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Published in:
Ambio: a Journal of the Human Environment

DOI:
10.1639/0044-7447%282004%29033%5B0386%3AKFAES%5D2.0.CO%3B2

2004

Citation for published version (APA):
Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Schaphoff, S., Sitch, S., & Zöckler, C. (2004). Climate Change and UV-B Impacts on Arctic Tundra and Polar Desert Ecosystems: Key Findings and Extended Summaries. *Ambio: a Journal of the Human Environment*, *33*(7), 386-392. https://doi.org/10.1639/0044-7447%282004%29033%5B0386%3AKFAES%5D2.0.CO%3B2

Total number of authors:
17

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Key Findings and Extended Summaries

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INTRODUCTION

The Arctic has become an important region in which to assess the impacts of current climate variability and amplification of projected global warming. This is because *i)* the Arctic has experienced considerable warming in recent decades (an average of about 3°C and between 4° and 5°C over much of the landmass); *i)* climate projections suggest a continuation of the warming trend with an increase in mean annual temperatures of 4–5°C by 2080; *ii)* recent warming is already impacting the environment and economy of the Arctic and these impacts are expected to increase and affect also life style, culture and ecosystems; and *iv)* changes occurring in the Arctic are likely to affect other regions of the Earth, for example changes in snow, vegetation and sea ice are likely to affect the energy balance and ocean circulation at regional and even global scales (Chapter 1 in ref. 1). Responding to the urgent need to understand and project impacts of changes in climate and UV-B radiation on many facets of the Arctic, the Arctic Climate Impact Assessment (ACIA) (1) undertook a four-year study. Part of this study (1–10) assessed the impacts of changes in climate and UV-B radiation on Arctic terrestrial ecosystems, both those changes already occurring and those likely to occur in the future. Here, we present the key findings of the assessment of climate change impacts on tundra and polar desert ecosystems, and extended summaries of its components.

KEY FINDINGS

- The dominant response of current Arctic species to climate change, as in the past, is very likely to be relocation rather than adaptation. Relocation possibilities vary according to region and geographical barriers. Some changes are occurring now.
- Some groups such as mosses, lichens, some herbivores and their predators are at risk in some areas, but productivity and number of species is very likely to increase. Biodiversity is more at risk in some subregions than in others: Beringia has a higher number of threatened plant and animal species than any other ACIA subregion.
- Changes in populations are triggered by trends and extreme events, particularly winter processes.
- Forest is very likely to replace a significant proportion of the tundra and this will have a great effect on the composition of species. However, there are environmental and sociological processes that will probably prevent forest from advancing in some locations.
- Displacement of tundra by forest will lead to a decrease in albedo which increases the positive feedback to the climate system. This positive feedback will generally dominate over the negative feedback of increased carbon sequestration. Forest development will also ameliorate local climate.
- Warming and drying of tundra soils in parts of Alaska have already changed the carbon status of this area from sink to source. Although other areas still maintain their sink status, the number of source areas currently exceeds the sink areas. However, geographical representation of research sites is currently small. Future warming of tundra soils would probably lead to a pulse of trace gases into the atmosphere, particularly in disturbed areas and areas that are drying. It is not known if the circum-Arctic tundra will be a carbon source or sink in the long term, but current models suggest that the tundra will become a weak sink for carbon because of the northward movement of vegetation zones that are more productive than those they displace. Uncertainties are high.
- Rapid climate change that exceeds the ability of species to relocate will very probably lead to increased incidence of fires, disease and pest outbreaks.
- Enhanced CO_2 and UV-B affect plant tissue chemistry and thereby have subtle but long-term impacts on ecosystem processes that reduce nutrient cycling with the potential to decrease productivity and increase or decrease herbivory.

EXTENDED SUMMARIES OF PAPERS

Past Changes in Arctic Terrestrial Ecosystems, Climate and UV-B Radiation (2)

At the last glacial maximum, vast ice sheets covered many continental areas. The beds of some shallow seas were exposed thereby connecting previously separated landmasses. Although some areas were ice-free and supported a flora and fauna, mean annual temperatures were 10–13°C colder than during the Holocene. Within a few millennia of the glacial maximum, deglaciation started but this was not a simple unidirectional change; instead a series of climatic fluctuations occurred during the period between about 18 000 and 11 400 years ago. During the Younger Dryas event, mean annual temperatures fell substantially in some areas and reglaciation occurred. At the end of the event, mean annual temperatures rose by > 5°C in less than 100 yrs in at least some parts of the Arctic. Following the general thermal maximum in the Holocene, there has been a modest overall cooling trend. However, superimposed upon the general longer-term patterns have been a series of millennial and centennial fluctuations in climate, the most marked of which occurred about 8200 years ago. The most recent of these climatic fluctuations was that of the "Little Ice Age", a generally cool interval spanning approximately the late 13th to early 19th centuries. At its most extreme, mean annual temperatures in some Arctic areas fell by several degrees and there were impacts on human settlements in the North.

