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Climate Change and UV-B Impacts on Arctic Tundra and Polar Desert Ecosystems

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

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The individual of a species is the basic unit which responds to climate and UV-B changes, and it responds over a wide range of time scales. The diversity of animal, plant and microbial species appears to be low in the Arctic, and decreases from the boreal forests to the polar deserts of the extreme North but primitive species are particularly abundant. This latitudinal decline is associated with an increase in super-dominant species that occupy a wide range of habitats. Climate warming is expected to reduce the abundance and restrict the ranges of such species and to affect species at their northern range boundaries more than in the South: some Arctic animal and plant specialists could face extinction. Species most likely to expand into tundra are boreal species that currently exist as outlier populations in the Arctic. Many plant species have characteristics that allow them to survive short snow-free growing seasons, low solar angles, permafrost and low soil temperatures, low nutrient availability and physical disturbance. Many of these characteristics are likely to limit species' responses to climate warming, but mainly because of poor competitive ability compared with potential immigrant species. Terrestrial Arctic animals possess many adaptations that enable them to persist under a wide range of temperatures in the Arctic. Many escape unfavorable weather and resource shortage by winter dormancy or by migration. The biotic environment of Arctic animal species is relatively simple with few enemies, competitors, diseases, parasites and available food resources. Terrestrial Arctic animals are likely to be most vulnerable to warmer and drier summers, climatic changes that interfere with migration routes and staging areas, altered snow conditions and freeze-thaw cycles in winter, climate-induced disruption of the seasonal timing of reproduction and development, and influx of new competitors, predators, parasites and diseases. Arctic microorganisms are also well adapted to the Arctic's climate: some can metabolize at temperatures down to -39°C . Cyanobacteria and algae have a wide range of adaptive strategies that allow them to avoid, or at least minimize UV injury. Microorganisms can tolerate most environmental conditions and they have short generation times which can facilitate rapid adaptation to new environments. In contrast, Arctic plant and animal species are very likely to change their distributions rather than evolve significantly in response to warming.

INTRODUCTION

The impacts of changing climate and UV-B in the Arctic (1) will be observed at many levels of organization of the biological system, from individual metabolic processes to changes in vegetation zones and exchanges of energy, water and trace gases between the

biosphere and the atmosphere (2, 3). However, it is the individual of a species that is the basic unit of ecosystems which responds to climate and UV-B changes. Individuals respond to environmental changes over a wide range of time scales from biochemical, physiological and behavioral processes occurring in less than a minute to the integrative responses of reproduction and death (Fig. 1 in ref. 2). Reproduction and death drive the dynamics of populations while mutation and environmental selection of particular traits in individuals within the population lead to changes in the genetic composition of the population and adaptation.

Current Arctic species have characteristics that have enabled them to pass various environmental filters associated with the Arctic's environment (4, 5), whereas species of more southern latitudes either cannot pass these filters or have not yet arrived in the Arctic. Changes in Arctic landscape processes and ecosystems in a future climatic and UV-B regime will depend upon the ability of Arctic species to withstand or adapt to new environments and upon their interactions with immigrant species that can pass through less severe environmental filters. This paper is part of an holistic approach to assess impacts of climate change on Arctic terrestrial ecosystems (1, 2). Here, we focus on the attributes of current Arctic species that are likely to constrain or facilitate their responses to a changing climate and UV-B regime.

IMPLICATIONS OF CURRENT SPECIES DISTRIBUTIONS FOR FUTURE BIOTIC CHANGE

Plants

Species diversity

About 3% (about 5900) species of the global flora occurs in the Arctic as defined in this paper and others in this Ambio Special Issue (0.7% of the angiosperms (flowering plants), 1.6% of the gymnosperms (cone-bearing plants), 4% of the bryophytes and 11% of the lichens) (Table 1). There are more species of primitive taxa (cryptogams) i.e. mosses, liverworts, lichens and algae in the Arctic than of vascular plants (6). Less than half of the Arctic plant species are vascular plants (about 1800 species). There are about 1500 species common to both Eurasia (6, 7) and North America (8). A similar number of nonvascular plants probably occurs in the Arctic on both continents, although their diversity has been less thoroughly documented. In the Russian Arctic, for example, 735 bryophyte species (530 mosses and 205 liverworts) and 1078 lichen species have been recorded (9–11). In general, the North American and Eurasian Arctic are similar to one another in their numbers of vascular and nonvascular

plant species, of which a large proportion (about 80%) of vascular plants occurs on at least two continents. An even larger proportion (90%) of bryophytes occurs in both the North American and Eurasian Arctic.

About 40% of vascular plants (and a much higher percentage of mosses and lichens) are basically boreal species that now barely penetrate the Arctic (Table 2). They currently occur close to the treeline or along large rivers that connect the sub-Arctic with the Arctic. These boreal species within the Arctic will probably be the primary boreal colonizers of the Arctic in the event of continued warming. Polyzoal (distributed in several zones), arctoboreal (in taiga and tundra zones) and hypoarctic (in the northern taiga and southern part of the tundra zone) species have even greater potential to widen their distribution and increase their abundance in a changing climate. The majority of cryptogams have wide distributions all over the Holarctic. Such species may survive a changing climate, although their abundance may be reduced (12).

In contrast to the low diversity of the Arctic flora at the continental and regional scales, individual communities (100 m² plots) within the Arctic have a diversity similar to or higher than those of boreal and temperate zones. These diversities are highest in continental parts of the Arctic such as the Taymyr Peninsula of Russia, where there are about 150 species of plants (vascular plants, lichens and mosses) 100 m² plot, 40–50 species m² plot and up to 25 species dm⁻² (13).

Latitudinal gradients of species diversity

Latitudinal gradients suggest that Arctic plant diversity is sensitive to climate. The number of vascular plant species declines 5-fold from South to North in the Taymyr Peninsula in Russia (14). Summer temperature is the environmental variable that best predicts plant diversity in the Arctic (15). Other factors are also important, however; as regions of different latitudes that have a similar maximum monthly temperature often differ in diversity. Taymyr biodiversity values are intermediate between the higher values for Chukotka and Alaska, which have a more complicated relief, geology, and floristic history, and the lower values in the eastern Canadian Arctic with its impoverished flora resulting from relatively recent glaciation. All diversity values on the Yamal Peninsula are even lower than in Canada because of a wide distribution of sandy soils and perhaps its young age. Similar patterns are observed for butterflies (Fig. 1) and spiders (16, 17). Therefore, latitudinal gradients of species diversity are best described as several parallel gradients, each of which depends on summer heat, but which may differ from one geographic region to another. This fact has to be taken into consideration when predicting future changes in biodiversity.

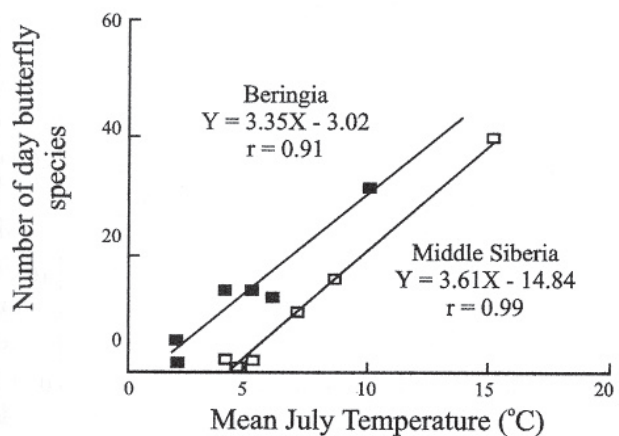
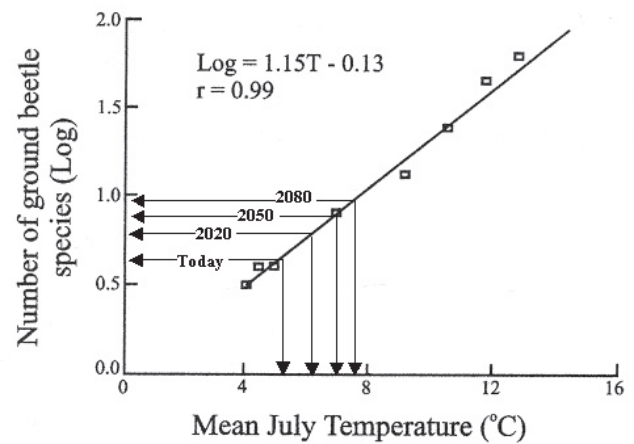
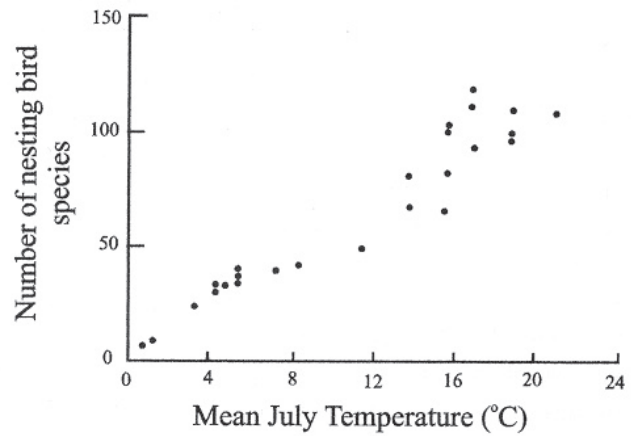


Table 1. Biodiversity estimates in terms of species richness (number of species) for the Arctic beyond the latitudinal treeline compared with world biota (6, 14).

