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

Past Changes in Arctic Terrestrial Ecosystems, Climate and UV Radiation

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 and Gus Shaver

At the last glacial maximum, vast ice sheets covered many continental areas. The beds of some shallow seas were exposed thereby connecting previously separated landmasses. Although some areas were ice-free and supported a flora and fauna, mean annual temperatures were 10–13°C colder than during the Holocene. Within a few millennia of the glacial maximum, deglaciation started, characterized by a series of climatic fluctuations between about 18 000 and 11 400 years ago. Following the general thermal maximum in the Holocene, there has been a modest overall cooling trend, superimposed upon which have been a series of millennial and centennial fluctuations in climate such as the "Little Ice Age" spanning approximately the late 13th to early 19th centuries. Throughout the climatic fluctuations of the last 150 000 years, Arctic ecosystems and biota have been close to their minimum extent within the most recent 10 000 years. They suffered loss of diversity as a result of extinctions during the most recent large-magnitude rapid global warming at the end of the last glacial stage. Consequently, Arctic ecosystems and biota such as large vertebrates are already under pressure and are particularly vulnerable to current and projected future global warming. Evidence from the past indicates that the treeline will very probably advance, perhaps rapidly, into tundra areas, as it did during the early Holocene, reducing the extent of tundra and increasing the risk of species extinction. Species will very probably extend their ranges northwards, displacing Arctic species as in the past. However, unlike the early Holocene, when lower relative sea level allowed a belt of tundra to persist around at least some parts of the Arctic basin when treelines advanced to the present coast, sea level is very likely to rise in future, further restricting the area of tundra and other treeless Arctic ecosystems. The negative response of current Arctic ecosystems to global climatic conditions that are apparently without precedent during the Pleistocene is likely to be considerable, particularly as their exposure to co-occurring environmental changes (such as enhanced levels of UV-B, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation) is also without precedent.

INTRODUCTION

An assessment of likely future climate and UV-B impacts on the Arctic's peoples, environment and biota (1), recognizes the importance of impacts on terrestrial ecosystems in terms of the biodiversity, ecosystem services, and feedbacks to the climate system (2). In order to understand the present biota and ecosystems of the Arctic, and to aid predictions of the likely nature of their responses to potential rapid future climate change, it is nec-

essary to examine at least the last ca. 21 000 yrs of their history. This paper is part of an holistic approach to assess impacts of climate change on Arctic terrestrial ecosystems (1, 2). We focus on the changes in environment and biota that occurred during the last ca. 21 000 yrs. This period, the late-Quaternary, extends from the present back to the last glacial maximum, encompassing the Holocene, or post-glacial, period that spans the last ca. 11 400 yrs. A review of this period of the history of the biota and ecosystems found in the Arctic today also must examine a spatial domain that is not restricted to the present Arctic regions. At the last glacial maximum many of these regions were submerged beneath vast ice sheets, whereas many of the biota comprising present Arctic ecosystems were found at lower latitudes.

LATE-QUATERNARY ENVIRONMENTAL HISTORY IN THE ARCTIC

At the last glacial maximum, vast ice sheets accumulated not only on many high latitude continental areas but also across some relatively shallower marine basins. The beds of relatively shallow seas such as the North Sea and Bering Sea were exposed as a result of the global fall of ca. 120 m in sea level, the latter resulting in a broad land connection between eastern Siberia and Alaska and closure of the connection between the Pacific and Arctic Oceans. The reduction in sea level also exposed a broad strip of land extending northwards from the present coast of Siberia. Most, if not all, of the Arctic Ocean basin may have been covered by permanent sea ice.

Although details of the extent of some of the ice sheets continue to be a matter for controversy (3–7), it is certain that the majority of land areas north of 60°N were ice-covered. The principal exceptions were in eastern Siberia, Beringia, and Alaska, although there is some geological evidence to suggest that smaller ice-free areas also persisted in the high Arctic, for example in the northernmost parts of the Canadian archipelago (8) and perhaps even in northern and northeastern Greenland (9). This evidence gains support from recent molecular genetic studies of Arctic species; for example, a study of the dwarf shrub *Dryas integrifolia* indicates glacial occurrences in the high Arctic (10) as well as in Beringia, and a study of the collared lemming *Dicrostonyx groenlandicus* indicates separate glacial populations east and west of the Mackenzie River (11, 12), the latter most probably in the Canadian archipelago. This latter conclusion is supported by the phylogeography (genetic and evolutionary relationships) of the *Paranoplocephala arctica* species complex, a cestode parasite of *Dicrostonyx* spp., indicating that two subclades probably survived the last glacial maximum with their host in the Canadian high Arctic (13). More controversial are suggestions that elements of the Arctic flora and fauna may have survived the last glacial maximum on nunataks in glaciated areas of high relief such as parts of Greenland, Svalbard, and Iceland