In the context of at least the last 150 000 years, Arctic ecosystems and biota have been close to their minimum extent within the most recent 10 000 years. They suffered loss of diversity as a result of extinctions during the most recent large-magnitude rapid global warming at the end of the last glacial stage. Consequently, Arctic ecosystems and biota are already stressed; some are extremely vulnerable to the current and potential future global warming. For example, migratory Arctic breeding birds today face maximal migration distances between their wintering and breeding areas.

Evidence from the past indicates that Arctic species, especially larger vertebrates, are very likely to be vulnerable to extinction if climate warms. The treeline will very probably advance, perhaps rapidly, into tundra areas of northern Eurasia, Canada and Alaska, as it did during the early Holocene, reducing the extent of tundra and contributing to the pressure upon species that may result in their extinction. Species that today have more southerly distributions will very probably extend their ranges northward, displacing Arctic species as in the past. Permafrost will decay and thermokarst develop, leading to erosion and degradation of Arctic peatlands. Unlike the early Holocene, when lower relative sea level allowed a belt of tundra to persist around at least some parts of the Arctic basin when treelines advanced to the present coast, sea level is very likely to rise in future, further restricting the area of tundra and other treeless Arctic ecosystems.

The expected negative response of Arctic ecosystems in the face of a shift to global climatic conditions that are apparently without precedent during the Pleistocene is likely to be considerable, particularly as their exposure to co-occurring environmental changes (such as enhanced levels of UV-B, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation) is also without precedent.

Biodiversity, Distributions and Adaptations of Arctic Species in the Context of Environmental Change (3)

Implications of current species distributions for future biotic change

Species diversity appears to be low in the Arctic, and decreases from the boreal forests to the polar deserts of the extreme north. Only about 3% (about 5 900 species) of the world's plant species (excluding algae) occur in the Arctic north of the treeline. However, primitive plant species of mosses and lichens are particularly abundant. Although the number of plant species in the Arctic is low in general, individual communities of small Arctic plants have a diversity similar to or higher than those of boreal and temperate zones: there can be 25 species dm^{-2}. Latitudinal gradients suggest that Arctic plant diversity is sensitive to climate, and species number is least sensitive to temperature near the southern margin of the tundra. The temperature gradient that has such a strong influence on species diversity occurs over much shorter distances in the Arctic than in other biomes.

The diversity of Arctic animals beyond the latitudinal treeline (about 6000 species) is nearly twice as great as that of vascular plants and bryophytes. The Arctic fauna accounts for about 3% of the global total, and, in general, primitive groups (e.g. springtails,) are better represented in the Arctic than are advanced groups such as beetles. In general, the decline in animal species with increasing latitude is more pronounced than that of plants (frequently greater than 2.5-fold). An important consequence of the decline in numbers of species with increasing latitude is an increase in dominance. Super-dominant plant and animal species (such as lemmings) occupy a wide range of habitats, and generally have large effects on ecosystem processes.

Microbial organisms are more difficult to enumerate. Arctic soils contain large reserves of microbial biomass, although diversity of all groups of soil microorganisms is lower in the Arctic than further south. Many common bacteria and fungi are rare or absent in tundra areas. As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, and increasing dominance of the species that occur.

The latitudinal temperature gradient within tundra is stronger than for any other biome, and outlier populations of more southerly species frequently exist in favorable microenvironments far north of their centers of distribution. Consequently, migration of southerly taxa is very likely to occur more rapidly in the Arctic than in other biomes. Temperature-induced biotic change will probably occur most strongly at the northern extreme of tundra, where species distributions are most temperature-sensitive.

The initial response of diversity to warming will likely be an increase in diversity of plants, animals, and microbes and reduced dominance of species that are currently widespread. Taxa most likely to expand into tundra are boreal taxa that currently exist in river valleys and could spread into the uplands or animal groups such as wood-boring beetles that are presently excluded due to lack of food resources. Although current extreme environmental conditions restrain the metabolic activity of Arctic microbes, they preserve huge potential that is ready to display the same activity as boreal analogs immediately after climate warming. Warming could cause extinction of some few Arctic plants that currently occur in narrow latitudinal strips of tundra adjacent to the sea. Some animals are Arctic specialists and could possibly face extinction. Those plant and animal species that have their centers of distribution in the high- or mid-Arctic are most likely to show reduced abundance in their current locations in the face of projected warming.

