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Published in:
Ambio: a Journal of the Human Environment

DOI:
10.1579/0044-7447-33.7.418

2004

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

Terry V. Callaghan, Lars Olof Björn, Yuri Chernov, Terry Chapin, Torben R. Christensen, Brian Huntley, Rolf A. Ims, Margareta Johansson, Dyanna Jolly, Sven Jonasson, Nadya Matveyeva, Nicolai Panikov, Walter Oechel, Gus Shaver, Josef Elster, Ingibjörg S. Jónsdóttir, Kari Laine, Kari Taulavuori, Erja Taulavuori and Christoph Zöckler

Environmental manipulation experiments showed that species respond individualistically to each environmental-change variable. The greatest responses of plants were generally to nutrient, particularly nitrogen, addition. Summer warming experiments showed that woody plant responses were dominant and that mosses and lichens became less abundant. Responses to warming were controlled by moisture availability and snow cover. Many invertebrates increased population growth in response to summer warming, as long as desiccation was not induced. CO_2 and UV-B enrichment experiments showed that plant and animal responses were small. However, some microorganisms and species of fungi were sensitive to increased UV-B and some intensive mutagenic actions could, perhaps, lead to unexpected epidemic outbreaks. Tundra soil heating, CO_2 enrichment and amendment with mineral nutrients generally accelerated microbial activity. Algae are likely to dominate cyanobacteria in milder climates. Expected increases in winter freeze-thaw cycles leading to ice-crust formation are likely to severely reduce winter survival rate and disrupt the population dynamics of many terrestrial animals. A deeper snow cover is likely to restrict access to winter pastures by reindeer/caribou and their ability to flee from predators while any earlier onset of the snow-free period is likely to stimulate increased plant growth. Initial species responses to climate change might occur at the sub-species level: an Arctic plant or animal 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. Indigenous knowledge, air photographs, satellite images and monitoring show that changes in the distributions of some species are already occurring: Arctic vegetation is becoming more shrubby and more productive, there have been recent changes in the ranges of caribou, and "new" species of insects and birds previously associated with areas south of the treeline have been recorded. In contrast, almost all Arctic breeding bird species are declining and models predict further quite dramatic reductions of the populations of tundra birds due to warming. Species–climate response surface models predict potential future ranges of current Arctic species that are often markedly reduced and displaced northwards in response to warming. In contrast, invertebrates and microorganisms are very likely to quickly expand their ranges northwards into the Arctic.

INTRODUCTION

The distributions of species that currently occur in the Arctic represent a snapshot of a dynamic and ongoing process driven by historical climate changes such as glaciations and deglaciations (1). We know from the ways in which species distributions have changed in the Arctic under past climates, and from the characteristics of current Arctic species selected by current environmental factors (2), that the performance, abundance and distribution of current Arctic species will change as the future climate of the Arctic becomes warmer (3). Indeed, monitoring and indigenous observations are already recording current species changes that are occurring in the Arctic. However, it is difficult to determine the causes of these changes, while predicting current Arctic species responses to *future* climate change is still more complex.

Species respond individualistically to environmental variables such as temperature (4) and even various processes within one species (e.g. reproductive development, photosynthesis, respiration, leaf phenology in plants) respond individualistically to any one environmental change. Knowledge on how species respond to changes in temperature come from many sources including indigenous knowledge (IK), current species distributions related to climate, and experimental manipulations of temperature in the laboratory and field. Often, however, the ways in which a species responds to changes in temperature are moderated by how its neighbors, competitors, facilitators, herbivores, food, pests and parasites and future immigrant species respond to the same environmental change (5). Responses of species to changes in temperature are also likely to be modified by changes in a co-occurring environmental variable such as UV-B radiation (3).

Despite the daunting complexity of understanding future ecosystem change from the complex interactions among its components species, a knowledge of species-level responses is essential to those people using particular species as a resource (3). This knowledge is also important for understanding the relationship between biodiversity responses to climate change and the functioning of future, changed, ecosystems that could have implications beyond the southern borders of the future Arctic region (6).

This paper is part of an holistic approach to assess impacts of climate change on Arctic terrestrial ecosystems (3, 7). Here, we focus on current, short-term phenotypic, and longer-term genetic responses of plant, animal and microorganism species to a changing climate and UV-B regime. Our information is taken from indigenous observations, scientific monitoring, experiments and models.

PHENOTYPIC RESPONSES OF SPECIES TO CHANGE

Specific Responses of Plants to Changes in Climate and UV-B Radiation

The information presented below relates to individual plant species and how they have been found to respond to changes in various aspects of climate and UV. This information is taken mainly from experiments in which some climate variables or UV have been modified and the responses of the individual species have been determined while they are growing in natural communities.

Plant responses to current changes in climate
IK studies in Canada describe poor vegetation growth in eastern regions associated with warmer summers and less rain (8) while those in western regions describe increased plant biomass and growth, particularly in riparian areas and with moisture tolerant species such as shrubs (9, 10) due to lengthening of the active growing season, marked springtime warming and increased rainfall.

Inuit within the Tuktu Nogak project in the Kitikmeot region of Nunavut (9, 11) observed that vegetation is more lush, plentiful and diverse in the 1990s compared to earlier decades. Willows and alders are described as taller, with thicker stem diameter and producing more branches, particularly along shorelines. Other indigenous communities are also reporting increases in vegetation, particularly grasses and shrubs. They say there is grass growing in places where there used to be only gravel. On Banks Island, in the Canadian western Arctic, Inuvialuit use the fact that the *umingmak* (musk oxen) are staying in one place for longer periods of time as additional evidence that vegetation is richer (10). In addition, Riedlinger (10) has documented Inuvialuit observations of an increase in forbs such as *qungalik* (Arctic sorrel, *Oxyria digyna*), which is described as coming out earlier in the spring, and noticeably "bigger, fresher and greener".

Monitoring of the annual quality and quantity of salmonberries locally called akpiks (=cloudberry=*Rubus chamaemorus)* the Arctic Borderlands Ecological Knowledge Co-op, (12) documented recent observations of high temperatures early in the year that 'burn' berry plant flowers, early spring-melt that results in inadequate moisture for the plants later in the year and intense summer sun that 'cooks' the berries before they can be picked. On Banks Island in the Western Canadian Arctic, local residents report years where the grass remained green right into autumn, leaving it vulnerable to freezing (10). This corresponds to experiments that show the same effect on Svalbard (13).

In northern Finland, marshy areas are said to be drying up. Sami reindeer herders from Kaldoaivi in Utsjoki have observed that berries such as bog whortleberry (*Vaccinium uliginosum*) have almost disappeared in some areas. Other berries such as cloudberries (*Rubus chamaemorus*) and lingon berries (*V. vitis-idaea*) are said to have declined in the last 30 years (14). The indigenous peoples' observations on declining berry production from *Rubus chamaemorus* are supported by experiments which postulate declines in growth in warm winters (15) and provide detailed mechanisms for fruit production (16–18).

IK also records changes in species distribution; some existing species are becoming more widespread and new species are being seen. In addition to increased shrub abundance, Thorpe et al. (9, 19) documented reports of new types of lichens and flowering plants on Victoria Island in Nunavut and more individual plants of the same species (11). The increases in shrubs in this area correspond to aerial photographic evidence of increases in shrub abundance in Alaska (20). However, the reports of new types of plants, and lichens in particular, contrast with experimental evidence that shows a decrease in lichens and some mosses when flowering plant biomass increases (21, 22). A possible reason for this is that results from warming experiments cannot be extrapolated throughout the Arctic because of variations in recent and projected climate from cooling and warming (3). Warming experiments in continuous vegetation show declines of lichens whereas lichens can expand their distribution during warming in the high Arctic where vascular plant competitors are sparse (23).

In contrast to observed responses of plants to recent warming, remote sensing by satellites has shown that the start dates of birch pollen seasons have been delayed at high altitudes and in the northern boreal regions of Fennoscandia (24). Also, in the Faroe Islands, there has been a lowering of the alpine zone in response to a 0.25°C *cooling* in the past 50 years (25).

Predicted responses of plants to future changes in temperature
Warming *per se* is very likely to be favorable to the growth, development and reproduction of most Arctic plant species, particularly those with high phenotypic plasticity (flexible/responsive growth and development). However, other limiting factors such as nutrients and moisture or competition from immigrant species are likely to modify response to warming. In some cases, direct and indirect effects of warming are expected to generate negative responses.

- Increased respiration relative to photosynthesis, particularly in clonal plants that accumulate old tissues, can result in negative carbon balances (e.g. the cushion form ecotype (Fig. 3 in ref. 7)) of *Saxifraga oppositifiolia* (26) and some species of the herb *Ranunculus* (27)).
- Cushion forms of Arctic plants including mosses, that have low atmospheric coupling and experience high temperatures could experience thermal death during warming, particularly when combined with reduced cooling by evapotranspiration under drought conditions.
- Exposure to high radiation and increases in temperature could possibly cause damage and death to some species, particularly those of shady and wet habitats, that have low thermo tolerances (as low as 42°C in the herb *Oxyria digyna;* (28)).
- During warming, Arctic species with conservative nutrient-use strategies, slow growth and particularly strongly determined morphologies of plants such as those of cushion and mat plants, are likely to be at a competitive disadvantage with more responsive, faster growing, taller species immigrating from southern latitudes. After 6 years of shading (simulating competition), warming and fertilizing a heath and a fellfield community in Swedish Lapland, shading was found to have the greatest effect on aboveground growth (29). In another experiment, flowering of the dwarf heather-like shrub *Cassiope tetragona* stopped when it was shaded (30). In contrast, in a meta analysis by Dormann and Woodin (31), no significant effect of shading was found on biomass.

Populations at the most environmentally extreme boundary of their distributions (in terms of latitude, altitude and habitat mosaics within landscapes) tend to be responsive to amelioration of physical environmental factors such as temperature that limit their distributions and have the potential to expand their distribution. In contrast, populations at the most environmentally benign boundary of their distribution tend to be constrained by competition with more responsive species of more benign environments (32) and tend to be displaced by environmental amelioration.

An International Tundra Experiment (ITEX) (33) meta-analysis of Arctic vascular plant species responses to simulated summer warming (1.2°–1.8°C mean daily near surface and soil temperature increase) using standard open-top chambers compared key species from 13 sites over a period of one to four years (34). This increase can be compared with the expected increase in mean summer air temperature for the Arctic of 1.8°C by 2050

(Mean of the 5 ACIA scenarios). Phenology in terms of bud burst and flowering in ITEX and earlier experiments (35, 36) was advanced in warming treatments at some sites. In Swedish Lapland, growth accelerated and the period between thawing and anther appearance advanced by 2 weeks (37). In contrast, there was little change in growth cessation at the end of the season in response to warming. Nutrient addition, however, prolonged the period of growth of polar semidesert species in autumn on Svalbard, but reduced frost hardening leading to dramatic loss of aboveground biomass during the extreme warm, wet, November of 1993 (13). This corresponds to indigenous observations noted above.

ITEX experiments showed that initial increases in vegetative growth were generally, but not always, reduced in later years probably because warming stimulated the use of stored resources more than the uptake of new resources. Similarly, responses of sub-Arctic dwarf shrubs to soil warming increased initially but soon returned to former levels. This response followed an initial increase in nitrogen mineralization in response to soil warming that did not persist (38). In contrast, reproductive success improved in later years in the ITEX experiments (34) due to the extended period of flower bud initiation to seed set in Arctic flowering plants. Similarly, flowering of the widespread sedge *Carex bigelowii* was strongly correlated with July temperature over an 18 year period, but in the year before flowers are seen (39). *Eriophorum* species exhibit even more dramatic variation in flowering among years than *Carex* species, but there is no simple correlation with the current or previous year's weather (40).