Animals			Taxon			Fungi		
Group	Number of species	% of world biota	Group	Number of species	% of world biota	Group	Number of species	% of world biota
Mammals	75	1.7	Angiosperms	1735	0.7	Fungi	2500	2.3
Birds	240	2.9	Monocotyledons	399	0.6			
Insects	3300	0.4	Dicotyledons	1336	0.7			
Diptera	1600	0.9	Gymnosperms	12	1.6			
Beetles	450	0.1	Pteridophytes	62	0.6			
Butterflies	400	0.3	Mosses	600	4.1			
Hymenoptera	450	0.2	Liverworts	250	2.5			
Others	400	—	Lichens	2000	11.0			
Springtails	400	6.0	Algae	1200	3.3			
Spiders	300	1.7						
Mites	700	1.9						
Other Groups*	600	—						
Total Estimate	6000	—		5859	3			

*Amphibians & reptiles (7 species), Centipedes (10 species), terrestrial Molluscs (3 species), Oligochaetes (earth worms and enchytraeids) (70 species), and Nematodes (~500 species).

Figure 1. Top: The relationship between the number of nesting bird species and July mean temperature in western and middle Siberia. **Middle:** Correlation between July mean temperature and number of ground beetle species in local faunas of the Taymyr Peninsula. **Bottom:** Correlation between July mean temperature and number of day butterflies in the middle Siberian and Beringian sectors of the Arctic (modified from Matveyeva and Chernov (6), Chernov (16) and Chernov (17)). The middle figure illustrates how current bioclimatic distributions are related to climate change scenarios by plotting the likely changes in the number of ground beetles for three time slices of mean July temperature derived from the mean of the five ACIA scenarios.

At the level of the local flora (the number of species present in a landscape of about 10 x 10 km), there is either a linear or an "S"-shaped relationship between summer temperature and species number (Fig. 2). Species number is least sensitive to temperature near the southern margin of the tundra and most sensitive to temperatures between 3–8°C. This suggests that the main changes in species composition will occur in the northern part of the tundra zone and in the polar desert, where species are now most restricted in their distribution by summer warmth and length of growing season. July temperature, for example, accounts for 95% of the variance in number of vascular plant species in the Canadian Arctic (18) (although extreme winter temperatures are also important (12). In general, summer warmth, length of the growing season and winter temperatures all affect the growth, reproduction and survival of Arctic plants. The relative importance of each of these varies from species to species, site to site and year to year.

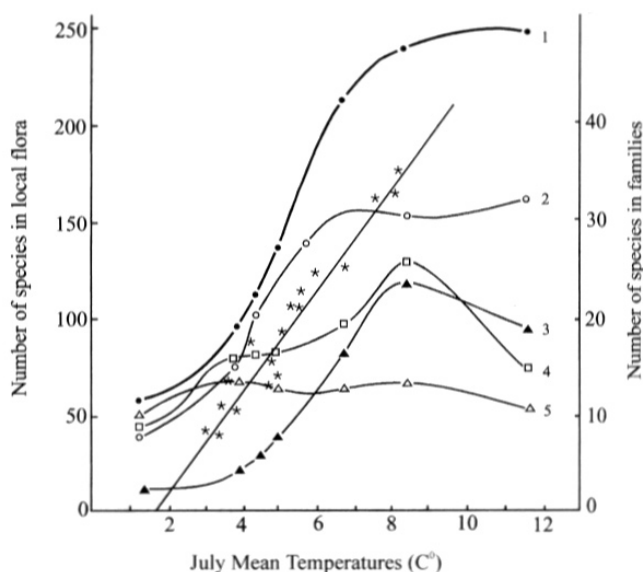


Figure 2. The relationship between July mean temperature and the number of vascular plant species in local floras of the Taymyr Peninsula and the Canadian Arctic Archipelago. 1. The whole flora 2. Poaceae 3. Cyperaceae 4. Brassicaceae 5. Saxifragaceae (modified from Matveyeva and Chernov (6), Rannie (18)).

The steep temperature gradient that has such a strong influence on species diversity occurs over much shorter distances in the Arctic than in other biomes. North of the treeline in Siberia, mean July temperature decreases from 12°C to 2°C over 900 km, whereas a 10°C decline in July temperature is spread over 2000 km in the boreal zone, and decreases by less than 10°C from the southern boreal zone to the equator (16). The temperature decrease of 10°C can be compared with the expected mean 2.5°C (range of the two extremes of the five ACIA climate scenarios – 1.1 to 4.2°C (1) increase in mean July temperature by 2080. Much of the region is very likely therefore to remain still within the Arctic summer climate envelope (although the increase in winter temperature is expected to be higher).

Because of the steep temperature gradients with latitude in the Arctic, the distance that plants must migrate in response to a change in temperature is much less in the Arctic than in other biomes, particularly where topographic variations in microclimate enable plants to grow far beyond their climatic optima. The low sun angle and presence of permafrost make topographic variations in microclimate and associated plant community composition particularly pronounced in the Arctic. Thus, both the sensitivity of Arctic species diversity to temperature and the short distance over which this temperature gradient occurs suggest that Arctic diversity will very probably respond strongly

and rapidly to high-latitude temperature change.

Latitudinal patterns of diversity differ strikingly among different groups of plants (Table 2). Many polyzonal, boreal and Hypoarctic species have ranges that extend into the Arctic. Some of these, e.g. the moss *Hylocomium splendens* and the sedges *Eriophorum angustifolium* and *E. vaginatum* are important dominants within the Arctic. Tussocks of *E. vaginatum* structure the microtopography of broad areas of tussock tundra (19), and *Hylocomium splendens* exerts a control over nutrient cycling (20). Tall willow (*Salix* spp.) and alder (*Alnus fruticosa*) shrubs as well as dwarf birch *Betula exilis*, *B. nana* form dense thickets in the southern part of the tundra zone and often have outlier populations that extend far to the north in favorable habitats (6). Those species that are important community dominants are likely to have a particularly rapid and strong effect on ecosystem processes where regional warming occurs. Hemi-arctic species are those that occur throughout the entire range of the Arctic. Many of these species are common community dominants, including *Carex bigelowii/arctisibirica*, *C. stans*, *Dryas octopetala/punctata*, *Cassiope tetragona*, and the moss *Tomentypnum nitens*. Due to their widespread current distribution, their initial responses to climatic warming are likely to be increased productivity and abundance followed by probable later movement further to the north. The most vulnerable are likely to be Euarctic (e.g. *Salix polaris*) and Hyperarctic species that now have the largest abundance and widest ecological amplitude in the northernmost part of the tundra zone (the former) or in polar deserts (the latter). These groups of species are best adapted to the climate conditions of the high Arctic where they are distributed in a wide range of habitats where more competitive species of a general southerly distribution are absent. In the more southerly regions of the tundra zone, they are able to grow only (or mainly) in snowbeds. It is probable that their ecological amplitude will narrow and abundance decrease during climate warming.

Thus, responses to climate changes will be different in various groups of plants. Some currently rare boreal species can move further north and the more common species increase in their relative abundance and in the range of habitats that they occupy. When southern species with current narrow niches penetrate into the poorer ecosystems at high latitudes, therefore, there can be a broadening of their ecological niches there. In contrast, some true Arctic species (endemics) that are widely spread in the high latitudes will probably become more restricted in their local distribution within and among ecosystems. They could possibly even disappear in the lower latitudes where the tundra territories are particularly narrow. Only few high Arctic plants of Greenland are expected to become extinct, for example *Ranunculus sabinei* that is limited to a narrow outer coastal zone of North Greenland (21). However, temperature is not the only factor that currently prevents some species from being distributed in the North. Even in future warmer summer periods, the long period of daylight will support the existence of Arctic species but initially restrict the distribution of some boreal ones (12). The actual latitudinal position is important, and life cycles depend not only on temperature but on the light regime as well. New communities with a peculiar species composition and structure are therefore, very likely to arise and these will not be the same as those existing now.