General characteristics of Arctic plant species in relation to climate and implications for their responses to climate change

Plant adaptations to the Arctic climate are absent or rare: many species are pre-adapted. The first filter for Arctic plants is freezing tolerance, which excludes approximately 75% of the world's vascular plants. Short growing seasons and low solar angles select for long life cycles in which slow growth often uses stored resources while development cycles are often extended over multiple growing seasons. Some plant species occupy microhabitats, or exhibit behavior or growth forms that maximize plant temperatures compared with ambient. Low soil temperatures reduce microbial activity and the rates and magnitude of nutrient availability to higher plant roots. Mechanisms to compensate for low nutrient availability include the conservation of nutrients in nutrient poor tissues, resorption of nutrients from senescing tissues, enhanced rates of nutrient uptake at low temperatures, increased biomass of roots relative to shoots, associations with mycorrhizal fungi, uptake of nutrients in organic forms, and uptake of nitrogen by rhizomes. Temperature fluctuations around 0°C cause frost-heave phenomena that can uproot ill-adapted plants.

Snow distribution determines the period over which plants can intercept solar radiation and can grow. A snow-cover insulates plants against low air temperatures in winter, extremes of temperature in spring, protects plants from physical damage from abrasion by ice crystals and provides a source of water and often late into the growing season. Where snow-cover is thin, for example in exposed ridge tops, growing seasons are usually long but water can become limiting: where snow accumulates in sheltered depressions, snowbeds form in which specialized plant communities occur: these are vulnerable to climate warming.

Many Arctic plants are pre-adapted to relatively high levels of UV-B radiation. They exhibit various mechanisms to protect DNA and sensitive tissues from UV-B and an ability to repair some UV-B damage to DNA. Thick cell walls and cuticles, waxes and hairs on leaves, and the presence or induction of UV-B absorbing chemical compounds in leaves, protect sensitive tissues. There appear to be no specific adaptations of Arctic plant species to high CO_2 concentrations.

Arctic plants species do not show the often complex interactions with other organisms prevalent in southern latitudes. Arctic plants are adapted to grazing/browsing mainly by chemical defenses rather than the possession of spines and thorns. Facilitation increases in importance relative to competition at high latitudes and altitudes.

Many of the characteristics of Arctic species to their current environments are likely to limit their responses to climate warming and other environmental changes. Many characteristics are likely to cope with abiotic selective pressures (e.g. climate) more than biotic (e.g. inter-specific competition). This is likely to render Arctic organisms more susceptible to biological invasions and they are very likely to change their distributions rather than evolve significantly in response to warming.

General characteristics of Arctic animal species in relation to climate and implications for their responses to climate change

Terrestrial Arctic animals possess many adaptations that enable them to persist in the Arctic climate. Physiological and morphological traits in warm-blooded vertebrates (mammals and birds) include thick fur and feather plumages, short extremities, extensive fat storage before winter and metabolic seasonal adjustments, while cold-blooded invertebrates have developed strategies of cold hardiness, high body growth rates together with pigmented and hairy bodies. Arctic animals can survive under an amazingly wide range of temperatures, including high temperatures. A short growing season represents a challenge for most Arctic animals and life history strategies have evolved to enable individuals to fulfill their life cycles under time constraints and high environmental unpredictability. The biotic environment (e.g. the ecosystem context) of Arctic species is relatively simple with few enemies, competitors, and available food resources. For those reasons, Arctic animals have evolved fewer traits related to competition for resources, predator avoidance and resistance towards diseases and parasites than their southern counterparts. Specifically adjusted life cycles to seasonal and multi-annual fluctuations in resources are particularly important because such fluctuations are very pronounced in terrestrial Arctic environments. Many Arctic animals possess adaptations for escaping unfavorable weather, resource shortage or other unfavorable conditions by winter dormancy or by selection of spatial refuges at a wide range of spatial scales from microhabitat selection at any given site, through seasonal habitat shifts within landscapes, to long distance seasonal migrations within or across geographic regions.

Based on the above general characteristics, if climate changes, terrestrial Arctic animals are likely to be most vulnerable to following conditions: *i)* warmer climate in summer that induces desiccation in invertebrates; *ii)* climatic changes that interfere with migration routes and staging sites en route for long distance migrators; *iii)* climatic events that alter snow conditions and freeze-thaw cycles in winter resulting in unfavorable conditions of temperature, O_2 and CO_2 for animals below the snow, and limited resource availability (e.g. vegetation or animal prey) for animals above the snow; *iv)* climate changes that disrupt behavior and life history adjustments to the timing of reproduction and development that are currently linked to seasonal and multi-annual peaks in food resource availability; *v)* influx of new competitors, predators, parasites and diseases.