(14). Although a recent molecular genetic study of the Alpine cushion plant *Eritrichium nanum* (15) provides strong evidence for survival of that species on nunataks within the heart of the European Alps, similar studies of Arctic species have so far not supported the hypothesis of survival on nunataks in areas such as Svalbard (16), which experienced extreme climatic severity as ice sheets extended to margins beyond the current coast in the last glacial maximum.

Direct evidence of the severity of the full glacial climate in the Arctic comes from studies of ice cores from the Greenland ice cap and other Arctic ice sheets which indicate full glacial conditions with mean annual temperatures 10–13°C colder than during the Holocene (1, 17). Paleotemperature reconstructions based upon dinoflagellate cyst assemblages indicate strong seasonal temperature fluctuations, with markedly cold winter temperatures (18, 19).

The last glacial maximum was, however, relatively short-lived; within a few millennia of reaching their maximum extent many of the ice sheets were decaying rapidly and seasonal temperatures had increased in many parts of the Arctic. Deglaciation was not, however, a simple unidirectional change; instead a series of climatic fluctuations occurred during the period between about 18 000 and 11 400 years ago, these fluctuations varying in intensity, duration, and perhaps also in geographical extent. The most marked and persistent of these fluctuations, the so-called Younger Dryas event (20–22), was at least hemispheric in its extent, and is marked by the reglaciation of some regions and re-advances of ice-sheet margins in others. Mean annual temperatures during this event fell substantially; although not as low as during the glacial maximum, they were nonetheless 4–6°C cooler than at present over most of Europe (23), and as much as 10–12°C colder than present in the northern North Atlantic and Norwegian Sea (24), as well as in much of northern Eurasia (25). The end of the Younger Dryas was marked by a very rapid rise in temperatures. At some individual locations mean annual temperature rose by > 5°C in less than 100 yr (26). The most rapid changes most probably were spatially and temporally transgressive, with the global mean change thus occurring much less rapidly. Nonetheless, in many areas summer temperatures during the early Holocene rose to values higher than those of the present day. Winter conditions remained more severe than today in many higher latitude areas, however, because the influence of the decaying ice sheets persisted into the early millennia of the Holocene.

Despite higher summer temperatures in the early to mid-Holocene in most Arctic areas, Holocene climate has not differed qualitatively from that of the present. Following the general thermal maximum there has been a modest overall cooling trend throughout the second half of the Holocene. Superimposed upon these general long-term patterns, however, have been a series of millennial and centennial fluctuations in climate (27). The most marked of these, which occurred about 8200 years ago, appears to have been triggered by catastrophic discharge of freshwater into the northern North Atlantic from proglacial lakes in North America (28, 29). A reduction in strength, if not a partial shut-down, of the thermohaline circulation in the northern North Atlantic and Norwegian Sea was also associated with this event, as well as with the series of less severe climatic fluctuations that continued throughout the Holocene (30).

The most recent of these climatic fluctuations was that of the “Little Ice Age”, a generally cool interval spanning approximately the late 13th to early 19th centuries. At its most extreme, mean annual temperatures in some Arctic areas fell by several degrees. Sea ice extended around Greenland and in some years filled the Denmark Strait between Greenland and Iceland (31–34); the Norse settlement of Greenland died out (35, 36) and the population of Iceland was much reduced (37, 38). Although

there was great temporal variability of climate on decadal to centennial time scales within the overall period of the Little Ice Age, and there was also spatial variability in the magnitude of the impacts, it was apparently a period of generally more severe conditions in Arctic and boreal latitudes; the marked impacts upon farming and fisheries (31) imply similarly marked impacts on other components of the Arctic ecosystem. Since the early 19th century, however, there has been an overall warming trend (39), although with clear evidence once again of both short-term temporal variability and of spatial variability (40). At least in those parts of the Arctic that have experienced the most rapid warming during the last 30 years or so, the magnitude of this recent warming is comparable to that during the warmest part of the Holocene.