Animals

Species diversity

The diversity of Arctic terrestrial animals beyond the latitudinal treeline (6000 species) is nearly twice as great as that of vascular plants and bryophytes (14, 16; Table 1). As with plants, the Arctic fauna accounts for about 2% of the global total, and, in general, primitive groups (e.g. springtails, 6% of the global to-

Table 2. Current diversity changes with latitude in the Arctic region, compiled and modified from information in Matveyeva and Chernov (6) excluding limnic and marine animals. Note: general information on how species within the various categories are likely to respond to climate and UV change is presented in the text, but insufficient information is available for most of the species in the Table.

Category	Optimum of distribution	Examples Plants	Birds	Mammals and invertebrates
Polyzonal	Different zones in the Holarctic and far to the North in tundra but usually in local habitats and wet depressions	Soil algae; the mosses <i>Hylacomium splendens sensu lato</i> , <i>Aulacomnium turgidum</i> , and <i>Racomitrium lanuginosum</i> ; the liverwort <i>Ptilidium ciliare</i> ; the lichens <i>Cetraria islandica</i> , <i>Psora decipiens</i> , and <i>Cladina rangiferina</i> ; the vascular species <i>Cardamine pratensis</i> , <i>Chrysosplenium alternifolium</i> , and <i>Eriophorum angustifolium</i> ; the sedge <i>Carex duriuscula</i> ; the herb <i>Helictotrichon krylovii</i> ; the moss <i>Tortula ruralis</i> (the last three are "steppe" species)	The common raven <i>Corvus corax</i> , the peregrine falcon <i>Falco peregrinus</i> , the white wagtail <i>Motacilla alba</i> , and the northern wheatear <i>Oenanthe oenanthe</i>	The wolf <i>Canis lupus</i> the ermine <i>Mustella erminea</i> , the weasel <i>M. nivalis</i> , the voles <i>Microtus gregalis</i> and <i>M. oeconomus</i> , and the mite <i>Chiloxanthus pilosus</i> (the last species is bizonal: steppe and tundra).
Zonal boreal	Not abundant and constrained to the South of the Arctic in benign habitats such as river valleys, South-facing slopes, and wet areas	Tree species of <i>Larix</i> ; the orchid <i>Corallorhiza</i> ; the shrub <i>Salix myrtilloides</i> ; the sedge <i>Carex chordorrhiza</i> ; the herbs <i>Allium schoenoprasum</i> , <i>Cortusa matthioli</i> , <i>Galium densiflorum</i> , <i>Sanguisorba officianalis</i> ; and forest mosses <i>Climacium dendroides</i> , <i>Pleurozium shreberi</i> , and <i>Rhytidiadelphus triquetrus</i>	The forest birds <i>Turdus iliacus</i> and <i>T. pilaris</i> (thrushes) leaf warbler Arctic warbler <i>Pyloscopus borealis</i> and Yellow-browed wabler <i>P. inornatus</i> ; and "river" ducks <i>Anas acuta</i> , <i>A. penelope</i> , and <i>A. crecca</i>	Reindeer (<i>Rangifer tarandus</i>) and the wolverine, <i>Gulo gulo</i> , Brown bear <i>Ursus arcticus</i>
Zonal Arctic				
Hypoarctic	Optima in the southern tundra subzone	This group characterizes the southern tundra subzone; the shrubs <i>Betula nana/exilis</i> and sedge <i>Eriophorum vaginatum</i>	The ptarmigan <i>Lagopus lagopus</i> , the spotted redshank <i>Tringa erythropus</i> , the little bunting <i>Emberiza pusilla</i> , and the bar-tailed godwit <i>Limosa lapponica</i>	The vole <i>Microtus midden-dorffi</i> , the ground beetle <i>Carabus truncatocollis</i> , the bumblebee <i>Bombus cingulatus</i> , and the spider <i>Alopecosa hirtipes</i>
Hemiarctic	Throughout the tundra zone but most frequent in the middle	Most of the dominant species: the grasses <i>Arctophila fulva</i> , <i>Dupontia fisheri</i> ; the sedges <i>Carex bigelowii/arctisibirica</i> and <i>Carex stans</i> ; the shrub willow <i>Salix reptans</i> , the dwarf shrubs <i>Dryas punctata/octopetala</i> and <i>Cassiope tetragona</i> ; the mosses <i>Tomenthypnum nitens</i> , <i>Drepanocladus intermedius</i> , and <i>Cinclidium arcticum</i> ; the herbs <i>Lagotis minor</i> and <i>Pedicularis hirsuta</i> , the moss <i>Polytrichum juniperinum</i>	The Lapland longspur <i>Calcarius lapponicus</i> , the lesser golden plover <i>Pluvialis dominica</i> , Pacific Golden plover <i>P. fulva</i> and the dunlins <i>Calidris alpina</i> and <i>C. minuta</i>	The lemming <i>Lemmus sibiricus</i> , the bumblebee <i>Bombus balteatus</i> , the ground beetles <i>Curtonotus alpinus</i> , <i>Pterostichus costatus</i> , and flower-fly <i>Syrphus tarsatus</i>
Euarctic	Northern part of the tundra zone, rare in the southern part	The dwarf shrubs <i>Salix polaris</i> and <i>S. arctica</i> (this group is relatively small, but it has an important value in the subdivision of the tundra zone into subzones)	The black-bellied plover <i>Pluvialis squatarola</i> , the curlew sandpiper <i>Calidris ferruginea</i> , the snowy owl <i>Nyctea scandiaca</i> , and the snow-bunting <i>Plectrophenax nivalis</i> and several more	The lemming <i>Dicrostonyx torquatus</i> , the bumblebees <i>Bombus hyperboreus</i> and <i>B. polaris</i> and the crane fly <i>Tipula carinifrons</i>
Hyperarctic	Polar desert and in the northernmost part of the tundra zone	Almost no plants are restricted to these zones: the following have their highest frequencies there. The grasses <i>Phippsia algida</i> and <i>Poa abbreviata</i> ; the herbs <i>Cerastium regelii</i> , <i>Draba oblongata</i> , <i>D. subcapitata</i> , <i>Saxifraga hyperborea</i> , and <i>S. oppositifolia</i> ; the mosses <i>Dicranoweisia crispula</i> , <i>Bryum cyclophyllum</i> , <i>Orthothecium chryseon</i> and <i>Seligeria polaris</i> ; and the lichens <i>Cetrariella delisei</i> , <i>Arctocetraria nigricascens</i> , <i>Dactylina ramulosa</i> , <i>D. madreporiformis</i> , and <i>Thamnotia subuliformis</i>	The wader species <i>Calidris alba</i> and <i>C. canutus</i>	No terrestrial mammal species are restricted to this zone. The collembolan <i>Vertagopus brevicaudus</i>

tal) are better represented in the Arctic than are advanced groups such as beetles (0.1%) (6, 16). There are about 315 species of vertebrates, of which about 75 species are mammals, 240 birds, 2 reptiles, and 5 amphibians. Insects are the most diverse group of Arctic animals (about 3300 species), of which about 50% are diptera, and 10% each of beetles (Coleoptera), butterflies (Lepidoptera), and hymenoptera. The Arctic has about 300 species of spiders (Arachnida), 700 species of mites (Acarina), 400 species of springtails (Collembola), 500 species of nematodes, 70 species of Oligochaetes (of which most are Enchytraeidae), only a few molluscs, and an unknown number of protozoan species.

In the Arctic region as defined by CAFF, which includes forested areas, some 450 species of birds have been recorded breeding. Some of them extend breeding from the south only marginally into the Arctic region. Others are not migratory and stay in the Arctic region all year around. About 280 species have their main breeding distribution in the Arctic and migrate regularly (22). An estimation of the total number of individuals involved is not possible. Too little is known about the population size of most species or their Arctic proportion. But a rough first approximation accounts for at least several hundred million birds. Water

birds are better known and the Arctic is of particular importance for most water birds, such as divers, geese and waders. Twelve goose species are breeding in the Arctic, 11 almost entirely and 8 exclusively. These comprise about 8.3 million birds. The total number of Arctic breeding sandpipers (24 species) exceeds 17.5 million birds (23). The total number of water birds, including other wader species, divers, swans, ducks and gulls is estimated to be between 85 and 100 million birds.