General characteristics of Arctic microorganisms in relation to climate and implications for their responses to climate change

Arctic microorganisms are not only resistant to freezing, but some can metabolize at temperatures down to -39°C. This process could be responsible for up to 50% of annual CO_2 emissions during winter from tundra soils. Cold-tolerant microorganisms are usually also drought-tolerant. Microorganisms are tolerant of mechanical disturbance and high irradiance. Pigmentation protects organisms such as lichens from high irradiance including UV radiation and pigments can be present in considerable concentrations. Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize UV injury. However, in contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.

As a group, microorganisms are highly adaptive, can tolerate most environmental conditions and they have short generation times which can facilitate rapid adaptation to new environments associated with changes in climate and UV-B radiation.

Responses to Projected Changes in Climate and UV-B at the Species Level (4)

Responses at the plant species level to changes in climate and UV-B radiation

Species responses to changes in temperature and other environmental variables are complex. Species respond individualistically to each environmental variable. Also, plant species respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations and interactions among species. Some species are already responding to recent environmental changes. Indigenous knowledge, air photographs and satellite images show that some Arctic vegetation is becoming more shrubby and more productive.

Summer warming experiments showed that initial increases in the growth of vascular species were generally reduced with time whereas reproductive success improved in later years. Over short periods (4 years), herbaceous plants responded more than woody plants but over longer periods, woody plant responses were dominant and could change the canopy height and structure. Mosses and lichens were generally disadvantaged by higher plant responses to warming.

Responses to warming are critically controlled by moisture availability and snow cover. Already, indigenous observations from North America and Lapland show a drying trend with reduced growth of economically important berries. However, experimental increases in summer precipitation produced few responses in Arctic plants, except for mosses which showed increased growth. An experiment that manipulated snow conditions showed that drifts increased winter-time temperatures and CO_2 flux and, surprisingly, that plant growth increased despite a shorter growing season. In general, however, any earlier onset of the snow-free period is likely to stimulate increased plant growth because of high solar angles whereas an increase in the snow-free period in autumn, when solar angles are low, will probably have little impact.

CO_2 enrichment experiments show that plant growth responses are dominated by early, transient responses. Surprisingly, enhanced CO_2 did not affect levels of herbivory but it significantly increased the leaf ice nucleation temperature (i.e. increased frost sensitivity) of 3 of 4 dwarf-shrub species and altered the composition of microbial communities after 5 years. A general lack of responses of mosses and lichens reflects their adaptation to the currently high levels of CO_2 that they experience close to the ground surface.

Ambient and supplemental UV-B produced complex, individualistic and somewhat small responses in species. Overall, Arctic species were far more tolerant of enhanced UV-B than previously thought, and the production of UV-B absorbing compounds showed no simple relationship with UV-B dose as expected from laboratory studies. There was increased frost sensitivity in some Arctic dwarf shrubs with increased UV-B. The Arctic photoperiod is not seen as a general constraint to species migrations from the south as trees and southern species previously occurred further north than at present.

Responses of animal species to changes in climate and UV-B radiation

Evidence for responses of animals to changes in climate are fewer than for plants because field experiments are less feasible for mobile animals, especially vertebrates. In many case inferences are made based on time-series analyses of data on population abundance of a few conspicuous species such as ungulates, and lemmings.

Winter climate impacts, especially those events that affect properties of snow and ice, are particularly important. Freeze-thaw cycles leading to ice-crust formation have been shown to severely reduce winter survival rate of a variety of species ranging from soil dwelling spring-tails (*Collembola*), through small mammals (lemmings and voles) to ungulates (in particular reindeer/caribou). Such icing induces conditions of anoxia that affect invertebrates, unfavorable thermal conditions for animals under the snow, and renders vegetation unavailable for herbivores. A deeper snow-cover is likely to restrict access to winter pastures by reindeer/caribou and their ability to flee from predators. An expected increased frequency of freeze-thaw cycles is very likely to disrupt the population dynamics of many terrestrial animals, and indications that this is already happening to some extent are apparent in the recent loss of the typical 3–4 year population cycles of voles and lemmings in sub-Arctic Europe.

Experimental elevation of summer temperature has shown that many invertebrates respond positively to higher temperatures in terms of population growth, as long as desiccation is not induced. Many invertebrates, such as insects, are very likely to quickly expand their ranges northwards into the Arctic if climate warming occurs because they have vast capacities to become passively or actively dispersed and host species (both plants and animals) are already present north of their present range borders.

Little is known about the responses in Arctic animals to expected increases in UV-B. However, there are some indications that Arctic animals are likely to be more exposed and susceptible to such changes than their southern counterparts. The effects of UV-B on animals are likely to be subtle and indirect such as reduced food quality for herbivores and increased disease resistance in insect pest species.