The ITEX experiment showed that responses of growth and reproduction varied among vascular plant life forms. Herbaceous species responded more strongly and consistently to warming than did woody forms over a four year period (34). Over longer time periods, the growth form, number and position of meristems in some woody plants such as *Betula nana* allows a much greater response that completely changes the height and structure of the whole canopy (41, but see Graglia et al. (42) for a different response). In the sub-Arctic, Graglia et al. (42) showed that initial plant responses (abundance) to warming and other treatments persisted throughout a ten year period. Graminoids were particularly responsive to fertilizer additions in the sub-Arctic and their increased growth and litter production suppressed the growth of mosses and lichens (21, 22, 43, 42). Evergreens were more responsive to nutrient addition and warming than deciduous species (34).

Mosses and lichens appear to be particularly vulnerable to climate warming, at least in areas of continuous vegetation cover. A meta-analysis of lichen responses to warming experiments across the Arctic showed that lichen biomass decreased as vascular plant biomass increased following warming (21). This group of plants is particularly important as a large proportion of global lichen diversity is found in the Arctic, because some species constitue important winter forage for reindeer, and because some are important nitrogen fixers in strongly nitrogen limited systems. A 22-year study of the lichen flora of The Netherlands similarly showed changes that are suggested to be related to an increase in temperature, although the subtropical species might be more sensitive to nitrogen (44). Of the Arctic-alpine/boreal-montane lichen species 50% were declining while sub-tropical species were invading (45). The widespread moss *Hylocomium splendens* shows a complex response to warming (46). Growth in warming experiments is reduced (22, 42) whereas growth increases in relation to mean annual temperature increases throughout its Arctic distribution range (Fig. 7; (47)). This suggests some limitation in the simulation of natural warming. If, however, moss growth and abundance are reduced by warming, then soil thermal regimes, biogeochemical cycling and energy and heat exchange between the biosphere and atmosphere will be significantly impacted (48).

Plant species respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations and interactions among species. Phenological responses to warming are greatest at cold, high Arctic sites (34, 35), whereas growth responses to warming are greatest at low Arctic sites. Growth responses of *Cassiope tetragona* to warming were greatest at a high Arctic and a high altitude-low Arctic site when compared with the warmest low latitude, low Arctic site (49). Over a period of 5 years, shoot elongation responses to warming were greatest in cold summers (50, 51). Laine (52) showed that the reproduction of *Vaccinium myrtillus* depended to some extent on the climate in the previous years (see chapter 13 in (52) for examples from trees) whereas Shetsova et al. (53, 54) showed no such response for co-occurring *V. vitis-idaea* and *Empetrum nigrum*.

Most information on plant responses to climate warming is limited to the short term and small plot – even if the short term is two decades. Because of the great longevity of Arctic plants and clonal growth, it is difficult to extrapolate plant responses from the individual plant to the population. However, climate change (temperature, nutrients, CO_2) impacts on demographic parameters and population growth statistics were determined for the sedge *Carex bigelowii* by Carlsson and Callaghan (55) and Callaghan and Carlsson (56) and showed that climate change increased tiller size, vegetative production of young tiller generations, survival of young tillers and flowering while reducing the age of a tiller at flowering and tiller life span. Two mathematical models showed that the changes in demographic parameters led to an increase in population growth rate, with young tillers dominating this increase. The rate of vegetative spread more than doubled while cyclical trends in flowering and population growth decreased substantially.

Responses of plants to precipitation changes

Precipitation in the Arctic is extremely variable among seasons and from place to place but the amount of snow is difficult to measure (3). Precipitation varies from over 1000 mm in coastal areas, e.g. Norway, Iceland, to less than 45 mm in the polar deserts where most of the annual precipitation occurs as snow. The interaction between precipitation and temperature is extremely important for plant growth and ecosystem processes and it is difficult to separate their effects.

Observations show that precipitation has increased by up to 15% in northern latitudes within the last 40 years (57) although the spring hemisphere snow cover has retreated by 10% in the last 20 years (3). The most recent climate scenarios for the North Atlantic Region suggest increased mean annual temperatures and precipitation for the entire region (3, 58).

Effects of changes in snow depth, duration and timing of the snow-free period: The interaction between snow amount and temperature will determine the start and duration of the snow-free period. The duration of the snow-free period at high northern latitudes has increased by 5–6 days per decade and the week of the last observed snow cover in spring has become earlier by 3–5 days per decade over the period 1972–2000 (59). Increased precipitation can therefore be associated with shorter duration of snow and less snow cover (3, 57) . (In contrast, the start of the growing season has been delayed by up to one week over the last 20 years in the high altitude and northern boreal regions of Fennoscandia) (60). Hydrological models applied to the Tana River Basin of northernmost Finland predict increases in the length of growing seasons from 30 days in the mountains to 70 days near the coast of the Barents Sea by 2100 (61). This change is associated with an earlier start of the growing season of about 3 weeks and a delayed end of 2 to 3 weeks.

The timing of the start of the snow-free period is of critical importance, and more important than the timing of autumn snow fall, because solar angles are already high when plants currently start growth and each extra snow-free day at the beginning of the growing season will enable plants to access high levels of PAR (Fig. 1; (6)). In an Alpine area, productivity decreased by about 3% per day delay in snow release date (62). The timing of snowmelt has also been found to have considerable effects on plant phenology (more so than temperature in some cases: (63)), with a contracting of development time that is associated with a decrease in productivity and reproductive output (64). Some plant species such as the Arctic deciduous shrub species, *Salix pulchra* and *Betula nana*, can respond to changes in timing of the growing season (65), but others, particularly evergreen and early flowering species appear to be particularly vulnerable (66, 67).

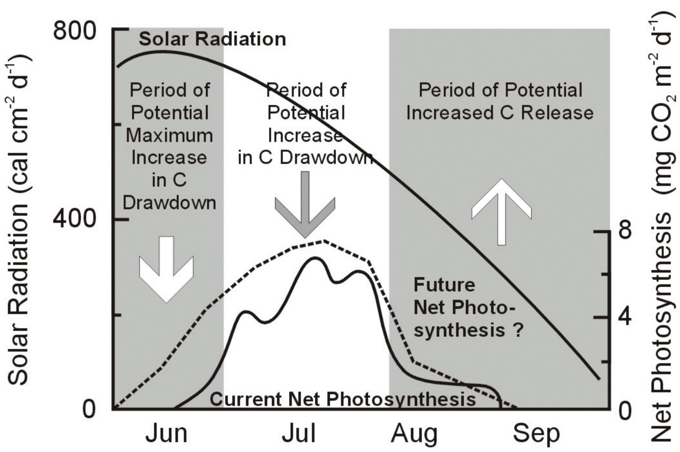

Figure 1. Schematic showing relationship between timing of the growing season and the seasonal pattern of irradiance together with an indication of where transient switches from carbon sink to carbon source could occur (modified from Chapin and Shaver (68)) as a result of increased soil microbial activity in prolonged autumns.

An experiment that manipulated snow conditions by using snow fences at Toolik Lake, Alaska, showed that drifts increased winter time temperatures and CO_2 flux (69–71). Under the drifts, temperatures were more constant than in control plots. Plant growth increased despite a shorter growing season, although this was thought to be a transitory response and contrasts with the reduced growth of late snow bed plants (Plate 7 in Callaghan et al. (5), this Ambio issue.

Frost resistance and avoidance: Changes in snow depth and duration are likely to cause hazardous impacts on the frost resistance and avoidance of many plants at high latitudes. Damage to foliage and apical meristems occur when they are "triggered" to premature bud burst and development by an earlier onset of the growing season, resulting from early snowmelt, when the annual hardening/dehardening is at its most sensitive phase, and when there is a risk of short periods of cold weather. Bilberry is a species whose requirements for cool temperatures to enable it to break dormancy (i.e. chilling requirement) are fulfilled early (72). Accelerated dehardening of bilberry was found as a consequence of a minor (2–3°C) elevation in temperature (73) suggesting that climatic warming is very likely to entail a real risk of early dehardening and subsequent shoot frost damage. The explanation for this may be the higher but fluctuating temperatures, which increase the cryoprotectant-consuming freeze-thaw cycles (74–76). In addition to frost resistance, frost avoidance may also be disturbed by a thin or lacking snow cover. The risk is likely to be highest at high latitudes, where plants that are genetically adapted to the presence of snow may have lost some potential for frost resistance during their evolution. Provenances of bilberry from the sub-Arctic, for example, have shown reduced frost resistance compared to provenances from southern Finland (72).

Other global change factors might affect frost resistance but few, and sometimes conflicting, reports have been published of studies performed at high latitudes. Nitrogen pollutant (or fertilizer) can impair the frost resistance of plants. Such an effect was demonstrated for *Dryas octopetala* on Svalbard during a warm period in early winter (3, 13). However, recent studies with *Calluna vulgaris* (77), *Vaccinium myrtillus* (78) and *V. vitis-idaea* (79) have demonstrated improved frost resistance caused by extra N. Probably, this is because these ericaceous species are plants adapted to low-nutrient habitats, such as those at high latitudes.

Snow depth and duration vary greatly with topography at the landscape level. High summer temperatures will decrease the abundance and sizes of snow beds. Current changes in snow patches recorded by IK are already causing concern in Baker Lake, Clyde River and Iqualiut. Fox (8) describes *aniuvak* (permanent snow patches) that are melting in the hills around the communities there. Aniuvak are good areas for caching meat and provide a sanctuary for reindeer against flying insects. Indigenous peoples' explanations for the melting are related more to changes in precipitation and mean relative humidity, rather than temperature increases. The specialized plants characteristic of late snow beds (80) will be at particular risk.

Summer precipitation: Altered timing and speed of snowmelt may differentially alter the availability of water in different facies of the tundra landscape mosaic which, may in turn impact greatly upon the predominant vegetation type and its growth dynamic through the active season (81). Artificial increases in summer precipitation produced few responses in Arctic plants compared with manipulations of other environmental variables (31). However, mosses benefited from moderate summer watering (22, 82, 83) and nitrogen fixation rates by blue-green algae associated with the moss *Hylocomium splendens* were increased (84). Addition of water in summer time to a polar semidesert community produced surprisingly few responses (85). In the high Arctic, comparisons were made of sites with high and low plant densities. Although there was little difference in soil moisture and plant water relations, and water availability did not constrain the adult vascular plants, surface water flow in snow flush areas allowed greater development of cyanobacterial soil crusts, prolonged their nitrogen fixing activity and resulted in greater soil nitrogen concentrations (86). Because of their importance in facilitating vascular plant community development, Gold and Bliss (86) predict that the effects of climate change on nonvascular species are very likely to be of great consequence for high Arctic ecosystems.

Responses of plants to increased atmospheric CO_2

There are very few manipulation experiments of atmospheric CO_2 concentrations in the field in the Arctic (87–89), but there are more laboratory experiments on Arctic vascular plants (90) and mosses and lichens (91–94).