Latitudinal gradients of species diversity

Latitudinal patterns of diversity in Arctic animals are similar to those described for Arctic plants. Species diversity declines in parallel with decreasing temperature in most animals groups (Fig. 1), including birds, ground beetles, butterflies, etc. (16). However, in some groups, for example, peat-land birds and sawflies in local sites of the European North, concentration per unit area both in species diversity and density can increase compared with more southern territories, perhaps because the habitat types appropriate to these groups are more diverse in the tundra than in the boreal forest. In general, the decline in animal species is more pronounced (frequently greater than 2.5-fold) than in

vascular plants. As with plants, there are more species in Beringia at a given temperature, with its complicated relief, geology, and biogeographic history than in the Taymyr Peninsula. Many animal species are restricted to the boreal zone because they depend on the crown, wood, roots, or litter of trees, which are absent in the tundra zone. These groups include wood-boring insects and wood-decaying fungi and their predators (24), as well as mammals and birds that specialize on tree-seeds and leaves. Other important animals, including the raven, wolf, red fox and ermine, are primarily boreal in distribution but remain an important component of many Arctic ecosystems. There are a few terrestrial animals restricted to the high Arctic such as the sand-erling, i.e. the wader *Calidris alba*, and a common Collembolan, *Vertagopus brevicaudis*. Other Arctic species have their centers of distribution in the northern, mid- or southern Arctic (Table 2). The more diverse patterns of animal than of plant distribution make it more difficult to project how animals will respond to climatic warming. Some herbivores have distributions that are more limited than those of their host plants (25), so warming may possibly allow these species to extend northward relatively rapidly.

As in the case of plants, latitudinal patterns of diversity differ strikingly among different groups of animals (Table 2). The common species tend to be more broadly distributed in the far north. In northern Taymyr there are only 12 species of springtails, but 80% of these occur in all microsites and topographic locations investigated (24). Some boreal birds, such as the American thrush *Turdus migratorius*, penetrate only into the southern part of tundra while others can occur far from their climatic optimum (climatic region associated with the center of distribution): in the vicinity of Dickson (Taymyr), forest thrushes *T. pilaris* and *T. iliacus* form populations in the northernmost part of the tundra zone that is 400 km distant from the last outposts of the forests. At the southern limits of the tundra, there is greater specialization among microhabitats. Many more species occur in intrazonal habitats, occupying relatively small and isolated sites, than in zonal habitats that contain only a small proportion of the regional fauna. Warming is therefore likely to lead to more pronounced habitat and niche specialization.

An important consequence of the decline in numbers of species with increasing latitude is an increase in dominance. For example, one species of collembolan, *Folsomia regularis*, may constitute 60% of the total collembolan density in polar desert (26). These "super-dominant" species are generally highly plastic, occupy a wide range of habitats, and generally have large effects on ecosystem processes. Lemmings (various *Lemmus* spp. and *Dicrostonyx* spp) are super-dominant species during peak years of their population cycles (27) and have large effects on ecosystem processes (27–29).

Microorganisms

Species diversity

Microbial organisms are critically important for the functioning of ecosystems, but are difficult to study and are poorly known compared with other species. However, the International Biological Program (IBP 1960–1970), significantly advanced our understanding of Arctic microorganisms, compared with those of other biomes, when an inventory of microbial communities was undertaken in the tundra (30). Currently, at the start of 21st century, the knowledge on microbial diversity in tundra remains the same or a little better than 30–40 years ago, and recent outstanding progress in molecular microbial ecology has rarely been applied to Arctic terrestrial studies.

Presently, there are 5000–6000 named bacterial species globally and about the same number of fungi (31) as compared with more than 1 million named plant and animal species (32, 33). Some scientists have interpreted this difference to mean that the bacteria are not particularly diverse (32). However, there are several reasons, listed in Callaghan et al. (34), to believe that the apparent limited diversity of microbes is an artifact.

Recent progress in molecular biology and genetics has revolutionized bacterial classification and our understanding of microbial phylogeny (family trees) and biodiversity in general. The DNA sequencing technique has reorganized bacterial classification and brought order to microbial taxonomy (35). Moreover, the microbial inventory can now be done without isolation and cultivation of the dominant microorganisms, because it is enough to extract from the soil the total community DNA, amplify, clone and sequence the individual genes. The described culture-independent approach has been applied occasionally for analysis of microbial communities in sub-Arctic and Arctic soils, most often to study relatively simple communities of hot springs, subsoils and contaminated aquifers. Analysis of Siberian subsurface permafrost samples (36, 37) resulted in the formation of a clone library of 150 clones which has been separated into three main groups of Eubacteria. From 150 clones so far analyzed, and several known species (*Arthrobacter*, *Clostridium*, and *Pseudomonas*) have been identified, while the most abundant phylotypes were represented by completely unknown species closely affiliated with Fe (iron)-oxidizing bacteria.

Another area of intensive application of molecular tools was northern wetlands (cold, oligotrophic (nutrient poor) and usually acidic type of habitats) as related to the methane cycle (38, 39). The most challenging and formidable tasks were to find out what particular microbial organisms are responsible for the generation and uptake of methane (so called methanogens and methanotrophs) in northern ecosystems and what can be their reaction to warming of the Arctic's soils. It was found that most of the boreal and sub-Arctic wetlands contain a wide diversity of methanogens (40, 41) and methanotrophs (42, 43), most of them being distantly related to known species. Only recently, some of these obscure microbes were obtained in pure culture or stable consortia (44, 45). The novel microbes of methane cycles are extreme oligotrophic species that evolved to function in media with very low concentrations of mineral nutrients. Taxonomically, the novel oligotrophic methanogens form new species, genera and even families within the *Archaea* domain (45). The acidophilic methanotrophs form two new groups: *Methylocapsa* and *Methylocella* (44, 46), the last one affiliating with heterotrophic *Beijerinckia indica*.

DNA-based techniques allow us to answer the question; What is the upper limit for variation of microbial diversity in the Arctic as compared with other natural ecosystems? How many species (both cultured and unculturable) do soils contain? This technique is called DNA reassociation (how quickly the hybrid double helix is formed from denatured single-stranded DNA).

Arctic desert and tundra contain considerable microbial diversity comparable with boreal forest soil and much higher than arable soils. Although extreme environmental conditions restrain the metabolic activity of Arctic microbes, they preserve huge potential that is ready to display the same activity as boreal

Table 3. The microbial genome size in Arctic habitats as compared with other habitats (after Torsvik et al. (47))

DNA source	Number of cells per cm ³	Community genome complexity (bp)*	Genome equivalents**
Arctic desert (Svalbard)	7.5 10 ⁹	0.5-1.0 10 ¹⁰	1200-2500
Tundra soil (Norway)	3.7 10 ¹⁰	0.5 10 ¹⁰	1200
Boreal forest soil	4.8 10 ⁹	2.5 10 ¹⁰	6000
Forest soil, cultivated prokaryotes	1.4 10 ⁷	1.4 10 ⁸	35
Pasture soil	1.8 10 ¹⁰	1.5 -3.5 10 ¹⁰	3500-8800
Arable soil	2.1 10 ¹⁰	5.7-14 10 ⁸	140-350
Salt-crystallizing pond, 22% salinity	6.0 10 ⁷	2.9 10 ⁷	7

*bp = base pair, which is the number of nucleotides in each strand in the DNA molecule.

** the number of genome equivalents is a measure of diversity specified at a molecular level.

analogs immediately after climate warming.

There is a much higher degree of genomic diversity in prokaryotic communities (prokaryotes such as cyanobacteria have a simple arrangement of their genetic material whereas eukaryotes such as microalgae have genetic material arranged in a more advanced way in that the DNA is linear and forms a number of distinct chromosomes) of heterogeneous habitats (virgin soils, pristine sediments) as compared with more homogeneous samples: the DNA diversity seen in 30–100 cc of heterogeneous samples corresponds to about 10^4 different genomes, while in pond water and arable soils the number of genomes decreases to 10^0 – 10^2 . Based on extrapolation and taking into account that listings of species can significantly overlap for microbial communities of different soils, a rough estimate is that there could be from 10^4 to 10^9 prokaryotic species globally (47, 48).