Responses of microorganisms to changes in climate and UV-B radiation

Tundra soil heating, CO_2 enrichment and amendment with mineral nutrients generally accelerate microbial activity. Enriched CO_2 tends to intensify root exudation, which is the main source of available C for soil and rhizosphere bacteria. Supplementation of UV-B in the field resulted in changes in the composition of microbial communities. Laboratory incubation of tundra soils had strong effects on community composition after a temperature shift of more than 10°C. Surprisingly, the effects of many factors on the soil microbial community were essentially less significant as compared with effects on the plant community. However, a mathematical simulation of the changes in microbial community structure in the tundra showed that soil warming resulted in stimulation of bacilli growth.

Effects of increased UV-B radiation on microorganisms include damage to high latitude strains of fungal spores, and damage to some species of leaf-dwelling fungi as well as soil-dwelling decomposer fungi that result in a change in the composition of the fungal communities.

Cyanobacteria are better adapted to changeable and harsh conditions than algae, and in milder climates are likely to be dominated by algae. However, herbivory of both cyanobacteria and algal biomass would increase in a warmer climate.

Genetic responses of species to changes in climate and UV-B radiation

Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels to very low levels. In widespread *Carex* taxa, levels of genetic variation were not related to climate, but were to a large extent explained by differences in glaciation history at the sampling sites: populations in areas deglaciated ca 10 000 years ago had significantly lower genetic variation than populations in areas deglaciated 60 000 years ago.

Plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution. On a microtopographical scale, extremely steep environmental gradients are frequent and ecotypic differentiation has been demonstrated over short distances for several widespread species. This heterogeneity, together with large phenotypic plasticity, is likely to contribute to resilience to change at the population and species levels. For plants with long-lived seed, further genetic variation related to former environments is preserved in the seed banks. Thus, there are several mechanisms for widespread Arctic plant species to respond to environmental change.

Experiments with plants from outside the Arctic have shown that increased UV-B may speed up genetic change and may lead to an increased tendency for mutations in future generations.

The present genetic differentiation of Arctic terrestrial animals that have been studied thoroughly, such as reindeer, lemmings, and Arctic fox, reflects to a large extent historic processes and the presence of current migration barriers. For mammals with relatively restricted mobility such as lemmings, even small-scale barriers (e.g. large rivers) can form the borders between subspecies while a very mobile animal such as the Arctic fox shows little genetic structuring at the circumpolar scale. A species with high genetic/racial diversity has proved an ability to adapt to different environmental conditions in the past and is likely to do so also in the future.

There is a paucity of studies on Arctic animals that have addressed the potential for rapid adaptations to climatic change. Elsewhere, it was shown that northern boreal red squirrels were able to respond genetically within a decade to increased spring temperatures.

Up to 1% of natural bacterial isolates have been found to be mutators and high mutation rates are associated with emerging pathogens causing spontaneous epidemic outbreaks. In the Arctic, intensive mutagenic actions are expected from UV radiation and also from aerosols and volatile chemical mutagens. Although the effect is probably not strong, possible mutants could lead to epidemic outbreaks that could possibly have profound and unexpected consequences for the whole ecosystem.

Recent and expected changes in species distributions and potential ranges

Monitoring of distribution ranges with a spatial representation as good as that for temperate latitudes is not available for the terrestrial Arctic region. Indigenous knowledge projects have documented recent changes in the ranges of caribou in relation to changes in weather. Hunters' explanations of caribou distributions may provide indications of potential range changes under scenarios of warming temperatures, such as overwintering of caribou in coastal areas during warm winters. Other Arctic indigenous observations include insects previously associated with areas south of the treeline and more frequent sightings of "mainland ducks". In contrast, almost all Arctic breeding species are declining. The reasons for the trends are not always clear and probably of multiple origins, although there are suggestions of a general trend that some species are shifting their distribution in response to changing climate that is altering habitats.

Quantitative monitoring of conspicuous and popular species such as birds and butterflies has demonstrated that many formerly southern species are quickly approaching the Arctic regions and some have already entered. Arctic birds, especially Arctic-breeding water and waders, that can be counted on staging and wintering grounds, show mostly declining population trends; some of them have declined dramatically. It can be suspected that these changes result from the combined action of eutrophication and habitat loss on wintering and staging sites as well as concurrent climate change although separating the relative contributions of these factors is difficult. Based on climate models, quite dramatic reductions of the populations of tundra birds can be predicted as generally warmer climate is likely to increase vegetation height and the Arctic's landmass will probably decrease in extent.