The first experiment that manipulated CO_2 in the Arctic concluded that elevated CO_2 had no long-term effects because photosynthetic acclimation (i.e. down-regulation) of *Eriophorum vaginatum* was apparent within 6 weeks and biomass did not increase, although there was prolonged photosynthetic activity in autumn and more biomass was allocated to roots (87). The lack of responses and enhanced root biomass were attributed to nutrient limitation (95). Increases in tiller production of *Eriophorum vaginatum* were not considered to be an important response but can lead to long-term increases in population growth (55).

Long-term CO_2 enrichment experiments in the sub-Arctic also show that growth responses are dominated by early, transient responses (96). Four dwarf shrubs were studied over the first 3 years of the experiment; one, the deciduous *Vaccinium myrtillus* showed increased annual stem growth (length) in the first year whereas two other evergreen dwarf *shrubs (Empetrum hermaphroditum* and *Vaccinium vitis-idaea*) showed reduced growth. In year 7, increased CO_2 significantly increased the leaf ice nucleation temperature (i.e. reduced the frost resistance which can be harmful during the growing season) of 3 of 4 dwarf shrub species tested (97). *Vaccinium uliginosum, V. vitis idaea* and *Empetrum hemaphroditum* showed increases of leaf ice nucleation temperature exceeding 2.5°C whereas *V. myrtillus* showed no significant effect as in another study, (78). Increased CO_2 interacted with a high UV-B treatment to give an increase in leaf ice nucleation temperature of 5°C in *V. uliginosum*. This effect coincides with indigenous knowledge and other experiments that show increased frost sensitivity of some Arctic plants to changes in climate and UV-B radiation (3).

An expected response to increased CO_2 was a change in leaf chemistry, e.g. an increase in C:N ratio, that would affect herbivory (98) and decomposition (99). Surprisingly, herbivory was not affected. However, increased CO_2 was found to play a role in nutrient cycling by altering the composition of microbial communities after 5 years (100) (3). This suggests that chemical changes are occurring in plants exposed to high CO_2, but these have not yet been identified.

In laboratory studies, the moss *Hylocomium splendens* that naturally experiences high CO_2 levels in the birch woodlands of the Swedish sub-Arctic, was shown to have photosynthetic rates that were limited by light, temperature and water for most of the growing season (92). Enhanced CO_2 for 5 months decreased photosynthetic efficiency, light compensation point and maximum net photosynthesis and, surprisingly, growth (94). Similar experiments on 3 lichen species, *Cladonia arbuscula*, *Cetraria islandica* and *Stereocaulon paschale* failed to show any response of fluorescence yield to enhanced CO_2 (1000 ppm) although there was an interaction between CO_2 and UV-B levels (93). Perhaps the lack of responses of the moss and lichens reflects their adaptation to the currently high levels of CO_2 that they experience close to the ground surface (92) *via* the process of down-regulation.

In contrast to some views that responses of plants (mainly growth) to increased CO_2 concentrations are relatively small and by inference insignificant (31), recent results show that increased CO_2 concentrations can have the wide ranging and important effects discussed above in the long-term (97, 100).

Responses of plants to increased UV-B

One common method for simulating the effects of ozone depletion has been to irradiate organisms and ecosystems with artificial UV-B radiation. Results are often repeated in relation to the % equivalent ozone depletion. It should be noted, however, that the radiation spectrum from the lamps used differs from the spectrum of the radiation increase that would ensue from real ozone depletion. Therefore the degree of simulated ozone depletion depends on the "weighting function" applied in the calculations, and the knowledge of the appropriate weighting function is very incomplete and is species-specific. A certain amount of artificial radiation applied does not correspond to the same ozone depletion for, e.g. a plant and a tadpole. The information in the following sections should be read with this in mind.

Relatively little is known about plant responses to changes in UV-B radiation. Field experiments on sub-Arctic and high Arctic ecosystems (Table 1) show species-specific responses to ambient UV-B and to enhanced UV-B simulating a 15% decrease in stratospheric ozone (1990 levels). (The 15% decrease is equivalent to losses of o zone expected to occur throughout much of the Arctic. However, the values do not apply to Beringia for April and October 2015 (101)) On the whole, the effects of UV-B are relatively few compared with effects of increased temperature and nitrogen (31).

A meta-analysis of plant responses to increased UV-B radiation globally, showed that there was a small but significant reduction in biomass and plant height (102). In the sub-Arctic, measurements of stem length, branching, leaf thickness, flowering, berry production, phenology and total UV-B absorbing compounds were affected significantly by ambient UV-B in only two of three dwarf shrubs i.e. *Vaccinium uliginosum* and *V. vitis-idaea* (103). *Empetrum hermaphroditum* and *Vaccinium vitis-idaea* showed no responses to enhanced UV-B after 7 years of exposure whereas *V. uliginosum* and *V. myrtillus* showed few responses (Table 1). Enhanced UV-B radiation has been shown to reduce the height growth, but not biomass, of the mosses *Sphagnum fuscum* and *Hylocomium splendens* in the sub-Arctic (104).

The UV-B studies (Table 1) showed that Arctic species were more tolerant of enhanced UV-B than previously thought, and that the production of UV-B absorbing compounds showed no simple relationship with UV-B dose as expected from laboratory studies. Another surprise effect was the responsiveness of frost hardiness in some Arctic dwarf shrubs to increased UV-B. Dunning et al. (105) made pioneering work to investigate the relationship between UV-B and frost resistance in a *Rhododendron* species and concluded that exposure to UV-B increases (although only marginally) cold resistance. In contrast, K. Taulavuori, E. Taulavuori and K. Laine (unpubl.) found decreased frost resistance in bilberry in response to elevated UV-B and Beerling et al. (97) showed decreased frost resistance in the ericaceous dwarf shrubs *Vaccinium uliginosum, V. vitis idaea* and *Empetrum hermaphoditum*. A combination of elevated CO_2 and UV-B reduced late season frost sensitivity of leaves *of V. uliginosum* from -11.5°C to -6°C. Increased frost sensitivity at the beginning and/or end of the short Arctic growing season is likely to curtail the season even further. As some models of vegetation redistribution related to temperature change use the critical freezing temperatures for leaf damage in temperate trees and shrubs (106), modeled past and future northwards migration of temperate vegetation should be reconsidered in relation to changing CO_2 and UV-B levels.

The resilience of the sub-Arctic dwarf shrubs to enhanced UV-B radiation probably reflects pre-adaptation to higher levels than currently experienced in the Arctic (103). The species currently extend southwards to about 40°N and they probably existed even further south in a higher UV-B regime during the early Holocene. The increased UV-B radiation currently applied in experiments is equivalent to the difference in ambient UV-B between the site of the experiment (68°N) and Helsinki (59°N)

Table 1. Summary of UV-B effects on sub-Arctic dwarf shrubs based on Phoenix (103) and other sources referred to in the text (↑ = increase, ↓ = decrease, 0 =no effect compared to control, - = no information).

	V. myrtillus		*V. uliginosum*		*V. vitis-idaea*		*E. hermaphroditum*	
Response	Zero to ambient UV	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B
Stem length	-	↓	0	0	0	0	0	0
Branching	-	0	0	0	0	0	0	0
Leaf thickness	-	↑	0	0	0	0	-	-
Flowering	-	↑	↑	-	0	0	-	-
Berry production	-	↑	0	-	0	0	0	0
Phenology	-	0	0	0	0	0	0	0
Total UV-B absorbing compounds	-	↓	↓	↓	↓	0	0	0
Leaf ice nucleation temperature	-	0	-	↑	-	↑	0	↑

(Fig. 2). In addition, many Arctic plants have thick leaves that might attenuate UV-B entering leaf tissues. However, one particular climate-UV interaction that could increase the damage experienced by plants is the combination of possible earlier snow-free periods (61) with higher spring UV-B radiation at the earth's surface (101). Such a combination of effects would expose young, potentially sensitive, plant shoots and flower buds to particularly high UV irradiation (107).

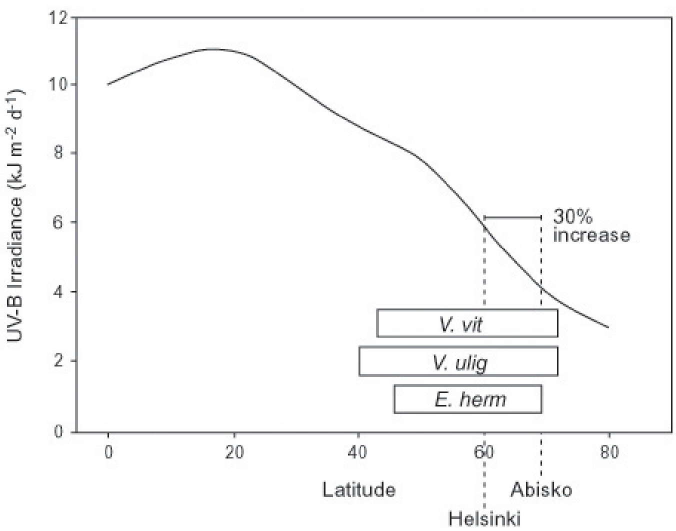

Figure 2. Dwarf shrub distributions (labeled boxes) in relation to latitude and solar UV-B radiation incident at the Earth's surface (89, 103, 108).

Plant responses to changes in cloudiness and photoperiod

A major characteristic of the Arctic environment is the daily and seasonal patterns of the light period or photoperiod. Intermediate latitudes (40–50°N) exhibit about 8-hour day length at mid-winter, whereas a polar night without sunrise prevails north of the Arctic Circle (66.5°N). Consequently, day length change during spring and autumn occurs much faster at high latitudes.

Frost resistance patterns change seasonally and are environmentally controlled, mainly by temperature and day length, the predominance of which depends on the seasonal growth cycle (109). The development of frost resistance by almost all woody plants at high latitudes is characterized by strong dependency on the photoperiod for growth cessation and cold hardening. Scots pine (*Pinus sylvestris*) seedlings from the northern boreal forest develop a high degree of frost resistance during the late summer as a consequence of the shortening days (110). The frost hardening process is initiated even at high temperatures (+ 20°C) in experimental conditions which mimic the ambient photoperiod (111). Due to the marked photoperiodic control of the frost hardening process of woody species at high latitudes, it is understandable that they harden more extensively compared to populations at lower latitudes under similar temperatures. For example, the lowest survival temperature of bilberry (*Vaccinium myrtillus* L.) in the Central Alps (ca. 50°N) at mid-winter is around -35°C (112 and references therein), while the same level of frost resistance is already achieved at the end September in northern Finland (65°C) (78).

Photoperiod will not change, but species that are migrating will experience changes in photoperiod. It is unlikely however, that this will constrain species initially as many northern boreal species, for example, experienced Arctic photoperiods earlier in the Holocene before they were displaced southwards by climate cooling (1). If and when species with a more southern distribution migrate into the Arctic, constraints of photoperiod might affect growth and flowering but this is largely unknown. However transplant experiments of herbs between the Austrian Alps, Abisko and Svalbard showed that allocation of biomass in some species such as *Rannunculus glacialis* was effected by photoperiod and this constrains any potential increases of vigor that might have occurred due to climate warming (113). In contrast herbs, such as *Geum* (113) and some grasses (114) not sensitive to photoperiod could benefit from climate warming.

It has been suggested that increased UV-B radiation effects might be small in the future because of increased cloudiness that would counteract to some extent decreasing ozone (31). However, predictions of increased cloudiness and particularly future cloud types are uncertain. Instead, UV-B effects will be reduced by decreases in albedo as snow and ice distribution and seasonal duration decline, and as the boreal forest displaces part of the current tundra.