The conventional inventory approach based on cultivation suggests that, in the Arctic, at the present time, we are able to identify in any particular soil no more than 100 prokaryotic species from the potential of 1000–3000 'genome equivalents' (Table 3) and no more than 2000 species of eukaryotes. Of the named fungi species (not including yeast and soil fungi) 1750 are known for the Russian Arctic (in the broad sense) (49). About 350 of these are macromycetes. However, their number in the Arctic proper is 20–30% less, but these data are far from complete. The Arctic has fewer species of bacteria, fungi, and algae than other major biomes; actinomycetes are rare or absent in most tundra sites (50). While most major phyla of microfloras are represented in tundra ecosystems, many species and genera that are common elsewhere, even in sub-Arctic ecosystems, are rare or absent in tundra. Gram-positive bacteria including gram-positive spore forms are absent or rare in most tundra sites. *Arthrobacter* and *Bacillus* can rarely be isolated and then only from drier areas. *Azotobacter*, the free-living nitrogen fixing bacterium, is extremely rare in tundra, and the moderate rate of N_2 fixation observed *in situ* is mainly due to the activity of cyanobacteria. Sulfur-oxidizing bacteria are also reported to be rare or absent. Even using enrichment techniques, Bunnell et al. (50) rarely found chemoautotrophic sulfur oxidizing bacteria. Photosynthetic sulfur bacteria have not been found in any IBP Tundra Biome Site and have been reported from only one sub-Arctic site (50, 51), although they are common in coastal areas of the west and south coasts of Hudson Bay. Sulfur-reducing bacteria, while not abundant in tundra sites, have been reported from Arctic and Antarctic sites. Iron-oxidizing bacteria are very rare in tundra sites. Despite ample iron substrate in tundra ponds and soils, chemoautotrophic ferrous iron oxidizers were not found in IBP tundra sites (51). In contrast, methanotrophic and methanogenic bacteria appear to be widely spread in tundra areas.

As with bacteria, many generally common fungi are conspicuous by their rare occurrence or absence in tundra areas. *Aspergillus*, *Alternaria*, *Botrytis*, *Fusarium* and *Rhizopus*, simply do not occur and even *Penicillia* are rare (52). Yeasts can be isolated readily but there is very low species diversity in culture media. Only three different species were reported for Pt. Barrow tundra (50). Aquatic fungi show high diversity, especially *Chytridiales* and *Saprolegniales*. However, they may not be endemic and reflect the annual migration into the Arctic of many avian species especially waterfowl. The so-called higher fungi, *Basidiomycetes* and *Ascomycetes*, also have low diversity. They are reduced to 17 families, 30 genera and about 100 species. In comparison, sub-Arctic and temperate regions would contain at least 50 families, not less than 300 genera and anywhere up to 1200 species (53). Mycorrhizal symbionts on tundra plants are common. Arbuscular, ecto-, ericoid, arbutoid and orchid mycorrhizal fungi are associated with plants in Arctic ecosystems (54). The ectomycorrhizal symbionts are important as they form mycorrhizal associations with *Betula*, *Larix*, *Pinus*, *Salix*, *Dryas*, *Cassiope*, *Polygonum* and *Kobresia*. Based on fungal fruitbodies, Borgen et al. (55) estimate 238 ectomycorrhizal fungal species in Greenland, which may increase to around 250 out of a total of 855

when some large fungal genera as *Cortinarius* and *Inocybe* have been revised. With the exception of *Eriophorum* spp. Flanagan (unpubl.) found endotrophic *Arbuscula*-like mycorrhizae on all ten graminoid plants examined. The number of fungal species involved in other mycorrhizal symbioses is not clear.

Tundra algae exhibit the same degree of reduction in species diversity seen amongst the fungi and bacteria (50, 56, 57), which document a diversity much reduced from that of the microflora of temperate regions. Cyanobacteria and microalgae are among the oldest, in evolutionary terms, and simplest forms of life on the planet that can photosynthesize. Mainly unicellular and filamentous photosynthetic cyanobacteria and microalgae are among the main primary colonizers adapted to conditions of the Arctic terrestrial environment. They are widespread in all terrestrial and shallow wetland habitats and frequently produce visible biomass. Terrestrial photosynthetic microorganisms colonize mainly the surface and subsurface of the soil and create the crust (58). Shallow flowing or static wetland algal communities produce mats or mucilaginous clusters that float in the water but are attached to rocks underneath (59). Terrestrial and wetland habitats represent a unique mosaic of cyanobacteria and algae communities that occur up to the highest and lowest possible latitudes and altitudes as long as liquid or vapor water is available for some time in the year (57). The Arctic soil and wetland microflora is composed mainly of species from Cyanobacteria, Chrysophyceae, Xanthophyceae, Bacillariophyceae, Chlorophyceae, Charophyceae, Ulvophyceae and Zygnemaphyceae. Species diversity reports from various sites range widely, between 53 to 150–160 species (57).

Latitudinal gradients of microbial species diversity

Arctic soils contain large reserves (standing crops) of microbial (mainly fungal) biomass, although the rate of microbial growth is generally lower than in the boreal zone. Surprisingly, under severe Arctic conditions, soil microbes fail to produce spores and other dormant structures (Fig. 3). The species diversity of all groups of soil microorganisms is lower in the Arctic than further south, decreasing from about 90 in grassland in Ireland, through

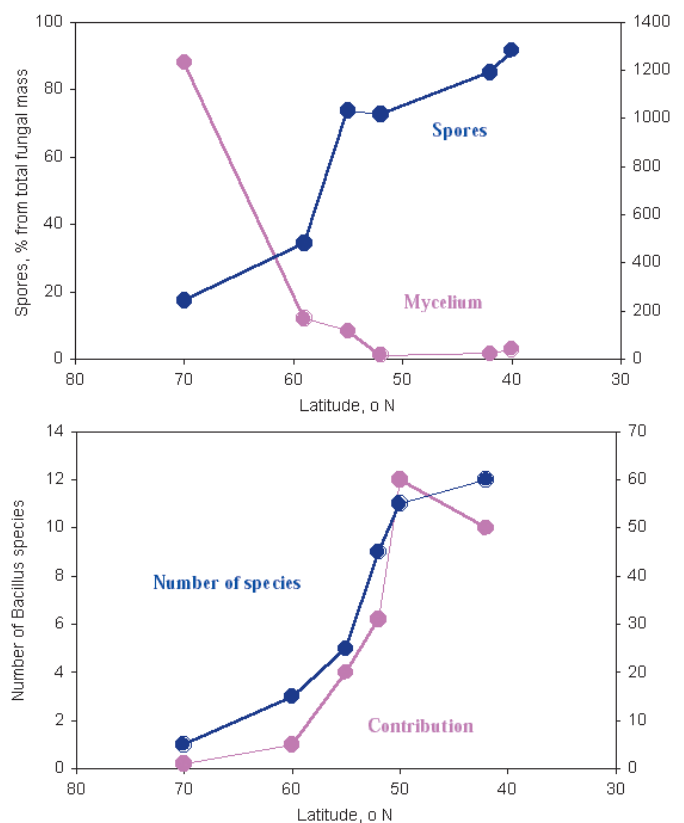


Figure 3. Latitudinal distribution of soil fungi (top) and bacilla (bottom). Recalculated from data in Mirchink (61).

about 50 in Alaskan birch forest to about 30 in Alaskan tundra (52). As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, although these patterns are less well documented. A correlate of the decreasing number of species with increasing latitude is increasing dominance of the species that occur, as with plants and animals. One yeast, *Cryptococcus laurentii*, for example, constitutes a large proportion of yeast biomass across a range of community types in the northern Taymyr Peninsula (60).

The hyphal length of fungi in the Arctic shows a latitudinal trend in which the abundance of fungi, as measured by hyphal length, decreases towards the north. Although it is not known if this trend also applies to the species diversity of fungal mycelia (the below ground network of fungal filaments or hyphae), it is clear that the amount of fungal hyphae is low in the Arctic (62). In the high Arctic, fungal hyphal length was $23 \pm 1 \text{ mg}^{-1}$ in a polar semidesert on Svalbard ($78^\circ 56' \text{N}$), 39 mg^{-1} on a beach ridge, and 2228 in a mesic meadow on Devon Island ($75^\circ 33' \text{N}$). At Barrow, Alaska hyphal length was 200 mg^{-1} . In a sub-Arctic mire in Swedish Lapland, hyphal length was 3033 mg^{-1} . These values can be compared with 6050–9000 for temperate uplands in the UK and 1900–4432 mg^{-1} for temperate woodland soils.

GENERAL CHARACTERISTICS OF ARCTIC SPECIES AND THEIR ADAPTATIONS IN THE CONTEXT OF CHANGES IN CLIMATE AND UV-B RADIATION

Plants

For the past 60 years, Arctic plant ecologists have been concerned with the adaptations and traits of Arctic plants that enable them to survive in harsh climates (e.g. 63–68). It is now important to consider how plants that are adapted to harsh environments can respond to climatic warming and particularly how former adaptations might constrain their survival when they compete with more aggressive species immigrating from the south. Only in the past 20 years have ecologists considered Arctic plant adaptations to UV-B radiation (e.g. 69, 70).