Species–climate response surface models are able to predict the recently observed range changes of at least some species of both birds and butterflies. At least in the case of butterflies, the extent to which species have realized their predicted range changes over the last 30–50 yrs is strongly related to their degree of habitat restriction, generalist species being much more able to achieve the predicted range expansions than are specialist species. Simulated potential future ranges are often markedly reduced in spatial extent compared to the species' present ranges. The range limits of boreal and temperate species shift polewards but the large magnitude of the simulated range margin shifts, however, results in many boreal species exhibiting potential future ranges of reduced spatial extent because they are limited to the north by reaching the shore of the Arctic Ocean. Species that experience some physiological constraint at their southern range margin are likely to be affected sooner than those that are affected by biotic relationships such as competition by immigrant species. Loss of habitat, such as tundra ponds for many Arctic birds, is a particularly important possibility that will very probably constrain species ranges. In contrast, plant populations that are outliers of more southern regions and restricted to particularly favourable habitats in the Arctic, may spread rapidly during warming. Models of a moss and dwarf shrub growth along latitudinal gradients show considerable potential for range expansion in the north, but considerable uncertainty, in relation to ACIA scenarios of warming.

Probably the great majority of microorganisms detected in northern ecosystems such as free-living bacteria are cosmopolitan in their geographic distribution, are readily disseminated from one location to another and the environment selects those that can proliferate. However, some species, particularly symbionts with endemic plants, can themselves be candidates for endemic status.

Effects on the Structure of Arctic Ecosystems in the Short- and Long-term (5)

Changes in climate and UV will very probably affect three important attributes of ecosystem structure: spatial structure such as canopy structure and habitat, trophic interactions and community composition in terms of biodiversity. Ecosystem structure varies along a latitudinal gradient from the treeline to the high Arctic polar deserts. Along this gradient there is a decreasing complexity of vertical canopy structure and ground-cover ranging from the continuous and high canopies (> 2 m) of the forest tundra in the south to the low canopies (ca 5 cm) that occupy less than 5% of the ground surface in the polar deserts. Within each Arctic vegetation zone there are often outliers of more southerly zones. Changes in distribution of vegetation in relation to climate warming are likely to occur by local expansion of these intra-zonal communities and northward movement of zones. Satellite measurements, aerial photographs and indigenous knowledge already show a recent increase in shrubbiness of parts of the Arctic.

Experimental manipulation of environmental factors expected to change at high latitudes show that some of these factors have strong effects on the structure of Arctic ecosystems, but the effects are regionally variable. Nutrient addition has the strongest effect on the productivity, canopy height and community composition of Arctic plant communities. Nutrients also increase biomass turnover, so biomass may or may not respond to nutrient addition. Summer warming of tundra vegetation within the range of expected temperature enhancement of 2–4°C for the next 100 years has generally led to smaller changes than fertilizer addition and always to greater responses than after water addition. Plant growth response increased from a climatically, relatively mild forest understorey through a treeline heath to a cold, high altitude fellfield. A 10-yr or more response to environmental manipulations at sites in sub-Arctic Sweden and in Alaska was a decrease in total nonvascular plant biomass and particularly the biomass of lichens. Warming experiments in the high Arctic had a greater effect on the fauna above ground than below ground and than on fauna in the sub-Arctic. Freeze-thaw events in spring were important and will probably cause differential mortality among species, thus altering community composition. In general, Arctic invertebrate communities are very likely to respond rapidly to change. In contrast long-term data on effects of summer warming of ecosystems by 2–4°C have not shown appreciable changes in microbial biomass and nutrient stocks. This suggests that temperature increase alone is unlikely to have any strong impact on microbial C and nutrient sequestration. Manipulations simulating enhanced UV-B radiation and a doubling of atmospheric CO_2 for 7 years altered the use of labile carbon substrates used by gram-negative bacteria suggesting a change in community composition. UV-B radiation also affects the structure of fungal communities. So far, no change in plant community structure has been found in the Arctic in response to manipulations of UV-B and CO_2.

Trophic interactions of tundra and sub-Arctic forest plant-based food-webs are centered on a few dominant animal species which often have cyclic population fluctuations that lead to extremely high peak abundances in some years. Small herbivorous rodents of the tundra (mainly lemmings) are the main trophic link between plants and carnivores. Small rodent population cycles with peak densities every 3–5 years induce strong pulses of disturbance, energy and nutrient flows, and a host of indirect interactions throughout the food-web. Lemming population cycles are crucial for nutrient cycling, structure and diversity of vegetation and for the viability of a number of predators and parasites that are specialists on rodent prey/hosts. Trophic interactions are likely to be affected by climate change. Ice crusting in winter may render vegetation inaccessible for lemmings, deep snow may render rodent prey less accessible to snow surface predators, and increased plant productivity due to warmer summers may dominate the food-web dynamics. Long-term monitoring of small rodents at the border of the Arctic region in Fennoscandia provides evidence already for a pronounced shift in small rodent community structure and dynamics that have resulted in a decline of predators that specialize in feeding on small rodents. These include the Arctic fox, snowy owls, buzzards, and skuas.