Arctic plants differ in the degree to which they gain or lose carbon in photosynthesis at "night time." In conditions of cloudy nights, those species that have carbon gain at nighttime e.g. *Dryas integrifolia, Alopecurus alpinus, Salix glauca* and *Salix arctica* (25–30% of diurnal carbon gain) (115) are likely to have a reduced competitive ability compared with species that do not. In contrast, increased cloudiness in daytime probably favors those species that have a carbon gain at night. Those species that lose carbon at nighttime (e.g. *Eriphorum angustifolium*) (115) would be disadvantaged by warming.

Plant responses to potential changes in pollinator abundance and activity

The rapid phenological changes that have been observed in response to simulated climate change have the potential to disrupt the relationships that plants have with animal, fungal, and bacterial species that act as pollinators, seed dispersers, herbivores, seed predators and pathogens (116). These disruptions are likely to have the strongest impact if the interacting species are influenced by different abiotic factors or if their relative responses to the same factors (e.g. elevated temperatures) are different. However, wind and self-pollination are more widespread among Arctic flowering plants so any mismatch between pollinator activity and flowering phenology would probably be of greater significance to any plants moving in to the Arctic during warming. Little appears to be known about these processes.

Specific Responses of Animals

In contrast to plants, there are relatively few experiments that have addressed how animal populations respond to simulated climatic change and UV-B levels in the Arctic. The few experiments have focused on invertebrates (e.g. insects and soil animals) for which the microclimate can be manipulated on small experimental plots. Experiments on free-ranging vertebrate populations may not be feasible for logistical reasons. On the other hand, time series of population data are available to a greater extent for conspicuous vertebrates such as reindeer and lemmings than, for example, soil invertebrates. Time series can be analyzed with respect to the influence of current climate variability (including recent changes).

Responses of animals to current changes in climate and UV

Ice crust formation on the tundra of a result as freeze-thaw events during the winters affects most terrestrial Arctic animals. Dense snow and ice severely limit forage availability for large ungulates such as reindeer and musk ox (117). Dramatic population crashes in reindeer resulting from periodic ice-crusting have been reported from the western, coastal part of the Russian Arctic, Svalbard, and Fennoscandia, (118–121). Similar events have been reported for musk ox in the southern parts of their range in Greenland (122). Inuit in Nunavut report that caribou numbers decrease in years when there are many freeze-thaw cycles (9) and the probability of such freeze-thaw events is said to have increased as a result of more short-term fluctuations in temperature. In central Siberia, where winter climate is colder and more stable, reindeer population dynamics are less climate driven (119). Swedish Saami note that over the last decade, autumn snow lies on unfrozen ground rather than on frozen ground in the summer grazing areas and this results in poor quality spring vegetation that has rotted (E. Nutti pers comm.). Certain micro-fungi seem to be responsible for such instances (123).

Long and accurate time series data on population sizes for the Svalbard reindeer (124, 120) show that the amount of precipitation during the winter, which is highly variable and is well described by the Arctic Oscillation (AO) index (125), provides the most important check on reindeer population growth rate in concert with population density. Winters with freezing rain were associated with severe population crashes both in one population of the reindeer (although the natural dynamics of an introduced herd may have contributed to this) and an introduced population of *Microtus* voles (Fig. 3).

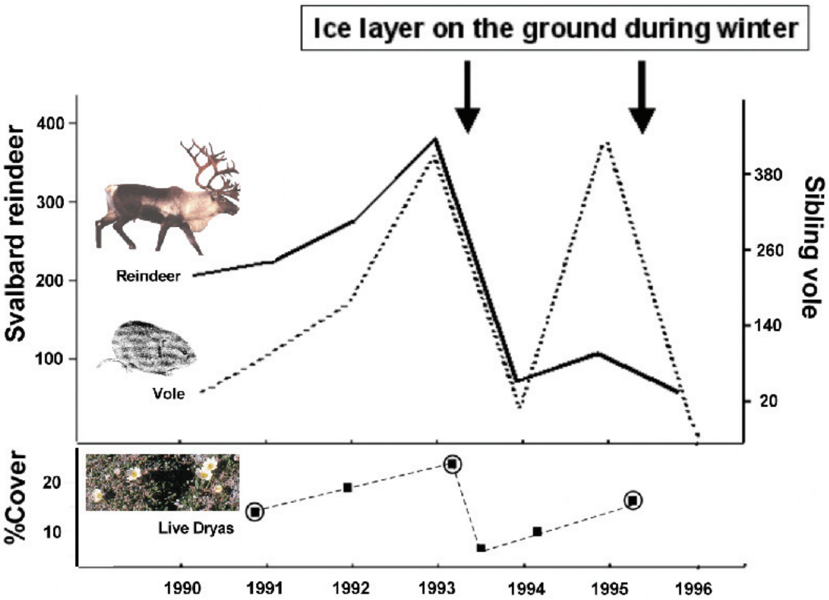

Figure 3. Population dynamics of Svalbard reindeer (solid line) at Brøggerhalvøya and sibling voles (broken line) at Fuglefjella on Svalbard (120, 126). Also included are data from Robinson et al. (13) and Callaghan et al. (46) showing observed (circles) and projected (squares) changes in vegetation.

Episodes with mild weather and wet snow lead to a collapse of the subnivean space and subsequent frost encapsulates food plants in ice, making them unavailable to small mammal herbivores, and even killing plants in some cases (13, 46). Accordingly, the survival rate of tundra voles decreases dramatically in winters with many alternating periods of melting and frost (127, Fig. 4). For example, the last two lemming increases at Kilpisjärvi (NW Finnish Lapland) in 1997 and 2001 were probably curtailed by warm spells and rain in January resulting in freezing of the ground layer (Henttonen unpubl.). Inuit residents of the western Canadian Arctic are also concerned with the impacts of thaw slumping on lemming populations and their predators (owls). Thaw slumps at lake edges are occurring more extensively and at a faster rate in recent years, linked to warmer temperatures and an increase in wind activity and rain while melting ice-bound soil destroys burrows of lemmings (128).

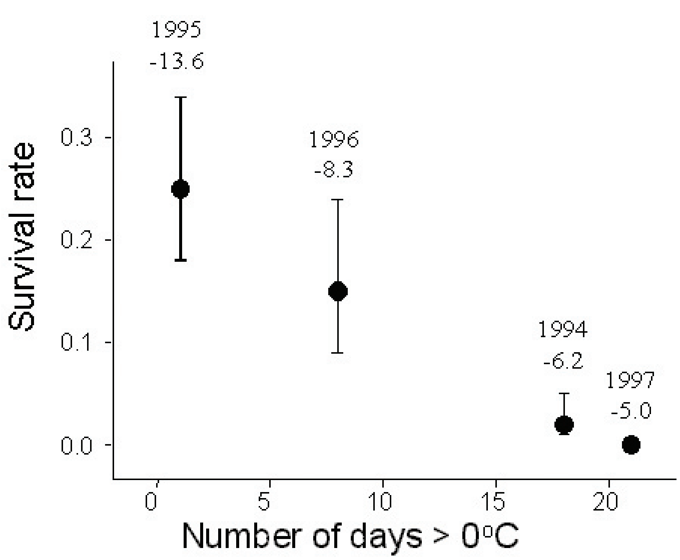

Figure 4. Yearly winter survival rate (with 95% confidence intervals) of experimental tundra vole *Microtus oeconomus* populations plotted against the number of days with temperatures above 0°C during mid winter (December-February). Mean winter temperature and the year are denoted above the survival rate estimates (127).

It has been speculated whether the recent dampened amplitude of population cycles and more spatially asynchronous dynamics of voles and lemmings in northern Fennoscandia (Fig. 5) could result from occasionally unfavorable winters disrupting the normal population dynamics (126). In long qualitative time series (up to 100 yrs), periods with loss of cyclicity and synchrony (129–131) are evident, but it is unclear whether this is related to periods with fluctuations in climate. There is a correlation between sunspot activity and snow-shoe hare cycles in North-America (132), but no such relation for the mountain hare in northern Finland (133). There are no relationships between sunspot activity and outbreak years in the autumnal moth in Fennoscandia (134), although the role of climatic variability in Arctic insects and soil arthropods has been hardly studied because of a lack of long quantitative time series.

The native people of the Arctic are rich sources of information about recent changes in animal health and behavior, in particular concerning the caribou/reindeer. Increases in vegetation (longer grass, thicker riparian areas) are linked to increased forage availability and more mosquitoes and flies, resulting in increased insect harassment of caribou (10). Changes in "the warmth of the sun", length of daylight and the timing of the season may trigger caribou to cross a frozen lake or river when the ice is no longer thick enough to support their weight (9). However, some of the environmental changes may be beneficial. Stronger and more frequent winds are said to provide caribou with relief from insect harassment, meaning they can spend more time inland and not in coastal areas (10). Qitirmiut in Nunavut know that caribou adapt to the heat by staying near coastal areas and shorelines, lying on patches of snow, drinking water, standing in the water, eating moist plants, and sucking mushrooms (9). However, increases to the number of extremely

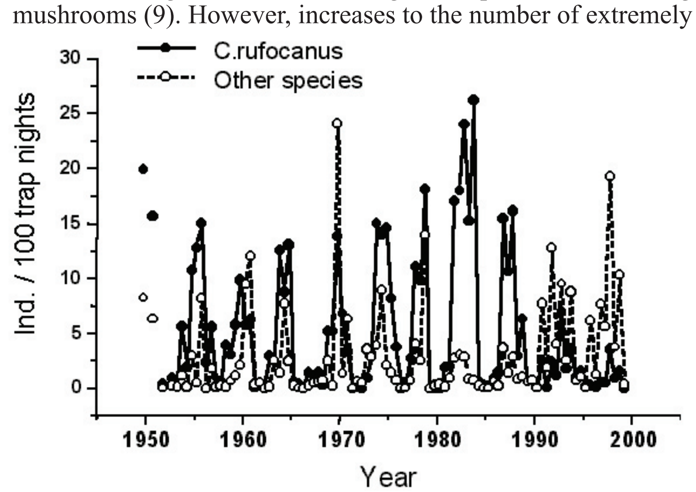

Figure 5. Evidence from the beginning of the 1990s for change in the population dynamics in the formerly cyclic and numerically dominant grey-sided vole and other vole species (combined) at Kilpisjärvi, N-Finland (135).

hot days combined with changing water levels and vegetation patterns may impact the ability of caribou to respond in these ways.

Climatic cooling is to some extent involved in the degradation of habitat in some coastal habitats as a result of grubbing by snow geese on their staging ground. The lesser snow goose (*Anser caerulescens caerulescens*) breeds in coastal areas of the Hudson Bay region which has experienced climatic cooling since the mid-1970s. This has delayed migration of the breeding populations (136). Huge aggregations of staging and local geese in the coastal marshes has led to intense grubbing and degradation of salt-mash swards (137). Long-term observations and modeling have shown that goose reproductive variables are both directly and indirectly dependent on selected climatic variables, and particularly those relating to the early season (138). Nest initiation date, hatching date, and clutch size were associated with date of last snow on the ground, and mean daily temperature between 6 and 20 May. Early snowmelt allows geese to forage and for females to build up nutrient stores before nest initiation. Also, goslings that hatch earlier in the spring have a higher probability of survival than those hatching later. Inclement weather, such as cumulative snowfall, freezing rain and northerly and easterly winds can result in nest abandonment by females and even adult starvation while on nest incubating eggs.