The solar variability thought to be responsible for The Little Ice Age, and for other similar centennial to millennial climatic fluctuations, probably also affected the ozone layer and UV-B radiation. UV-B irradiance at ground level relevant to absorption by DNA could have been between 9% and 27% higher during low-radiation (cool periods) than during high-radiation periods of the sun (41).

LATE-QUATERNARY HISTORY OF ARCTIC BIOTA

At the time of the last glacial maximum, when most land areas in the Arctic were ice covered, biomes able to support the elements of the Arctic biota, including some species that are now extinct, were extensive south of the Fennoscandian ice sheet in Europe (42). Similar biomes apparently were extensive south of the Eurasian ice sheets of northern Russia, eastwards across Siberia and the exposed seabed to the north, and *via* Beringia into Alaska and adjacent northern Yukon (43), although they were much more restricted south of the Laurentide ice sheet in central and eastern North America (44). The most extensive and important of these glacial biomes, the steppe–tundra, has been interpreted and referred to by various authors as “tundra–steppe” or “Mammoth steppe” (45–47). The vegetation of this biome comprised a no-analog combination of light-demanding herbaceous and dwarf-shrub taxa that are found today either in Arctic tundra regions or in the steppe regions that characterize central parts of both North America and Eurasia (46). The association with this biome of evidence of an abundance of grazing herbivores of large body mass, some extant (e.g. *Rangifer tarandus* – reindeer, caribou; *Ovibos moschatus* – musk oxen) and others extinct (e.g. *Megaloceros giganteus* – giant deer, ‘Irish elk’; *Mammuthus primigenius* – woolly mammoth; *Coelodonta antiquitatis* – woolly rhino), is interpreted as evidence that the biome was much more productive than is the contemporary tundra biome. This productive biome, dominated by non-tree taxa, corresponded to a no-analog environment that was relatively cold throughout the year, with a growing season short enough to exclude even cold-tolerant boreal trees from at least the majority of the landscape. The “light climate”, however, was that of the relatively lower latitudes (as little as 45°N in Europe) at which this biome occurred, rather than that of the present Arctic latitudes. The greater solar angle and consequent higher insolation intensities during the summer months probably made an important contribution to the productivity of the biome.

The productive steppe–tundra and related biomes were much more spatially extensive during the last glacial stage than is the tundra biome today (Fig. 1). The glacial was thus a time when many elements of the present Arctic biota thrived, almost certainly in greater numbers than today. Fossil remains of both Arctic plants (48) and mammals (49–51) found at numerous locations attest to their widespread distribution and abundance. Similar conclusions have been reached on the basis of phylogeographic studies (studies of the relationships between genetic identity and

geographical distribution) of Arctic breeding waders (52). Species such as *Calidris canutus* (red knot) and *Arenaria interpres* (ruddy turnstone) are inferred to have had much larger populations and more extensive breeding areas during glacial stages, although others, such as *C. alpina* (dunlin), exhibit evidence of range fragmentation during glacial stages leading to evolution of distinct geographically restricted infra-specific taxa. Phylogeographic studies of other Arctic taxa reveal a picture of individualism of response of different species (see ref. 51 for a recent review). Some species, such as *Salvelinus alpinus* (Arctic char) (54), and genera, such as *Coregonus* spp. (whitefish) (55), exhibit evidence of sub-taxa whose origins are apparently related to recurrent periods of isolation of populations throughout the Pleistocene history of alternating glacial and interglacial stages. *Dicrostonyx* spp. (collared lemmings), however, apparently parallel *C. alpina* in exhibiting genetic differentiation principally as a consequence of the relatively recent geographical isolation of populations during the last glacial stage (12, 56). Others, such as *Ursus maritimus* (polar bear) (57), exhibit little or no evidence of genetic differentiation that might indicate past population fragmentation, and Eurasian *Lemmus* spp. (true lemmings) (58) are inferred to have experienced no effective reduction in population size during recent glacial–interglacial cycles.