In sub-Arctic forests, a few insect defoliators such as the autumnal moth *Epirrita autumnata* that exhibit cyclic peak densities at approximately 10-year intervals are dominant actors in the forest food-web. Insects can devastate large tracts of birch forest at outbreak densities, and play a crucial role in forest structure and dynamics. Trophic interactions with either the mountain birch host plant or its insect parasitoids, are the most plausible mechanisms generating cyclic outbreaks in *Epirrita*. Climate is likely to alter the role of *Epirrita* and other insect pests in the birch forest system in several ways. Warmer winters may act to increase survival of eggs and expand the range of the insects into areas outside their present outbreak ranges. Alternatively the distribution range and activity of natural enemies like parasitic wasps is likely to keep the insect herbivore populations below outbreak densities.

Climate change is likely to also affect the important interaction between parasitic insects and reindeer/caribou. Insect harassment is already a significant factor affecting the condition of reindeer in the summer. These insects are likely to become more widespread, abundant and active during warmer summers while refuges for reindeer/caribou on glaciers and late snow patches will probably disappear. There are large uncertainties about the outcome of the potential spread of new trophic interactants, especially pests and pathogens into the Arctic.

Disease in plants is likely to increase in those parts of species distribution ranges where a mismatch between the rate of relocation of the species and the northward/upward shift of climatic zones results in populations remaining in supra-optimal conditions. The incidence of new diseases from increasing mobility of pathogens with a southern distribution is a possibility but UV-B could possibly reduce the impact of viral and fungal pathogens.

Microbe-plant interactions can be competitive for nutrients and also mutualistic through mycorrhizal associations. Warming will probably affect both types of relationship but information is scarce.

Effects on the Function of Arctic Ecosystems in the Short- and Long-term (6)

Arctic ecosystems tend to accumulate organic matter and elements despite low inputs because organic matter decomposition is very slow. As a result, soil-available elements like N and P are key limitations to increases in C fixation and further biomass and organic matter accumulation. Key issues for prediction of whole-system responses to climate change include the importance of C-nutrient interactions, the interactions of C and nutrient cycles with temperature, water, and snow cover, the magnitude of DOC and DIC losses in soil water, and the magnitude and role of wintertime processes. Most disturbances are expected to increase C and element turnover, particularly in soils, which may lead to initial losses of elements but eventual, slow recovery. Individual species and species diversity have clear impacts on element inputs and retention in Arctic ecosystems but their magnitude relative to climate and resource supply is still uncertain. Similarly, the current information on long-term effects of CO_2 and UV-B on whole ecosystems indicates that direct effects of these variables will be probably small relative to changes in soil resources and element turnover. Indirect effects of CO_2 and UV-B are likely to be more important at the ecosystem level, such as through changes in species composition.

The most important trace gases in Arctic ecosystems are CO_2 and CH_4. Trace gas exchange with the atmosphere occurs through a set of coupled soil ecosystem processes. The dominant form of C loss is as CO_2, produced by both plants and soil biota: autotrophic plant respiration accounts for about half the C lost from the ecosystems and heterotrophic soil microbial respiration accounts for most of the other half. Wet and moist tundra environments are known to be significant contributors to atmospheric CH_4. However, methane is also consumed in aerobic parts of the soil. Methane emissions from the ecosystems are a balance between production and consumption. Production is more responsive to warming than consumption. Soil warming in the absence of any other changes will very likely accelerate emissions. Winter processes and vegetation type also affect CH_4 emissions. N_2O emissions are also sensitive to winter conditions and potential winter warming.

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation, to summer when the ecosystem absorbs most incoming radiation. Vegetation profoundly influences the water and energy exchange of Arctic ecosystems. Vascular plants account for most CO_2 flux, whereas mosses account for most water vapor flux; albedo during the period of snow-cover declines from tundra to forest tundra to deciduous forest to evergreen forest; shrubs, and trees increase snow-depth which in turn increases winter soil temperatures; ground heat fluxes ecosystems with a large leaf area and insulating moss carpets reduce ground heat fluxes and conserve permafrost. Future changes in vegetation driven by climate change are very likely to profoundly alter regional climate.