Responses of animals to possible changes in climate

Despite adaptations to low temperatures, warming experiments have shown that temperatures higher than normal do not present any physiological problem for Arctic arthropods given that water is available (139). Arctic aphids were more successful in terms of number of completed generations through the summer when temperature was experimentally elevated (140). The effects of experimental warming were more pronounced in the high Arctic at Svalbard than in the sub-Arctic at Abisko (141). However, the combination of high temperatures and drought seem to be very problematic for terrestrial invertebrates (142) but the hydrological aspect of climate change in tundra habitats is an important issue that has rarely been addressed in studies on Arctic animals (143).

Some of the most important effects of higher summer temperatures in Arctic terrestrial animals are likely to be mediated through intensified inter-specific interactions (parasitism, predation and competition). Higher temperatures in the Arctic will lead to invasions of more southerly-distributed species. Such range expansions are expected to be particularly rapid in those species for which food resources (e.g. host plants) are already present (144). For instance, the mountain birch, the main food plant of the autumnal moth *Epirrita autumnata*, occurs in the continental parts of the Fennoscandian forest tundra where winter temperatures are occasionally lower than the tolerance limit for over-wintering eggs (145) but warmer winters could lead to the exploitation of this existing food source. Already, many insects belonging to the boreal forest invade the low Arctic tundra in quite large quantities every summer (146) and the Arctic region is subject to a "steady rain" of wind-dispersed small invertebrates (147) that may rapidly establish when the environmental conditions are adequate. Due to the lack of long-term monitoring programs, there are presently no Arctic equivalents of the detailed and quantitative documentation of the northward spread of insects in Europe (e.g. 148). Several generalist predators not yet present in the Arctic are likely to spread northwards with increased ecosystem productivity due to warming. The red fox has already expanded into the Arctic, probably at the expense of the Arctic fox (149).

Winter warming will alter snow cover, texture and thickness. A deeper snow cover is likely to restrict access to winter pastures by reindeer/caribou, their ability to flee from predators and energy expenditure traveling across snow. Changes in snow depth and texture will also determine whether warm-blooded small vertebrates may find thermal refuges when resting in snow dens (ptarmigan and hares) or by being active in the subnivean space (150). Ice crust formation reduces the insulating properties of the snow pack (151) and makes the vegetation inaccessible for herbivores. There is ample observational evidence that the current incidence of rate of winter ice crusting clearly affects the population dynamics patterns of both large and small mammal herbivore species (2). Moreover, there is experimental evidence that population densities of numerically dominating tundra Collembola (springtail) species such as *Folsomia quadrioculata* and *Hypogastrura tullbergi* may be halved following an episode of freezing rain on Spitzbergen (152). The expected winter temperature increase of 6.3°C for 2080 (mean of 5 ACIA scenarios: (3) is very likely to result in an increase of alternating periods of melting and freezing: Putkonen and Roe (121) found that such episodes with rain-on-snow in the winter presently covered an area of 8.4 x 10^6 km^2 in the Arctic and they predicted a 40% increase by 2080–2089. This expected increasing frequency of such climatic events is very likely to severely suppress population densities, distort the cyclic dynamics degree of geographic synchrony in lemming, voles and geometrid moths and in some cases even lead to population extinctions.

Responses of animals to possible increases in UV-B

The extent to which animals are adapted to UV-B must be inferred in most cases. Hairs and feathers necessary for insulation against low temperatures also presumably protect the skins of mammals and birds from UV-B while white winter hair and feathers will reflect UV-B radiation to some extent. Eyes of non-migratory animals must be extremely well-adapted to UV-B in order to be effective in the dark Arctic winter yet also cope with high UV-B in the bright, snowy spring. Invertebrates have coloring that might serve many functions. Melanic forms of invertebrates might have advantages in thermoregulation and UV-B protection (153).

Four species of collembola on Svalbard were investigated by Leinaas (153) with respect to UV-B tolerance: *Hypogastrura viatica*, *Folsomia sexoculata*, *Onychiurus groenlandicus* and *O. arcticus*. The first-mentioned three species coexist in wet shore habitats, with the very heavily pigmented *H. viatica* on the surface and *F. sexoculata*, which is as adult also very heavily pigmented lower down. *O. groenlandicus* is a soil-living, unpigmented species. *O. arcticus* is most commonly found under small stones and in rock crevices, and thus living rather unexposed, but has some pigmentation. In an experiment with UV-B radiation (0.5 W m^{-2} in the 300–320 nm band for 12–14 h day^{-1}, approximately equivalent to clear sky summer conditions in southern Norway) the unpigmented *O. groenlandicus* had 100% mortality within 1 week, while the heavily pigmented *H. viatica* was not affected.

Caterpillars of sub-Arctic moths have skins that absorb UV-B to varying extents and the degree of absorption can respond to preconditioning in high UV-B (154). However, UV-B affects animals indirectly *via* the quality and quantity of food that is available to them as a result of UV-B impacts on plant growth and secondary metabolite production (5).

It is possible to infer some responses of animals to future increases in UV-B by comparing relationships of animals to natural UV-B along latitudinal gradients. Along these gradients, ambient UV-B radiation reduced hatchling size of frogs at sites up to 66°N and no latitudinal gradient in UV-B tolerance existed (155). Surprisingly, for a given time of the year, although the UV-B decreases with increasing latitudes, they are in fact exposed to more UV-B during their sensitive stages at high as compared to low latitude (156). These studies suggest that an increase in UV-B radiation due to anthropogenic causes is likely to reduce the populations of those amphibians that have distribution ranges extending into the Arctic.

Enhanced UV-B is thought to improve the immune system of the autumn moth in the sub-Arctic and to destroy the polyhydrosis virus. As this virus, together with the parasitoid wasp *Cotesia jucunda* are both important controllers of the survival of moth caterpillars, increased UV-B radiation could potentially lead to increased population sizes and birch forest defoliation. However, no direct effects of enhanced UV-B were detected on fecundity or survival of the moth (154).

The model generates realistic patterns of mass and energy flow (primary productivity, decomposition rates, soil respiration) under present-day conditions and in response to warming, pollution, fertilization, drying-rewetting of soil, etc. (Fig. 6). Soil warming results in acceleration of both primary productivity and organic matter decomposition, but the latter was more affected. The total C-balance of soil turned out to be negative: respiration exceeded photosynthesis leading to decline of accumulated organic C (Fig.6, right panel) under conditions of soil warming (this topic is addressed in detail in ref. 6). L-selected microbial species exemplified by *Bacillus* which, under normally cold conditions displayed only weak growth in spring, showed considerable stimulation of bacilli growth and a better competitive advantage under soil warming.

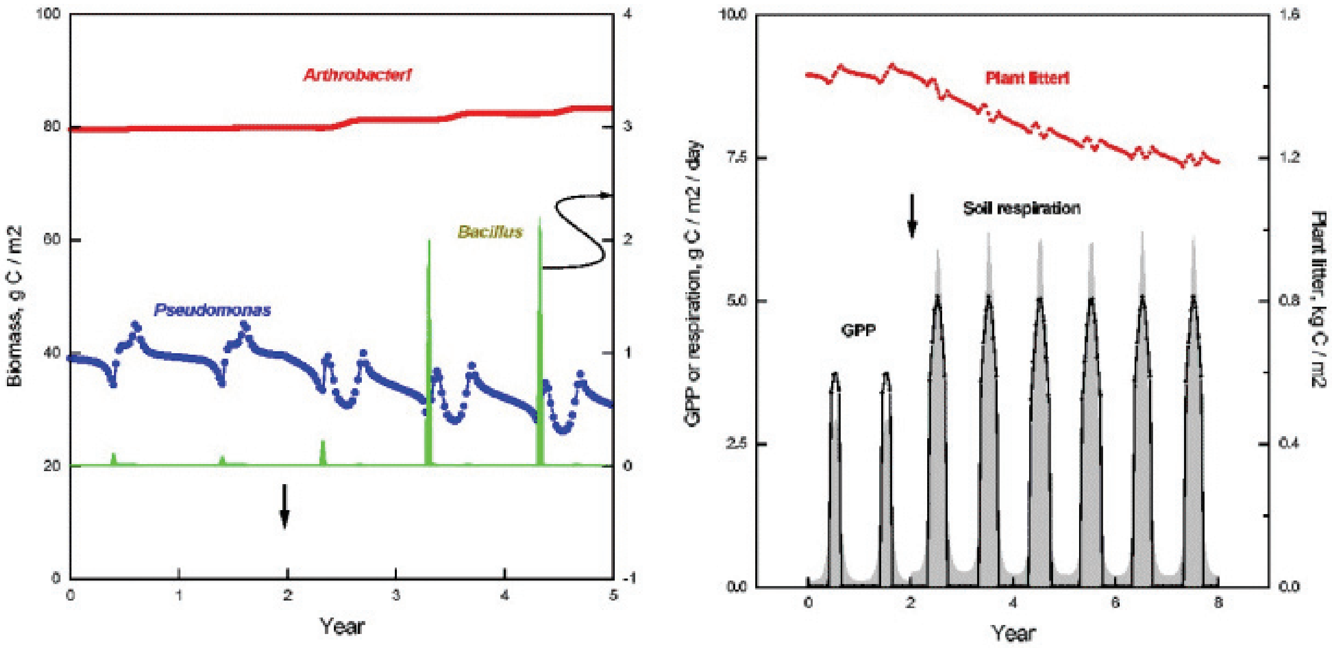

Figure 6. Simulation of changes in a tundra microbial community (Barrow, Alaska) induced by climate warming. Left: population dynamics of dominant soil bacteria; note that L-selected species (*Bacillus*) display only sporadic occurrence under normally cold conditions of the tundra, which is in agreement with observations, and attains high population density after soil warming. Right: carbon budget including net primary production (NPP), soil respiration and litter dynamics. It was assumed that average air temperature was instantly (see y-axes break) shifted by 10°C (159).

Specific Responses of Microorganisms to Changes in Climate and UV-B Radiation

Recent experiments that manipulate the environment, e.g. soil heating, changing watertable, CO_2 enrichment, UV-B supplementation and attenuation, etc. have added new information on the effect of environmental change on the soil microbial community at the species level. In general, climate change is likely to alter microbial community composition and substrate utilization (157). Tundra soil heating, CO_2 enrichment and amendment with mineral nutrients generally accelerate microbial activity (higher growth rate). Enriched CO_2 tends to intensify root exudation, which is the main source of available C for soil and rhizosphere bacteria. Much less is known about the transient changes in the species composition of soil microorganisms induced by manipulation, although supplementation of UV-B in the field resulted in changes in the composition of microbial communities (100). However, laboratory incubation of tundra soils (Barrow, Alaska) at different temperatures had strong effects on community composition assessed from the molecular biology approach called SSU 16S rRNA sequence and fatty acid profiling, but only after a temperature shift of more than 10°C (158).

A mathematical simulation of the changes in microbial community structure in the tundra (159, 160) showed, surprisingly, that the effects of many factors on the soil microbial community were essentially less significant compared with effects on the plant community. This is probably indicative of stronger stabilizing forces within microbial communities regulated by negative feedbacks.