Plant adaptations to the Arctic climate are relatively few compared with adaptations of plants to more southerly environments (67, 68) for several reasons (71): *i*) Arctic plants have inhabited Arctic regions (except for ice-free refugia) for a relatively short period of time, particularly in Canada and Yamal; *ii*) life spans and generation times are long, with clonal reproduction predominating; *iii*) flowering and seed set are relatively low and insecure from year to year; *iv*) the complexity of the plant canopy is relatively small and the canopy is low so that climbing plants with tendrils, thorns, etc. are not present. Annuals and ephemeral species are very few, e.g. *Euphrasia frigida* and *Koenigia islandica*. Many Arctic plants are pre-adapted to Arctic conditions (72) and have migrated to the Arctic along mountain chains (73) or have migrated along upland mires and bogs. Although specific adaptations to Arctic climate and UV-B are absent or rare, the Arctic's climate and UV-B regime have selected for a range of plant characteristics (Table 4).

The first filter for plants that can grow in the Arctic is freezing tolerance, which excludes approximately 75% of the world's vascular plants (4). However, many temperature effects on plants, particularly those with roots are indirect (74). Plant nutrients in Arctic soils, particularly nitrogen, are available to higher plants (with roots) at low rates (64) because of slow microbial decomposition and mineralization rates of organic matter constrained by low temperatures (30). Arctic plants use different strategies for nutrient uptake (75), and different sources of nitrogen, which reduces competition among plants and facilitates greater plant diversity (76).

Many of the adaptations of Arctic species to their current environments, such as slow and low growth, are likely to limit their responses to climate warming and other environmental changes. If changes in climate and UV adversely affect species such as mosses, that play an important role in facilitation, then normal community development and recovery after disturbance could be constrained. Many Arctic plant characteristics are likely to cope with abiotic selective pressures (e.g. climate) more than biotic (e.g. inter-specific competition). This is likely to render Arctic organisms more susceptible to biological invasions at their southern distributional limits, while populations at their northern range limit (e.g. boreal species in the tundra) will probably respond more than species at their southern limit to warming *per se*. Thus, as during past environmental changes (3), Arctic species are very likely to change their distributions rather than evolve significantly.

Animals

Classical Arctic zoology typically focused on morphological and physiological adaptations to a life under extremely low winter temperatures (129, 130). Physiological studies contribute to a mechanistic understanding of how Arctic animals cope with extreme environmental conditions (especially low temperatures), and what makes them different from their temperate counterparts. Ecological and evolutionary studies focus on how life history strategies of Arctic animals have evolved to tolerate environmental variation in the Arctic, how flexible life histories (both in terms of phenotypic plasticity and genetic variation) are adapted to environmental variation, and how adjustments in life history parameters such as survival and reproduction translate in to population dynamics patterns.

Animal adaptations to low temperatures

Arctic animals have evolved a set of adaptations that make them able to conserve energy at low winter temperatures. Warm-blooded animals that persist throughout the Arctic winter have thick coats of fur and feathers that often turn white (130). The body shapes of high Arctic mammals such as reindeer, collared lemmings, Arctic hares and Arctic foxes are rounder and their extremities shorter than their temperate counterparts (Allen's rule). The body size within some vertebrate taxa increase towards the north (Bergman's rule), but there are several notable Arctic exceptions to this (e.g. reindeer (131); muskox (132)) There are few physiological adaptations in homeotherms (i.e. warm blooded) that are unique to Arctic animals. However, several adaptations may be considered to be typically Arctic including fat storage (e.g. reindeer and Arctic fox (133)) and lowered body-core temperature and reduced basal metabolism in the winter (e.g. Arctic fox (134)). While hibernation during the winter is found in a few Arctic mammals such as the Arctic ground squirrel, most homeothermic animals are active year round. Small mammals such as shrews, voles and lemmings with relatively large heat losses due to a high surface-to-volume ratio stay in the subnivean space (a cavity below the snow) where they are protected from low temperatures during the winter. Even medium-sized birds and mammals such as ptarmigan and hares seek thermal refuges in snow caves when resting. In high Arctic areas, the normal diurnal activity patterns known from more southern latitude, are replaced by activity patterns that are independent of the time of the day (e.g. Svalbard ptarmigan (135)).

In heterothermic (i.e. cold-blooded) invertebrates hairiness and melanism (dark pigmentation) enable them to warm up in the summer season. Invertebrates survive low winter temperatures in dormancy mainly due to two strategies of cold hardiness; i.e. freeze tolerance and freeze avoidance (25). Typically, super-cooling points are lower in Arctic than in temperate invertebrates. Freeze tolerance, which appears to be an energetically

Table 4. Summary of major current characteristics of Arctic plants related to climate and UV-B radiation

Climatic factor	General effects on plants	Adaptations/characteristics of Arctic plants	References
1) Aboveground environment			
Freezing temperatures	Plant death	Evergreen conifers tolerate temperatures between -40°C and -90°C; Arctic herbaceous plants between -30°C and -196°C	(77)
Ice encapsulation	Death through lack of oxygen	Increased anoxia tolerance	(72)
Low summer temperatures	Reduced growth	Increased root growth, nutrient uptake and respiration	(78-80)
		Minimized coupling between the vegetation surface and the atmosphere: cushion plants can have temperature differentials of 25 °C	(81)
		Occupation of sheltered microhabitats and south-facing slopes	(66)
Short, late growing seasons	Constraint on available photosynthetically active radiation and time for developmental processes	Long life cycles	(82)
		Slow growth and productivity	(83)
		Dependence on stored resources	(84)
		Long flowering cycles with early flowering in some species	(63)
		Increased importance of vegetative reproduction	(85)
		Clonal growth: clones surviving for thousands of years	(82, 86)
		Long-lived leaves maximizing investment of carbon	(87)
Interannual variability	Sporadic seed set and seedling recruitment	Dependence on stored resources	(84)
		Long development processes buffer effects of any one year	(63)
		Clonal growth	(82, 88-90)
Snow depth and duration	Negative: constrains length and timing of growing season.	Where snow accumulates, snowbeds form in which specialized plant communities occur	(91)
		Where snow is blown off exposed ridges (fellfields), plants are exposed to summer drought, winter herbivory and extreme temperatures	(92, 68)
	Exerts mechanical pressure on plants	Responses and adaptations not measured	-
	Positive: Insulation in winter (it is seldom colder than -5°C under a 0.5 m layer).	Low plant stature	(93)
	Reduction of plant temperature extremes and freeze-thaw cycles	Low stature to remain below winter snow cover reduces the risk for premature dehardening	(94, 95)
	Protection from wind damage, abrasion by ice crystals and some herbivory.	Low stature to remain below winter snow cover: growth in sheltered locations	(96)
	Protection from winter desiccation when water loss exceeds water supply from frozen ground.	Low stature to remain below winter snow cover, deciduous growth	(97, 98, 94, 99, 100)
	Protection from chlorophyll bleaching due to light damage in sunny habitats	Low stature to remain below winter snow cover; deciduous growth	(101)
	Source of water and nutrients late into the growing season	Zonation of plants species related to snow depth and duration	(91, 102)
Increased UV-B radiation	Damage to DNA that can be lethal or mutagenic	Reflective/absorptive barriers such as thick cell walls and cuticles, waxes and hairs on leaves, and physiological responses such as the induction or presence of UV-B absorbing pigments (e.g. flavonoids) and an ability to repair some UV-B damage to DNA.	(69, 103)
		Repair is mediated through the enzyme photolyase that is induced by UV-A. There is so far no indication of any specific adaptation of plants in the Arctic to UV-B radiation.	(104, 105)
Variable CO ₂ concentrations	Increased CO ₂ concentrations usually stimulate photosynthesis and growth if other factors are non-limiting. Increased C:N in plant tissues	Photosynthesis of Alaskan graminoids acclimated to high CO ₂ concentrations in 6 weeks with no long term gain	(106)
		The dwarf willow (<i>Salix herbacea</i>) has been able to alter its carbon metabolism and morphology in relation to changing CO ₂ concentrations throughout the last 9 000 years	(107)
		Species such as the moss <i>Hylocomium splendens</i> are already adapted to high CO ₂ concentrations; they frequently experience 400-450 ppm, and sometimes over 1 100 ppm, to compensate for low light intensities under mountain birch woodland	(108)
2) Soil environment			
Availability of nutrients, particularly nitrogen, at low rates	Reduced growth and reproduction	Conservation of nutrients in nutrient poor tissues	(109)
		High nitrogen retention time resulting from considerable longevity of plant organs and resorption of nutrients from senescing tissues and retention of dead leaves within plant tufts and cushions	(110)
		Substantial rates of nutrient uptake at low temperatures.	(111)
		Increased surface area for nutrient uptake by increased biomass of roots relative to shoots (up to 95% of plant biomass can be below ground)	(79, 112)
		associations with mycorrhizal fungi	(113)
		and uptake of N by rhizomes	(114)
		Some Arctic plants can take up nutrients in organic forms, thereby by-passing some of the slow decomposition and mineralization processes	(115)
		Dependence on atmospheric nutrient deposition in mosses and lichens	(116)
Soil movement at various spatial scales resulting from freeze-thaw cycles, permafrost dynamics and slope processes	Freeze-thaw cycles heave ill-adapted plants from the soil and cause seedling death	Areas of active movement select for species with elastic and shallow roots or cryptogams without roots.	(117-119)
Shallow active layer	Limits zone of soil biological activity and rooting depth. Shallow rooting plates of trees can lead to falling.	Shallow rooting-species, rhizome networks	(112)
3) Biotic environment			
Herbivory	Removal of plant tissue sometimes leading to widespread defoliation and death	Arctic plants do not have some morphological defenses e.g. thorns found elsewhere.	(67)
		Many plants have secondary metabolites that deter herbivores. Some substances are induced by vertebrate and invertebrate herbivores	(120, 121)
		Protected growing points, continuous leaf growth in summer, rapid modular growth in some graminoids, regeneration from torn fragments of grass leaves, mosses and lichens.	(63, 68)
Competition	Suppression of some species and increased dominance of others leading to changes in community structure	Secondary metabolites in some Arctic species inhibit the germination and growth of neighboring species.	(122, 123)
Facilitation	Mutual benefits to plant species that grow together	Positive plant interactions are more important than plant competition in severe physical environments	(124, 125)
		Nitrogen fixing species in expanding glacial forefields facilitate the colonization and growth of immigrant plants species	(126)
		Plant aggregation can confer advantages of shelter from wind	(127)
		Hemiparasites can stimulate nutrient cycling of potential benefit to the whole plant community	(128)