Effects on Landscape and Regional Processes and Feedbacks to the Climate System (7)

Biological and physical processes in the Arctic system operate at various temporal and spatial scales to impact large-scale feedbacks and interactions with the earth system. There are four main potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system: albedo, greenhouse gas emissions or uptake by ecosystems, greenhouse gas emissions from methane hydrates, and increased freshwater fluxes that could affect the thermohaline circulation. All these feedbacks are controlled to some extent by changes in ecosystem distribution and character and particularly by large-scale movement of vegetation zones. However, it is difficult to assess the consequences of the interacting feedbacks, and even of individual feedbacks.

There are currently too few full annual measurements available to give a solid answer to the question as to whether the circumpolar Arctic is an atmospheric source or a sink of CO_2 at the landscape scale. Indications are, however, that currently the source areas exceed sink areas in geographical distribution. CH_4 sources are also lacking study but the available information indicates emissions at the landscape level that are of great importance for the total greenhouse balance of the circumpolar North. In addition to the effect of greenhouse gases, the energy and water balances of Arctic landscapes encompass important feedback mechanisms in a changing climate. Increasing density and spatial expansion of the vegetation cover will cause a lowering of the albedo and more energy to be absorbed on the ground that is likely to exceed the negative feedback of increased C sequestration in greater primary productivity. The degradation of permafrost has complex consequences. In areas of discontinuous permafrost, warming will lead to a complete loss of the permafrost. Depending on local hydrological conditions this may in turn lead to a wetting or drying of the environment with subsequent implications for GHG fluxes. Models projecting vegetation change in response to future climate change scenarios indicate a 7–18% decrease in the area occupied with polar dessert and a 4–11% northward migration of the treeline over the coming 80 years. This in turn leads to an increased carbon storage over this same period due to productivity being stimulated more than respiration. However, this balance critically depends on the degree of warming predicted. With warmer climate change scenarios the heterotrophic respiration is stimulated more and the carbon gained will be less. There are very few models available for projections of future CH_4 emissions but the importance of these emissions for the total greenhouse gas balance and functioning of the circumpolar Arctic will be huge.

Synthesis of Effects in Four Arctic Subregions (8)

North-south gradients in temperature dominate the geographical variability of species diversity, ecosystem structure and function, and carbon storage in the Arctic. However, these latitudinal patterns vary also longitudinally in relation to differences in geography, environmental history, and recent climate variability. Assessments of impacts of changes in climate and UV-B radiation within 4 subregions of the Arctic determined by large-scale differences in weather and climate-shaping factors, showed that geographical barriers to species relocation, particularly the distribution of land masses and separation by seas, will affect the northward shift of vegetation zones. The geographical constraints—or facilitation—of northward movement of vegetation zones will affect the future storage and release of carbon, and the exchange of energy and water between biosphere and atmosphere. In addition, differences in the ability of vegetation zones to re-locate will affect the biodiversity associated with each zone while the number of species threatened by climate change varies greatly between subregions with a significant hot-spot in Beringia. Overall, the subregional synthesis demonstrates the difficulty of generalizing projections of responses of ecosystem structure and function, species loss, and biospheric feedbacks to the climate system for the whole Arctic region and implies a need for a far greater understanding of the spatial variability of the responses of terrestrial arctic ecosystems to climate change.

Uncertainties in Making Assessments and Recommendations for Future Research (9)

An assessment of the impacts of changes in climate and UV-B radiation on Arctic terrestrial ecosystems, made within the Arctic Climate Impacts Assessment (ACIA), highlighted the profound implications of projected impacts for future ecosystem services, biodiversity and climate. However, despite some strengths in our capabilities, the assessment is based on a range of approaches that each have uncertainties and data sets that are often far from complete. Uncertainties arise from methodologies and conceptual frameworks, from unpredictable surprises, from lack of validation of models, and from the use of particular scenarios, rather than predictions, of future greenhouse gas emissions and climates. Recommendations to reduce the uncertainties are wide-ranging and relate to all disciplines within the assessment. However, a repeated theme is the critical importance of achieving an adequate spatial and long-term coverage of experiments, observations and monitoring of environmental changes and their impacts throughout the sparsely populated and remote region that is the Arctic.

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11. Acknowledgements. We thank Cambridge University Press for permission to reproduce this paper. TVC and MJ gratefully acknowledge the grant from the Swedish Environmental Protection Agency that allowed them to participate in ACIA. Participantion of K. Laine and E. Taulavuori have been facilitated by financial support from the Academy of Finland and Thule Institute, University of Oulu. Phycology research in the Arctic by J. Elster and colleagues has been sponsored by two grants; the Natural Environment Research Council (LSF-82/2002), and the Grant Agency of the Ministry of Education of the Czech Republic (KONTAKT - ME 576). We thank the participants, reviewers and particularly the leaders of the ACIA process for their various contributions to this study.

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