Conidia (spores) of the fungus *Metarhizuim* are sensitive to UV-B. There are great differences between strains but strains from high latitudes are less tolerant than those from lower latitudes (161, 162). In one species (*M. anisopliae*) it was shown that UV-A also had a negative effect and when comparing strains the sensitivity to UV-A did not correlate with that of UV-B (163). Several groups have studied effects of UV- B on phylloplane (leaf surface-dwelling) fungi and litter decomposing fungi. Moody et al. (164) found that five of the investigated species were sensitive and seven relatively insensitive. The spore production in the litter decomposers was generally inhibited by UV-B (except for one species), while that in phylloplane species was unaffected. However, the sensitivity of spores is not equivalent to sensitivity of metabolic machinery of the vegetative body of a fungus (i.e. the thallium or mycelium), which produces the spores.

In the sub-Arctic (Abisko), a study of the decomposition rates of a standard litter type showed that there was a change in the composition of fungal species resulting from elevated UV-B levels (164). These results to some extent resemble those from an earlier experiment on decomposition of dwarf shrub litter from the same site (104).

The Arctic periglacial environment represents a unique mosaic of unstable habitats (graduation between terrestrial and shallow wetland environments) where large variations in cyanobacteria and algal diversity, productivity and life strategy exist (165–169). Prokaryotic cyanobacteria and eukaryotic algae have different life strategies with respect to their susceptibility to severe unstable conditions (170). Cyanobacteria are well adapted to changeable conditions involving low and high radiation (including UV-B), cycles of desiccation, rehydration, salinity and freeze-thaw episodes. This gives them a great ecological advantage and allows them to be perennial. Eukaryotic algae, in contrast, have higher rates of photosynthesis and lower resistances to changes in irradiation, desiccation, rehydration and freeze-thaw cycles. This pre-determines their annual behavior. It can be expected that with increasing severity of the Arctic terrestrial environment, the cyanobacteria will probably become the dominant community. In contrast, if the conditions become milder, the eukaryotic algae will probably start to predominate. In addition, the ongoing temperature rise in the Arctic may also influence cyanobacteria and algal production, as well as the balance between cyanobacteria and algae and invertebrate herbivore activity. Invertebrate grazing pressure is likely to increase and much of the visible cyanobacteria and algae biomass could possibly disappear from Arctic localities (171).

GENETIC RESPONSES OF SPECIES TO CHANGES IN CLIMATE AND UV-B RADIATION

Many widely distributed Arctic species show large ecological amplitude (broad niches), are taxonomically complex, often representing many subspecies, while species of narrower distribution range often show more restricted amplitude. It is necessary to know the extent of genetic variation in Arctic species and the underlying causes of differentiation/ homogenization (biogeography, historical bottle necks, reproductive biology and demography) in order to assess responses of species to climate change.

Plants

In spite of a fast development in recent years of different molecular techniques suited for population genetic studies, there are still rather few studies on Arctic plants. Most have focused on biogeographical and phylogeographical questions related to vascular plant species. Such studies may reveal the migratory potential of the species in response to climate change. During the Pleistocene glaciations, Arctic plants were restricted to refugia, either within or south of present day Arctic regions, from where they could recolonize areas as conditions improved during interglacial periods (172, 173). The rate of colonization by different species during the Holocene probably depended on where their closest refugia were situated, their dispersal biology and genetic makeup. Genetic phylogeographical studies provide evidence for relatively fast migration rates in most vascular species (174–176) and possibly bryophytes as well (177). However, in the modern context of fast climate change, migration rates need to be considered on somewhat shorter time scales than thousands of years.

The level of genetic variation within and between populations indicates the potential for local adaptation to environmental change and hence population resilience to environmental change. Based on the relatively young age of populations and low recruitment of sexually reproduced offspring it was long believed that genetic variation in Arctic plants would be low. However, the number of genetic studies is limited and no such general pattern of genetic variation has been identified. Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels (178–183) to very low levels of variation (183, 184–187). However, genetic variation among Arctic plants may be of greater value in terms of biodiversity due to much lower species diversity than in other biomes. Furthermore, high levels of polyploidy in many Arctic vascular plant species may promote the proportion of the genetic variation partitioned within individuals which may be important when passing through evolutionary bottlenecks (188).

By comparing 19 different populations of three rhizomatous *Carex* taxa, distributed among 16 sites along a major circumpolar sector in Eurasia, ranging from northern Scandinavia in the West to Wrangel Island in the East, Stenström et al. (183) showed that the 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 or those in areas not glaciated at all during the Weichselian. Relatively young population age may also be responsible for a low genetic variation in some other populations (e.g. 184, 187), while in yet others, breeding systems apparently play a large role (e.g. 185, 186). In general, populations of insect pollinated or self-pollinated plant species have lower genetic variation than populations of wind pollinated species (189) and this seems to apply to Arctic plants as well.

Those plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution, as for example *Saxifraga oppositifolia* (190), *Saxifraga cernua* (182), *Silene acaulis* (181, 190), *Carex bigelowii* sensu lato (180, 183) and *Carex stans* (183). In these species, the genetic variation among populations (G_{ST}) is a relatively small proportion of the total genetic variation, i.e. they show low degrees of population differentiation. Large variation within populations, however, increases possibilities for ecotypic differentiation. In the Arctic, extremely steep environmental gradients are frequent on a microtopographical scale and ecotypic differentiation has been demonstrated over such short distances for *Phleum alpinum* (64), *Carex aquatilis* (191), *Dryas octopetala* (192), and *Saxifraga oppositifolia* (193), all widely distributed plant species in the Arctic. Ecotypic differentiation to this small-scale heterogeneity may preserve genetic variation and in that way contribute to resilience to change at the species, rather than the population level. Thus, an initial response to climate change in such species is likely to be a change in the distribution and abundance of ecotypes within a species distribution (193). In addition, many Arctic plants show large phenotypic plasticity, which would further increase their resilience (194) (Table 4 in Callaghan et al. (2)).

If the degree of genetic variation can be used as an indication of resilience of populations to change, we would expect this resilience to be greatest among plants in old populations of widely distributed, wind-pollinated vascular species as for example rhizomatous *Carex* populations in eastern Siberia. However, generation time and seedling recruitment may affect the adaptation rate. Many of the dominating Arctic plants like the rhizomatous *Carex* species are clonal, i.e. they do not rely on seed production through sexual reproduction for short-term population maintenance. The genetic individual of these plant species may become thousands of years old (195) which may slow down the adaptation rate. However, experiments with plants from outside the Arctic have shown that UV-B may speed up genetic change. High UV-B exposure can activate mutator transposons that amplify the mutation effect beyond the immediate UV-B damage (196), and increased UV-B may lead to increased tendency for mutations in future generations (197).

For plants with long-lived seed, further genetic variation is preserved in the seed banks. Dormant seed populations may be genetically different from the aboveground populations (198) and potentially able to better exploit a new climate.

Genetic variation has been studied in fewer moss and lichen species than in vascular plants. However, boreal and Antarctic bryophytes usually show high levels of variation (199, 177, 200,

201) but the partitioning of genetic variation among and within populations depends on species. Scandinavian populations of the widely distributed moss *Hyolocomium splendens*, including two sub-Arctic-alpine populations showed high genetic variation within populations, low G_{ST} and a similar pattern as in widely distributed, wind pollinated vascular species (199). In contrast, North American and European populations of *Polytrichum commune* have low within population variation and high G_{ST} (0.51) (177).

Animals

The genetics of Arctic terrestrial animals have been studied thoroughly mainly for a few well-known mammal species such as reindeer (202), lemmings (203–205) and Arctic fox (206). These studies have focused on phylogeographical patterns and the relative roles of present gene flow and historic processes (especially concerning glacial-interglacial cycles, (1) based on neutral genetic markers (especially mtDNA). The present genetic differentiation 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 sub-species (203, 204), while a very mobile animal such as the Arctic fox, which readily moves among continents and islands on sea ice, appears to be relatively panmictic (i.e. shows little genetic structuring) at the circumpolar scale (206).

Current gene flow (an indication of mobility) and population history (origin and differentiation) indicate a species' ability to track the location of their habitats through time. A mobile species will have better prospects than a relatively sedentary species. Moreover, 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. It should be noted, however, that markers of genetic variation/differentiation currently used (e.g. mtDNA) may have little bearing on the genetic variation in morphology and life-history traits (202). It is these latter traits that decide whether a species or a morph will be able to adapt to future changes. Currently, there is a paucity of studies on Arctic animals using a quantitative genetics approach (207) that have addressed the potential for rapid adaptations to climatic change. Elsewhere, using a quantitative genetic research protocol, Réale et al. (208) recently showed that northern boreal red squirrels were able to respond genetically within a decade to increased spring temperatures.

Microorganisms

Assessment of genetic responses of microorganisms to climate change is based on laboratory models as data from observations within Arctic terrestrial ecosystems are absent. Short generation times and impressive genetic plasticity of bacteria make them one of the favorite objects in theoretical studies of general population genetics. Because most mutations are deleterious, mutation rates are generally thought to be low and, consequently, mutator alleles should be counter-selected. However, up to 1% of natural bacterial isolates have been found to be mutators. A mutator can be viewed as behaving altruistically because, although it reduces individual fitness, it increases the probability of an adaptive mutation appearing. These results may help to explain observations that associate high mutation rates with emerging pathogens causing spontaneous epidemic outbreaks (209, 210).

In the Arctic environment, intensive mutagenic actions are expected from UV radiation and also from aerosols and volatile chemical mutagens brought to the cool polar air from the mid- and low latitudes. The direct mutagenic effect is probably not strong, especially if we take into account the protecting shielding effects of soil particles and population mechanisms discussed above. However, possible mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the whole ecosystem.

RECENT AND EXPECTED CHANGES IN SPECIES DISTRIBUTIONS AND POTENTIAL RANGES

Paleoecological research (1) and observations over many decades demonstrate that the geographical ranges of terrestrial species in general can be correlated well with bioclimatic variables. Furthermore, the strength of these relationships is independent of trophic level (211). Major climate-related species distributions at the large scale include the limit of trees (associated with the isoline for mean July air temperatures of about 10°C (212 discussed in 213) and soil temperature of 7°C (214)) and the limit of woody plants such as dwarf shrubs that are one indicator of the boundary of the polar deserts zone (215). Such relationships suggest that species distributions at the macro-geographical and landscape scales will change as temperature changes. Here, we assess the impacts of climate change on recent changes in species distributions and those expected in the future.

Recent Changes

Indigenous knowledge projects have documented recent changes in the ranges of caribou in relation to changes in weather based on hunters' understandings of how environmental conditions affect seasonal caribou distribution patterns (12). Hunters' explanations of caribou distributions may provide indications of potential range changes under scenarios of warming. For example, in the El Niño year of 1997/98, several thousand Porcupine Caribou over-wintered on the Yukon Coast in Arctic Canada. Hunters in Aklavik, Northwest Territories explained this phenomenon in terms of the Beaufort Sea ice pack, which was farther from the Yukon North Slope than in most years, resulting in warmer coastal temperatures and thus more abundant forage for caribou. In July of 1997, as the caribou moved into Canada from their Alaskan calving grounds, several large groups remained on the coast, taking advantage of the rich forage opportunities. A mild fall and the lack of icing events that push the caribou south for the winter kept the caribou in the area into October, as the animals could continue to access summer forage. The herd remained on the coast for the winter, and was reported to be in better condition than the herd wintering in the usual locations.

IK has also documented recent changes in the ranges of other animals in relation to changes in weather. In the Canadian Arctic, Inuit in communities such as Baker Lake report insects previously associated with areas South of the treeline (8). In more western regions, there are more frequent sightings of "mainland ducks" such as pintail ducks and mallard (10).