less costly strategy than extended supercooling, is a common strategy in very cold regions. Wingless morphs occur frequently among Arctic insects, probably because limited energy during the short growth season is allocated to development and reproduction, rather than in an energetically costly flight apparatus. A short growth season also constrains insect body size and number of generations per year. Life cycles are often extended in time and/or simplified because invertebrates may need several seasons to complete their life cycles. Small body sizes in Arctic insects seem to be a strategy to shorten generation time (25). Moreover, individuals from Arctic populations are able to grow faster at a given temperature than southern conspecifics (e.g. 136). Thus Arctic invertebrates may be particularly efficient in utilizing relatively short warm periods to complete life-cycle stages.

A short breeding season also underlies several life history adaptations in birds and mammals such as synchronized breeding, shortened breeding season, specific molting patterns and mating systems (137). Although adjustments to low temperatures and short growth seasons are widespread in Arctic animals, successful species cannot be generalized with respect to particular life history traits (138). Both flexible and programmed life cycles are common in polar arthropods (139).

While there are many examples that show that winter-temperatures lower than species-specific tolerance limits set the northern borders of the geographic distribution of animals, there are hardly any examples that demonstrate that high temperatures alone determine how far south terrestrial Arctic animals are found. Southern range borders are typically set by a combination of abiotic factors (e.g. temperature and moisture in soil invertebrates) or, probably most often, by biotic factors such as food resources, competitors and natural enemies.

Animal migrations and habitat selection

Many vertebrates escape unfavorable conditions through movements, either long-distance migrations or more short-range seasonal movements, between different habitats in the same landscape. Seasonal migration to overwintering areas in the south is almost the rule in Arctic birds. Climate may in several ways interfere with migrating birds, such as mismatched timing of migration, habitat loss at stopover sites and weather *en route* (140) and a mismatch in the timing of migration and the development of invertebrate food in Arctic ponds (1). Many insects belonging to the boreal forest invade the low Arctic tundra in quite large quantities every summer (24), but few of these are likely to return in the fall. Year-round resident tundra birds are very few and include species such as Arctic redpolls, willow grouse, ptarmigan, raven, gyrfalcon and snowy owl. Like several other Arctic predators that specialize in feeding on lemmings and Arctic voles, the snowy owl emigrates when cyclic lemming populations crash to seek high-density prey populations elsewhere in Arctic and sub-Arctic areas. Such a nomadic life style is also found in small passerine seed-eating birds such as redpolls and crossbills in the forest tundra. These birds move between areas with asynchronous mast years in birch and conifers. Also a substantial fraction of Arctic foxes emigrates after lemming peaks and sometimes these emigrations may extend far into the taiga zone (141). Most reindeer and caribou populations perform seasonal migration from coastal tundra in summer to continental areas in forest tundra and taiga in the winter. Inuit ecological knowledge explains caribou migrations as triggered by seasonal "cues", such as the length of the day, temperature or ice thickness (142). Reindeer on isolated Arctic islands are more sedentary without pronounced seasonal migrations (143). Lemmings and ptarmigans shift habitat seasonally within the same landscapes (144). In population peak years these seasonal habitat shifts may turn into more long distance mass movements in the Norwegian

lemming (145). For small mobile animals, for example wingless soil invertebrates such as collembola and mites, habitat selection on a very small spatial scale (microhabitat selection) enables the individuals to find spatial refuges with temperature and moisture regimes adequate for survival (146, 147). The variability in microclimatic conditions may be extremely large in the high Arctic (148).

Animal adaptations to the biotic environment

Generalists in terms of food and habitat selection seem to be more common among Arctic animals than in communities further south (e.g. 25). This may be due either to fewer competitors and a less tightly packed niche-space in Arctic animal communities and/or because food resource availability is less predictable and the appropriate strategy is to opt for more flexible diets. Notable exceptions to food resource generalism are lemming predators (e.g. least weasels, several owls and raptors and skuas) and a number of host-specific phytophagous insects (e.g. aphids and saw flies). Many water birds, such as geese with 75%, and sandpipers (*Calidrids*) with 90% of the species breeding in the Arctic, are habitat specialists. Some species exhibit a large flexibility in their reproductive strategy based on food resources. Coastal populations of Arctic foxes with a relatively predictable food supply from the marine ecosystem (e.g. seabird colonies) have smaller litter sizes than inland "lemming foxes" relying on a highly variable food supply (149). Specialists on highly fluctuating food resources such as seeds from birch and conifers and lemmings/voles respond to temporary superabundant food supplies by having extraordinary high clutch/litter sizes.

High Arctic environments contain fewer natural enemy species (e.g. predators and parasites) and some animals seem to be less agile (e.g. Svalbard reindeer (143)) and are possibly less disease resistant (150).

UV-B radiation

Little is known about animal adaptations to UV-B radiation. Clearly, nonmigrant species such as reindeer, Arctic foxes, hares and many birds have white feathers and fur that presumably reflect some UV-B radiation. There is some evidence, however, that feathers can be affected by high UV-B (151) although this early research needs to be repeated. There is also a possibility that fur absorbs UV-B. Eyes of Arctic vertebrates experience extremes of UV-B from dark winter conditions to high UV-B environments in springtime. However, mechanisms of tolerance are unknown. Invertebrates in general have DNA that is robust to UV-B damage (152) and various adaptations to reduce UV-B absorbance. Some caterpillars of the sub-Arctic possess pigmented cuticles that absorb in the UV-B wavelengths while pre-exposure to UV-B can induce pigmentation (153). Collembolans and possibly other invertebrates have dark pigmentation that plays a role in both thermoregulation and UV-B protection (154).

Population dynamics patterns

In tundra habitats, population cycles in small- to medium-sized birds and mammals are the rule, with few exceptions. The periods of the cycle in lemmings and voles vary geographically and are between 3 and 5 years. Cyclicity such as spatial synchronicity and period between population peak years all seem to be associated with geographic climate gradients in Fennoscandia (coast-inland and South-North; (155, 156), although the biotic mechanisms involved are still much debated (157). Lemming populations may show geographic variation in the period of the cycle within the Arctic Siberia; also for example a long period of 5 years on Wrangel Island and relatively short period of 3 years between peak years in Taymyr (24). Within regions (for example northern Fennoscandia) small rodent cycles may show distinct interspecific synchrony over large spatial scales (158).

However, recent spatially extensive surveys in northern Canada (159) and Siberia (160) have indicated that the spatial synchrony of lemming populations is not as large-scale as the snow-shoe hare cycles in boreal N-America (161). This is at least partly due to the geographically variable cycle period.

