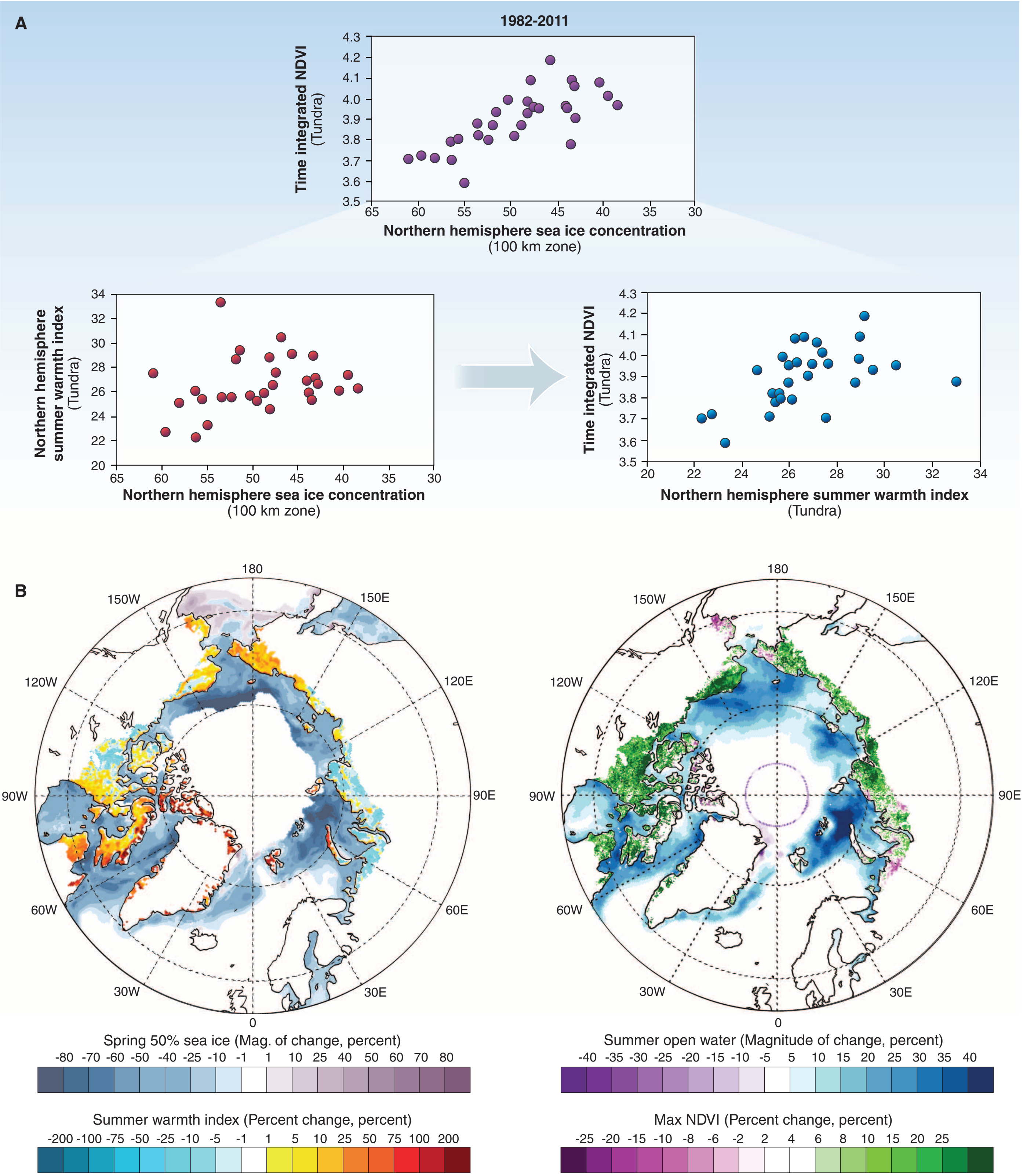

Fig. 5. Increasing arctic terrestrial primary production associated with sea-ice decline. (**A**) Coastal tundra primary productivity, shown as time-integrated NDVI, has increased in association with declining arctic sea-ice concentration or area (top). This is presumed to be driven by the relations between sea-ice area and SWI (bottom left) and between SWI and NDVI (bottom right). (**B**) Pan-Arctic trends in SWI (left) and NDVI (right) [adapted from (*4*, *5*)] vary spatially across the Arctic, but almost all locations experienced an increase in maximum NDVI and an increase in summer open water (right).

increased (*42*) and relates inversely to sea-ice extent during the previous growing season (Fig. 3B). Inferring causality between correlated time series is difficult but may be supported when the response displays a lagged relation to the presumed driver, as in this instance.