Working in the Canadian Arctic, and using the "conventional science approach", Morrison et al. (216) summarized the trends in data for breeding waders. Almost all Arctic breeding species are declining. The reasons for the trends were not always clear and probably of multiple origin. Long-term monitoring in Finland has shown a substantial decline in the populations of many Arctic and sub-Arctic bird species over the past 20 years (217), but the trend is not always negative. Zöckler et al. (218) found that almost half of the long distance Arctic breeding migrants studied are presently in decline. For many species there are still insufficient data available, and only a few (8%) show an increasing trend. In most cases, it is not easy to correlate trends with climate change. As the trends in some species are different outside and inside the Arctic region, there is an indication that factors of a more global nature are involved. An example is the drastic decline of the Ruff (*Philomachus pugnax*) in almost all breeding sites outside the Arctic in contrast to their stable or even increasing populations in some (but not all) northern Arctic areas (219). This coincides with the recent northern expansion of other wet grassland waders, such as Common Snipe in the Bolshemelzkaya tundra (220), Black-tailed Godwit and Northern Lapwing *Vanellus vanellus* in northern Russia concomitant with a northward expansion of agriculture including sown meadows (221). Several other bird species have recently been recorded in more northern locations in the Arctic (222) suggesting a general trend that some species are shifting their distribution in response to changing climate that is altering habitats. The emerging picture is that the Ruff is being forced to retreat to its core Arctic habitats through the effect of global climate change in combination with increasing nutrient enrichment on the quality of wet grassland habitats (219).

same future climate scenarios. However, the large magnitude of the simulated range margin shifts results in many boreal species also exhibiting potential future ranges of reduced spatial extent because they are limited to the north by reaching the shore of the Arctic Ocean.

The extent to which Arctic plant species may suffer the rapid range reductions simulated by such models will depend principally upon two factors. Firstly, such reductions are likely to happen most rapidly in species that experience some physiological constraint at their southern range margin (e.g. the winter thermal constraint postulated for *Rubus chamaemorus* (15, 231) or the summer thermal constraints postulated for *Catharacta skua* (232)); species that have their southern range margin determined by biotic interactions are likely to be affected less rapidly. Secondly, such reductions very probably happen more rapidly where the northward migration of boreal or temperate species is not limited either by habitat availability or propagule dispersal. 'Fugitive' species of the early successional communities that characteristically follow disturbance of the boreal forests will have the required dispersal ability to achieve rapid poleward range expansions. Unless other factors, such as herbivore pressure or a lack of microsites for successful seedling establishment, exclude them then these species potentially will extend into the Arctic rapidly, forming transient ecosystems that will persist until the arrival of the more slowly expanding late successional boreal species.

Table 2. Scenarios of habitat loss of breeding area in % for 23 Arctic water-bird species applying two different circulation models (HadCM2GSa1 = moderate warming; UKMO = extreme warming); their globally threatened status (VU = Vulnerable as a globally threatened species, according to Collar et al. (223); EN = suggested to be upgraded as Endangered as a globally threatened species; ! = suggested for inclusion into the Red List) based on Zöckler and Lysenko (224)

Species		HadCM2GSa1*	UKMO*	Red List
Tundra Bean Goose	*Anser fabalis rossicus/serrirostris*	76	93	
Red-breasted Goose	*Branta ruficollis*	67	85	VU
Spoon-billed Sandpiper	*Eurynorhynchus pygmaeus*	57	57	VU/EN
Emperor Goose	*Anser canagicus*	54	54	!
Ross's Gull	*Rhodosthetia rosea*	51	73	
Red-necked Stint	*Calidris ruficollis*	48	68	
Sharp-tailed Sandpiper	*Calidris acuminata*	46	74	
Little Stint	*Calidris minuta*	45	65	
Curlew Sandpiper	*Calidris ferruginea*	41	70	
Pectoral Sandpiper	*Calidris melanotos*	38	60	
Dunlin	*Calidris alpina*	36	58	
White-fronted Goose	*Anser albifrons*	36	57	
Long-billed Dowitcher	*Limnodromus scolopaceus*	31	54	
Great Knot	*Calidris tenuirostris*	31	42	
Lesser White-fronted Goose	*Anser erythropus*	28	29	VU
Barnacle Goose	*Branta leucopsis*	21	27	
Western Sandpiper	*Calidris mauri*	19	21	
Brent Goose	*Branta bernicla*	16	44	
Knot	*Calidris canutus*	16	33	
Greater Snow Goose	*Anser caerulescens*	14	46	
Canada Goose	*Branta Canadensis*	13	22	
Pink-footed Goose	*Anser brachyrhynchus*	10	10	
Sanderling	*Calidris alba*	5	25	

*Value could be substantially higher as unclassified areas in this GIS analysis may contain different tundra types, e.g. mountain tundra.

A recent global meta-analysis of plants claims that a climate change signal has been identified across natural ecosystems (225). Range shifts of plants averaging 6.1 km per decade towards the poles and 6.1 m per decades upwards have been identified in response to a mean advancement of spring by 2 to 3 days per decade. Although some northern treeline data were included, little information was available for Arctic ecosystems.

Expected Future Changes in Species Distributions

Species–climate response surface models based upon correlations between species ranges and bioclimatic variables are able to project scenarios of the recently observed range changes of at least some species of both birds (224) and butterflies (225–228). Related studies have shown that, at least in the case of butterflies, the extent to which species have realized their predicted range changes over the last 30–50 yr 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 (229).

Such models (227, 230) simulated potential future ranges of Arctic species that are often markedly reduced in spatial extent compared to the species' present ranges. The range limits of boreal and temperate species shift polewards in response to the same future climate scenarios. However, the large magnitude of the simulated range margin shifts results in many boreal species also exhibiting potential future ranges of reduced spatial extent because they are limited to the north by reaching the shore of the Arctic Ocean.

Loss of habitat is a particularly important possibility that will constrain species ranges. The change in habitat that is most dramatic for many waterbirds is the loss of tundra habitat, varying between 39% and 57% (233, 234). Vegetation models (235) applied with GIS distribution maps of waterbirds show a large variation in the impact of predicted changes in vegetation on 25 selected species (224). According to the HadCM2GSa1 model, 76% of Tundra Bean Geese (*Anser fabalis rossicus/serrirostris*) will be affected by the alteration of tundra habitats, whilst only 5% of the Sanderling will be affected. However, the Sanderling, in a similar way to many other high Arctic breeders, might even be affected more strongly, as southern tundra types will replace their specific high Arctic habitats. Whereas the more southerly breeding species can shift northwards, it is increasingly difficult for High Arctic breeders to compete. For two of the three waterbird species which are considered globally threatened, namely the Red-breasted Goose (*Branta ruficollis*) and the Spoon-billed Sandpiper (*Eurynorhynchus pygmaeus*), 67% and 57% of their current breeding range is expected to change from tundra to forest, respectively (see summary in Table 2). This additional loss of habitat will place these two species at a higher risk of extinction. The Emperor Goose (*Anser canagica*), already in decline and with 54% of its small range affected, is highlighted as needing further conservation attention.

Geographical ranges of plants

Strong relationships between growth and temperature in the circumpolar ericaceous dwarf shrub *Cassiope tetragona* and the feather moss *Hylocomium splendens* can be used to model range changes. The growth of *C. tetragona* is strongly related to mean July temperature (236) and that of *H. splendens* is related to mean annual temperature (47) throughout their northern ranges

(Fig. 7a). (Mean July and mean annual temperatures are to some extent equivalent to latitude as they decrease towards the north in the above examples.) The natural climatic warming from the beginning of the Little Ice Age to the present is the equivalent of only a minor shift in latitude for *C. tetragona*. On the other hand, scenarios of future warming would produce an equivalent greater displacement of latitude which, at the northern current ranges of the two species, could result in a northern range extension (Fig. 7a). In contrast, at the southern edge of the ranges, future warming could not increase growth beyond the genetic capabilities of the species and the dynamics of the species at this part of their ranges would be potentially determined by the responses of competitors to warming. A similar analysis for the moss *H. splendens* shows how a current alpine population would resemble a population from a lowland forested area under climatic warming (Fig. 7b).

At the landscape scale, plants are distributed in mosaics associated with microhabitats and the larger-scale latitudinal range changes will be associated with initial changes in landscape mosaics. Cushion plants and other species characteristic of wind-exposed patches might become restricted in distribution by increased snow cover. In contrast, plants of snow beds might become more restricted if snow duration decreases. Wetland species will become restricted by drying and so on. Plants currently restricted to south-facing slopes and warm springs (to some extent analogs of future warmer habitats and hot spots of biodiversity) north of their main distribution areas, can provide "an inoculum" for rapid colonization of surrounding habitats when climate becomes warmer, although they themselves are likely to be displaced from their current niches by less diverse shrub-thicket communities. Examples include orchids, ferns and herbs in warm springs on West Greenland (although orchids and ferns are unlikely to become widely distributed), ericaceous dwarf shrubs in some inner fjords of Svalbard and the large shrub/small trees of the North Slope of Alaska.

Geographical ranges of animals

Often observed trends of migrant bird population numbers cannot easily be distinguished from local, site-related factors in and outside the Arctic, such as drainage, land-use change, hunting and persecution by humans, as well as predation. Even among global factors, climate change is one in an array of impacts, such as eutrophication, often working in synergy with climate change and reinforcing the effect. In addition, migratory birds are also heavily impacted by climate change outside the Arctic breeding grounds. Desertification, droughts and the loss of wetlands, the eutrophication of staging and wintering wetlands, changes in land use and application of chemicals and nutrients on wintering grounds, lead to changes in vegetation and biomass on coastal staging and wintering grounds. Sea level rise impacts on the extent of coastal staging and wintering grounds will be particularly harmful, and the hunting pressure on wintering waders in certain areas will also reduce bird populations.