Small- and medium-sized bird and mammal predators follow numerically the dynamics of their lemming and vole prey species (162). The signature of the lemming and vole dynamics can also be found in the reproductive success and demography of mammals and birds, for example waders and geese (e.g. 163), that serve as alternative prey to the predators of lemmings. Among northern insects, population cycles are best known in geometrid moths, particularly *Epirrita autumnata*, a species exhibiting massive population outbreaks with approximately 10 year intervals that extend into the forest tundra (164, 165). On the tundra, no herbivorous insects are known to cycle (24). However, the population dynamics of tundra invertebrates is poorly known due to the lack of long-term time series data. It is clear, however, that soil invertebrates such as Collembola (166, 167) sometimes exhibit large inter-annual fluctuations in population density. Large fluctuations in numbers are also known in the Arctic ungulate populations (reindeer/caribou and musk oxen) and seem to be the outcome of several biotic factors in combination with climatic variation (131, 168, 169).

Microorganisms

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

Adaptations to cold

The development to resist freezing (and to restore activity after warming) and the ability to metabolize below the freezing point are fundamental microbial adaptations to cold climates prevailing at high latitudes.

Cell viability depends dramatically on the velocity of freezing, which defines the formation of intracellular water crystals (170, 171). Cold-adapted microbial species are characterized by remarkably high resistance to freezing due to the presence of specific intracellular compounds (metabolic antifreeze), stable and flexible membranes and other adaptations. Lichens are extreme examples (172): the moist thalli of such species as *Xanthoria candelaria* and *Rhizoplaca melanophthalma* fully tolerated gradual or rapid freezing to -196°C , and even after storage up to several years, almost immediately resumed normal photosynthetic rates when warmed and wetted. For 5–7 months of cold and continuous darkness, they remain green with intact photosynthetic pigments. However, freeze-resistance is not a unique feature of Arctic organisms.

The ability of microorganisms' to grow and metabolize in frozen soils, subsoils or water, is generally thought to be insignificant. However, microbial growth and activity below freezing point has been recorded in refrigerated food (173) as well as in Arctic and Antarctic habitats such as sea ice, frozen soil and permafrost (174, 175). Such activity has important implications for ecosystem function (38). The year-round field measurements of gas fluxes in Alaska and northern Eurasia revealed that winter CO_2 emissions can account for up to half of the annual emissions of CO_2 (176–179), implying a significant cold-season activity of psychrophilic (cold-loving) soil microbes. Soil fungi (including mycobionts in lichens) have been considered as the most probable candidates for the majority of the below-zero tundra soil respiration (180) because their live biomass was estimated to be ten times larger than that of cohabiting bacteria.

Winter CO_2 emissions have been also explained by other mechanisms, e.g. the physical release of summer-accumulat-

ed gases or abiotic CO_2 formation due to cryoturbation (181). Most recent studies (171, 182–184, 185), agree that microbial growth is limited at about -12°C and that occasional reports of microbial activity below -12°C (e.g. continuous photosynthesis in Arctic and Antarctic lichens down to -17°C (174, 175) and photosynthetic CO_2 fixation at -24°C (186)) were not carefully recorded and confirmed. Under laboratory conditions, Rivkina et al. (185) quantified microbial growth in permafrost samples at temperatures down to -20°C . However the data points below -12°C turned out to be close to the detection limits of the highly sensitive technique that they employed. The authors concluded that nutrient uptake at -20°C could be measured, but only transiently 'whereas in nature (i.e., under stable permafrost conditions)... the level of activity, if any, is not measurable ...' (185, p. 3232).

Recently, a new, precise, technique was applied to frozen soil samples collected from Barrow, Alaska, and incubated at a wide range of subzero temperatures under laboratory conditions (187). The rate of CO_2 production declined exponentially with temperature and unfrozen water content when soil was cooled down below zero, but it remained surprisingly positive and measurable, e.g. $8 \text{ ng CO}_2\text{-C day}^{-1} \text{ kg}^{-1}$, at -39°C . A range of experimental results and treatments confirmed that this CO_2 production at very low temperatures was due to microbial respiration, rather than to abiotic processes.

Dark pigmentation causes higher heat absorption in lichens, being especially favorable in the cold polar environment (188, 189).

Adaptations to drought

Freezing is always associated with deficiency of available water. Thus, true psychrophilic organisms must also be *xerotolerant*, i.e. adapted to extremely dry environments. A number of plants and microorganisms in polar deserts, such as lichens (symbionts of algae and fungi) are termed *poikilohydrous*, meaning that they tend to be in moisture equilibrium with their surroundings (190). They have high-desiccation tolerance and are able to survive water loss of more than 95% and long periods of drought. Quick water loss inactivates the thallus and then in the inactive state, the lichen is safe from heat-induced respiratory loss and heat stress (191, 192). In unicellular microorganisms, drought-resistance can also be significant, although mycelial forms of microbial life (fungi and actinomycetes) seem to have a much higher capability due to their more efficient cytoplasm compartmentalization and spore formation.

Adaptations to mechanical disturbance

Wind, sand and ice-blasts, and seasonal ice oscillations are characteristic features of Arctic environments that affect colonization and survival of organisms. Most lichens are adapted to such effects by forming a mechanically solid thallus firmly attached to the substrate. Windswept habitats such as hillsides can be favorable if they provide suitable rough substrate and receive sufficient moisture from the air. In contrast, shallow depressions or small valleys, although more sheltered, are bare of lichens because snow recedes from them only for very brief periods each season or persists over several years. This phenomenon is one reason for the so-called trimline effect (193–195). The abrasive forces of the ice at the bottoms of glaciers may destroy all epilithic (rock-attached) lichen vegetation, but lichens once established are able to survive long periods of snow cover, even glacial periods (172).

Adaptations to irradiance

Strong pigmentation is typical for numerous microorganisms of tundra and polar deserts, especially for those which are frequently or permanently exposed to sun on the soil surface (lichens and

epiphytic bacteria). Pigments (melanin, melanoids, carotenoids, etc) are usually interpreted as a protection against strong irradiation. Pigmentation may be constitutive for particular species or appear as a plastic response to irradiance, e.g. originally colorless *Cladonia* and *Cladina* lichens quickly develop dark-pigmented thalli after exposure to stronger sun radiation (196). Buffoni Hall et al. (197) demonstrated that in *Cladonia arbuscula* ssp. *mitis* an increase in phenolic substances is specifically induced by UV-B radiation, and that this increase leads to attenuation of the UV-B radiation penetrating into the thallus. Also the accumulation of the protective pigment parietin in *Xanthoria parietina* is induced specifically by UV-B radiation (198), while in *Cladonia uncialis* and *Cladina rangiferina* only UV-A radiation had a stimulating effect on the accumulation of usnic acid and atranorin, respectively. Photo-repair of radiation-damaged DNA in *Cladonia* requires not only light, but also high temperature and that the thallus is hydrated (197). As in higher plants, carotenoids protect against excessive photosynthetically active light (199), and perhaps also have a role in protection from ultraviolet radiation. In contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.

Braga et al. (200, 201) survey the UV sensitivity of conidia (spore-forming bodies) of thirty strains of the fungus *Metarhizium* (belonging to four species). This fungus is an important agent of insect disease. Exposure to UV-B within an ecologically relevant range, showed great differences between the strains: strains from low latitudes were generally more tolerant than those from high latitudes.

Algae

Seven interrelated stress factors (temperature, water, nutrient status, light availability and/or UV radiation, freeze/thaw events, length of growing season and unpredictability) are important for life in Arctic terrestrial and shallow wetlands (138). Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize injury. Three main strategies for coping with living in the Arctic terrestrial and wetland habitats are avoidance, protection, and the formation of partnerships with other organisms (202). Poikilohydricity (tolerance of desiccation) and shelter strategies are frequently interconnected, and when combined with cell mobility and development of complex life cycles, afford considerable potential for avoidance. The extracellular production of protective compounds and structures such as multi-layered cell walls, sheets of mucilage that together with intracellular control of cell solute composition and viscosity (changes in the cell's carbohydrate and polyols composition) is also a very common phenomenon. The association of cyanobacteria/algae with fungi in lichens gives a benefit of physical protection.

CONCLUSIONS

This paper is part of an holistic approach to assess impacts of climate change on Arctic terrestrial ecosystems. It focuses on the attributes of current Arctic species that are likely to constrain or facilitate their responses to a changing climate and UV-B regime. Overall, it is apparent that many Arctic species should be able to withstand the direct effects of increased temperature and UV-B radiation. However, the indirect effects of warming and UV-B increases, and particularly those mediated by species interactions such as competition with more aggressive immigrants from the South, are likely to dominate Arctic species' responses to environmental change. Such inferences derived from existing relationships between species and current climate give information on *potential* responses to climate change, but often fail to identify the operative mechanisms and time frames underpin-

ning the responses. To derive this type of information, other approaches are required such as experimental manipulation and simulation of future environments.

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