Increases in the abundance and cover of shrubs are occurring across the Arctic (*43*). In coastal and near-coastal areas, these increases are likely related to local warming driven by sea-ice loss. The entire arctic tundra biome is coupled with the marine system because of its extensive coastline (Fig. 4) and is especially vulnerable to sea-ice decline because of the strong climatic influence of the nearby sea ice. A unique area that will be particularly sensitive to sea-ice loss is bioclimate subzone A (Fig. 4) (*44*). Floristically depauperate and experiencing some of the largest and fastest temperature changes in the Arctic, this zone is likely to experience complete loss of summer sea ice in the next few decades, rendering it an endangered bioclimate subzone (*45*).

Associations between sea-ice decline and terrestrial primary productivity are also evident at larger scales across the Arctic. Biome-scale evidence for a relationship between sea-ice decline and increases in terrestrial primary productivity derives mainly from satellite data. Between 1982 and 2011, as near-coastal sea-ice area declined, the summer warmth index (SWI) for low-elevation tundra along the Arctic Ocean increased, precipitating an increase in vegetation production captured by Normalized Vegetation Difference Index (NDVI) data (*4*, *5*) (Fig. 5A). The relationship between SWI and sea-ice extent is largely negative for the entire Northern Hemisphere, indicating warming associated with sea-ice loss, but varies among regions such as Eurasia and North America (fig. S1). Moreover, NDVI trends and relations to sea-ice extent vary across the Arctic (*46*) (Fig. 5B), suggesting that other factors likely interact with abiotic drivers associated with sea-ice loss to influence variation in terrestrial primary productivity across the tundra biome.

Increases in terrestrial primary productivity related to sea-ice decline and the consequent increase in land surface temperatures have the potential to alter ecosystem carbon flux (*47*). Modeling of measurements of CO_2 flux from West Greenland indicates a doubling of carbon uptake concordant with shrub increases there between 2003 and 2010 (*48*). Moreover, ecosystem process models indicate increases in arctic tundra methane emissions matching sea-ice fluctuations and trend for the period from 1979 to 2006 (*47*). Projecting carbon dynamics in terrestrial systems with future sea-ice declines is, however, complicated by the unknown extent to which respiration may increase with warming (*47*). A recent link between sea-ice decline and the annual extent of tundra fires in Alaska (*49*) also suggests that ice loss may contribute to periodic massive pulses of terrestrial carbon release.

Future Challenges

Despite numerous examples of effects of declining sea ice on dynamics, abundance, and interactions among species, foreseeing the consequences of continued sea-ice loss remains difficult. A considerable challenge is to assign attribution, with greater certainty, to sea ice as a driver of ecological dynamics. The associations that we have drawn are weakened by reliance on patterns of covariation between sea-ice dynamics and ecological dynamics. Increasing emphasis on sea-ice decline as a contributing factor to regional warming (*11*) will improve the potential for increased recognition of sea-ice decline as a driver of ecological dynamics (*4*, *45*). The field of joint attribution (*50*) in studies of ecological response to climate change can be informative here. Joint attribution is a statistical approach for assigning causation by anthropogenic forcing in recent warming and causation by warming in observed ecological dynamics (*50*). Further development and application of this approach will improve our ability to detect ecological responses to sea-ice decline.

A second challenge is to foresee and anticipate the human dimension as sea-ice decline increasingly facilitates access to coastal and near-shore areas for increased industrial development and extended-season shipping. In the Arctic, loss and thinning of sea ice is anticipated to increase accessibility of near-coastal and remote marine zones of all eight arctic nations by up to 28% by the middle of this century (*51*). Increased human access to formerly remote areas of the Arctic could have negative consequences for many species and their habitats, including those exploited by humans. Increased marine access will also likely accelerate the pace of arctic mineral and petroleum exploration in both terrestrial and marine systems (*52*), with increased threats to marine species such as bowhead whales (*53*) and Pacific walrus (*51*). Viewing sea ice as an important indicator of climatic warming and as an integrator and driver of ecological dynamics in the Arctic will improve our understanding of the systems-level functioning of this region and our basis for anticipating and responding to further change.

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Acknowledgments: U.S.B., E.P., and D.A.W. thank NSF and NASA; E.P. thanks the National Geographic Society and the Polar Center at Pennsylvania State University; M.H. thanks NASA; J.K. and C.M.B. thank NSF. S.J.K. thanks National Sciences and Engineering Research Council of Canada (NSERC); the Nasivvik Centre for Inuit Health; the governments of the Northwest Territories, Nunavut, and Yukon; and the government of Canada's International Polar Year Program. I.S. thanks Environment Canada, the Polar Continental Shelf Project, NSERC, and the World Wildlife Fund. We thank Misty Wilt Graphic Design LLC for Fig. 1, A and B; M. Raynolds for Fig. 1C; and three anonymous referees for helpful comments.

Supplementary Materials

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Fig. S1

10.1126/science.1235225