The impact of climate change on migratory species has not

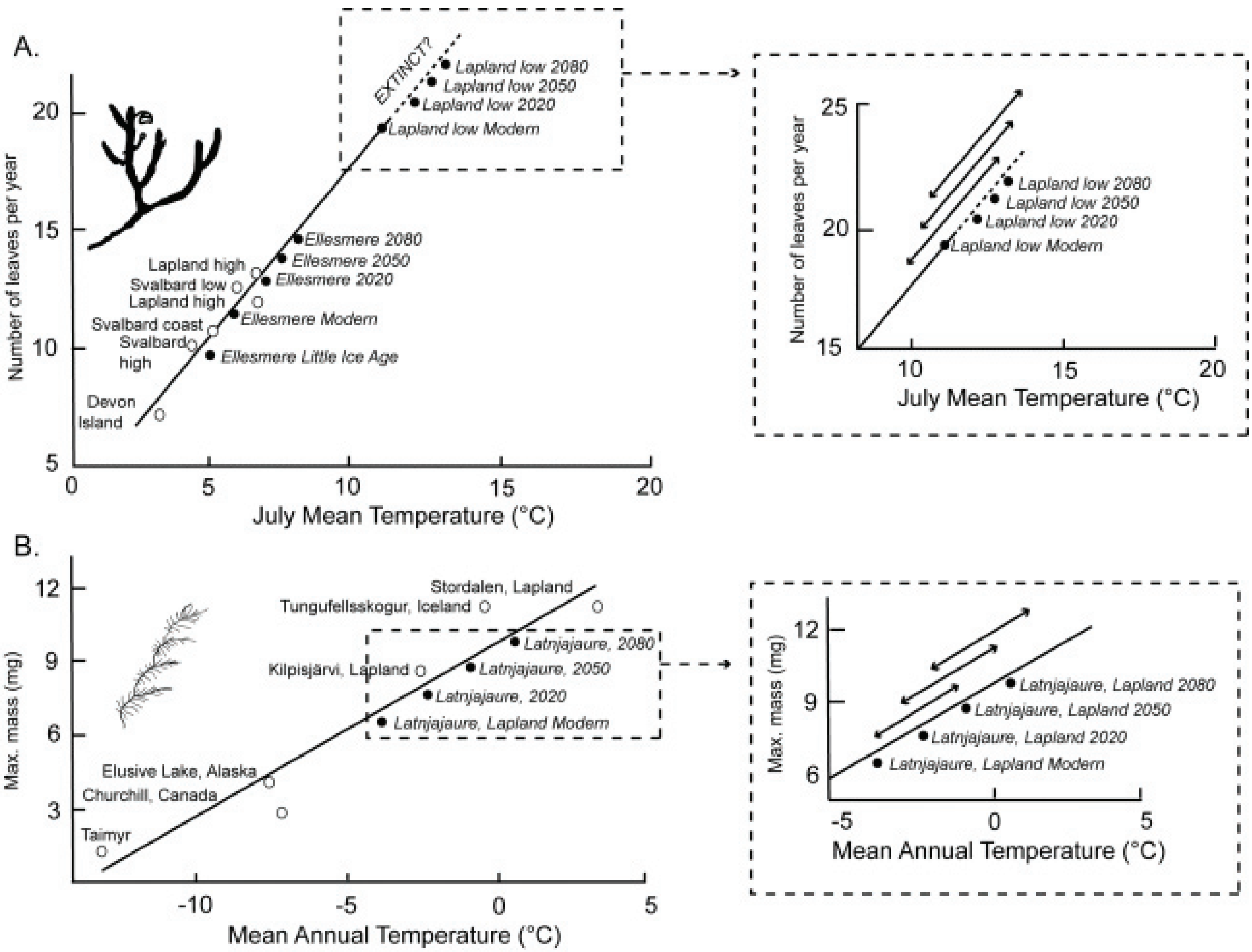

Figure 7 A) The number of leaves produced per year in shoots of *Cassiope tetragona* as a function of the average July temperature. B) Correlation between a growth parameter in *Hylocomium splendens* and mean annual temperature at seven Arctic/sub-Arctic sites. The boxes on the regression lines contain scenarios of growth for ACIA time slices resulting from temperature increases according to the five ACIA scenarios. The dotted line in a) depicts predicted growth probably outside the capability of the species. The expanded boxes to the right depict uncertainty ranges associated with each of the predictions. Filled circles denote populations for which scenarios have been applied. Based on Callaghan et al. (47) and Havström et al. (236).

been studied very much, although the recent trends in some species (e.g. Arctic geese) are well known (237). Very little can be concluded about observed impacts of current climate variability on migratory birds, as existing monitoring programs are few (e.g. 238) and often started only recently.

Analysis of Hadley Centre spring and summer data of temperature and precipitation over the last 50 years, interpolated over the currently known distribution areas of the White-fronted Goose (*Anser albifrons*) and the Taymyr population of the Knot (*Calidris canutus canutus)* in the Arctic, demonstrates a significant correlation between the mean June temperature and the juvenile percentage as a measure of breeding success. The Nearctic population of the Knot (*C. c. islandica*), as well as the Curlew Sandpiper (*Calidris ferruginea*) breeding on the Taymyr Peninsula, do not show such a correlation (224). Under the HadCM2GSa1 model, an increase of 1% CO_2 yr^{-1} results in a moderate increase of the mean June temperature scenario in the Taymyr-breeding area of the White-fronted Goose which is likely to favor the goose population. The conditions for the Taymyr population are particularly favorable for the period around 2020. However, a considerable early cooling and lack of warming over today's values by 2080 of the breeding grounds of the goose population in West Greenland is likely to lead to a drop in size of the fragile Greenland population. Although the ACIA climate scenarios (3) differ from those used in Zöckler and Lysenko (224), possible decreases in temperature in ACIA sub-region I are within the range of scenarios (Table 6 in reference (239)). This study has to be interpreted in relation to other factors, such as other weather parameters, and natural predation which often fluctuates in 3–4 year cycles according to the abundance of the main prey, i.e. the lemming (5). Furthermore, hunting by humans, mainly outside the Arctic, and the effects of climate change, in particular sea-level rise outside the Arctic, need to be taken into account.

Investigations of the breeding wader population in NE Greenland for over 30 years showed that spring snow cover is the main factor governing initiation of egg-laying in High Arctic waders, such as Red Knot and other sandpipers, while temperature appears not to be important in June (240, 241 and Meltofte, pers. comm.). In fact, waders breed earlier in the arid but cool far north of Greenland, than they do in the 'mild' south of the high Arctic zone because snow-cover is much deeper and extensive in the humid south. Predictions for northeast Greenland are cooler summers, later snowmelt, and less snow-free space to feed on for the arriving waders, leading to later breeding and smaller populations. Snow-cover must still be considered the prime regulating factor for initiation of egg-laying, but temperature—so important for determining invertebrate food availability—is involved as well, when sufficient snow-free habitat is already present.

Although global warming in synergy with global eutrophication will probably lead to an increase of biomass, a change in vegetation height and density and a general change in vegetation structure with shifts in species distribution that will have an enormous impact on water-birds that are highly dependant on open landscapes and lightly vegetated breeding sites, it will provide opportunities for other birds with more southerly distribution, such as owls and woodpeckers. Some birds, like most goose species and also a few waders have demonstrated a certain ability to adjust to new and changing habitats (242), but the majority of high Arctic breeding birds appears to be prone to be pushed to the edge with little habitat left.

Geographical ranges of microorganisms

Studies on geographical ranges of microbes related to extreme cold environments such as the Arctic, and also to climate change, are in their infancy. Contrary to plant and animal ecology, soil microbiology still does not have a solution to the central biogeographical problem: are soil microorganisms *cosmopolitan* (widely distributed) or *endemic* (restricted to one location) species? Until we know the ranges of species, we cannot identify which bacteria might be threatened by climate change (243).

The prevailing hypothesis for bacterial biogeography is based on the axiom of the Dutch microbiologists Baas-Becking and Beijerinck, who stated, "Everything is everywhere, but the environment selects" (244). This assumes that free-living bacteria are cosmopolitan in their geographic distribution; they are readily disseminated from one location on Earth to another by water and air currents or animal vectors such as birds that migrate between regions. Only recently has it been possible to rigorously test the cosmopolitan distribution of bacteria with unbiased molecular biological approaches. Studies outside the Arctic demonstrate that the cyanobacteria *Microcoleus chthonoplastes* is a cosmopolitan species (245). Using different molecular biology techniques, Stetter et al. (246) discovered that hyperthermophilic ("heat loving") archaea isolated from Alaskan oil reservoirs showed a high degree of DNA-DNA reassociation with selected *Archaeoglobus*, *Thermococcus*, and *Pyrococcus* species. Stetter et al. (246) concluded that the species were the same as those from European thermal marine sources. In a separate study, DNA-DNA reassociation of a strain isolated from North Sea crude oil fields showed 100% relatedness to an *Archaeoglobus fulgidus* strain from Italian hydrothermal systems (247). These two studies comprise some of the best evidence to date supporting the cosmopolitan hypothesis of Baas-Becking.

However, 3-chlorobenzoate–degrading bacteria isolated from soils in six regions on five continents (248) were found to have restricted/unique ranges. Also, plant species have been reported to harbor their own unique symbiotic species of fungi associated with leaves, bark, roots, etc. (249), so, by definition, the existence of endemic plants should imply the existence of respective microbial symbionts. Therefore, Arctic microbial communities may consist of a mixture of species, some of which are endemic and some of which are cosmopolitan.

CONCLUSIONS

This paper has assessed the current changes recorded for the distribution, abundance and performance of Arctic species, and has analyzed information from various approaches to project future changes of Arctic species related to a range of climate-related factors including UV-B radiation. Although species respond individualistically to environmental variables such as temperature, their responses are moderated by how neighbors, competitors, facilitators, herbivores, food, pests and parasites and future immigrant species respond to the same environmental change. To understand how species within communities and ecosystems respond to climate change, it is necessary to assess climate impacts on interactions between species that together determine ecosystem structure and dynamics (5).

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250. 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. We also thank the participants, reviewers and particularly the leaders of the ACIA process for their various contributions to this study. 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).

Terry V. Callaghan
Abisko Scientific Research Station
Abisko SE 981-07
Sweden
terry.callaghan@ans.kiruna.se

Lars Olof Björn
Department of Cell and Organism Biology
Lund University, Sölvegatan 35
SE-22362, Lund
Sweden
lars_olof.bjorn@cob.lu.se

Yuri Chernov
A.N. Severtsov Institute of Evolutionary Morphology and Animal Ecology
Russian Academy of Sciences
Staromonetny per. 29
Moscow 109017
Russia
lsdc@orc.ru

Terry Chapin
Institute of Arctic Biology
University of Alaska
Fairbanks, AK 99775
USA
terry.chapin@uaf.edu

Torben Christensen
Department of Physical Geography and Ecosystem Analysis
GeoBiosphere Science Centre
Lund University
Sweden
torben.christensen@nateko.lu.se

Brian Huntley
School of Biological and Biomedical Sciences
University of Durham, UK
brian.huntley@durham.ac.uk

Rolf A. Ims
Institute of Biology
University of Tromsö
N-9037 Tromsö, Norway
r.a.ims@bio.uio.no

Margareta Johansson
Abisko Scientific Research Station
Abisko, SE 981-07
Sweden
scantran@ans.kiruna.se

Dyanna Jolly Riedlinger
Centre for Maori and Indigenous Planning and Development
P.O. Box 84, Lincoln University
Canterbury
New Zealand
dyjolly@pop.ihug.co.nz

Sven Jonasson
Physiological Ecology Group
Botanical Institute, University of Copenhagen
Oester Farimagsgade 2D
DK-1353 Copenhagen K, Denmark
svenj@bot.ku.dk

Nadya Matveyeva
Komarov Botanical Institute
Russian Academy of Sciences
Popova Str. 2
St. Petersburg 197376
Russia
nadyam@nm10185.spb.edu

Nicolai Panikov
Stevens Technical University
Castle Point on Hudson
Hoboken, NJ 07030, USA
npanikov@stevens-tech.edu

Walter C. Oechel
Professor of Biology and Director
Global Change Research Group
San Diego State University
San Diego, CA 92182
oechel@sunstroke.sdsu.edu

Gus Shaver
The Ecosystems Center
Marine Biological Laboratory
Woods Hole, MA
02543 USA
gshaver@mbl.edu

Josef Elster
Institute of Botany
Academy of Sciences of the Czech Republic
CZ 379 82 Trebon
Czech Republic
jelster@butbn.cas.cz

Ingibjörg S. Jonsdottir
University of Svalbard
Norway
isj@unis.no

Kari Laine
Thule Institute
P.O.Box 7300
FIN-90014 University of Oulu, Finland
kari.laine@oulu.fi

Kari Taulavuori
Thule Institute
P.O.Box 7300
FIN-90014 University of Oulu, Finland

Erja Taulavuori
Thule Institute
P.O.Box 7300
FIN-90014 University of Oulu, Finland

Christoph Zöckler
UNEP-WCMC
219 Huntington Road
Cambridge CB3 ODL, UK
christoph.zockler@unep-wcmc.org