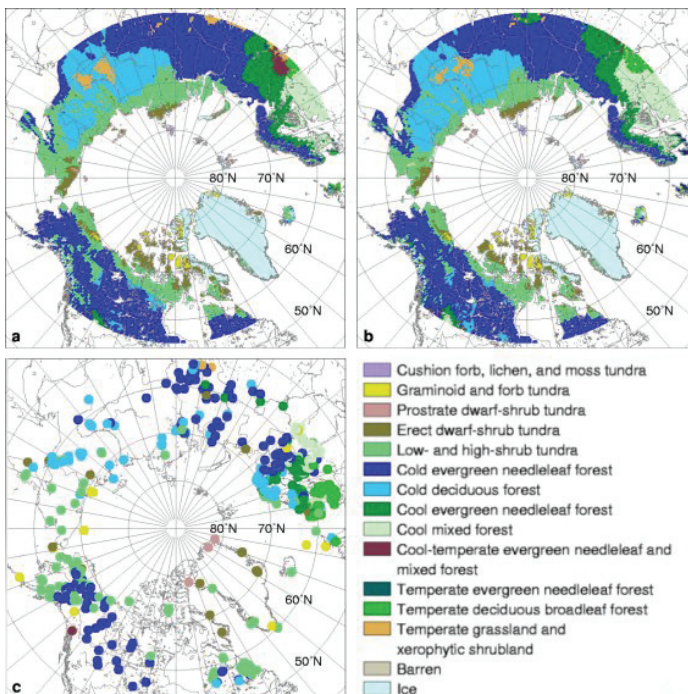


Figure 1. Northern vegetation in the Mid- Holocene a) simulated by the IPSL-CM1 AOJCM model, b) simulated by the HADCM2 AOJCM model, c) observed vegetation reconstructed from pollen data (modified from Kaplan et al. (86) and Bigelow et al. (87)).

In the context of their late-Quaternary history, the Arctic biota of the present day should be viewed as relatively restricted in range and population size. Although tundra areas were of even smaller extent at the time of the early Holocene period of greater northward extension of the Arctic treeline (59–61), that reduction was marginal when compared to that suffered at the end of the last glacial stage. Similarly, whereas at the lower taxonomic levels, extant Arctic taxa often exhibit considerable diversity that can be related to their late-Quaternary history, the biota as a whole has suffered a recent reduction of overall diversity through the extinctions of many species, and some genera, that did not survive into the Holocene. Of at least 12 large herbivores and 6 large carnivores present in steppe-tundra areas at the last glacial maximum (44, 51), only 4 and 3, respectively, survive today and of those, only 2 herbivores (reindeer and musk ox)

and 2 carnivores (brown bear and wolf) occur today in the Arctic tundra biome. The present geography also imposes extreme migratory distances upon many tundra-breeding birds because of the wide separation of their breeding and wintering areas (62, 63), in consequence rendering many of them, in common with much of the Arctic biota, extremely vulnerable to any further climatic warming (64).

LATE-QUATERNARY ECOLOGICAL HISTORY IN THE ARCTIC

Although relatively few in overall number, paleoecological studies of the late-Quaternary have been made in many parts of the Arctic (43, 61, 65–67). In areas that were by then ice free, the transition to the Holocene was marked by evidence of rapid ecological response to the environmental changes at that time. Elsewhere, in proximity to the decaying ice sheets the ecological changes lagged the global environmental change because of the regional influence of the persisting ice. Although the precise nature of the ecological changes depends upon the location, the overall picture was one of widespread rapid replacement of the open, discontinuously vegetated tundra and polar desert that had characterized most ice-free areas during the late-glacial period, by closed tundra. This was in turn replaced by shrub tundra and subsequently by Arctic woodlands or northern boreal forests in lower Arctic areas. In areas such as Alaska that were unglaciated at the last glacial maximum, the ecological transition began earlier, coinciding with the first rapid climatic warming recorded in Greenland at ca. 14 700 years ago (68, 69). In Alaska, tundra was replaced by shrub tundra during the late glacial and the first forest stands (of *Populus balsamifera* – balsam poplar) were present already before the transition to the Holocene (66). South of the Arctic the extensive areas of steppe-tundra that were present at the last glacial maximum were rapidly replaced by expanding forests. Only in parts of northernmost Siberia may fragments of this biome have persisted into the Holocene, supporting the last population of woolly mammoths that persisted as recently as 4000 years ago (70).

The early Holocene was characterized by enhanced summer insolation intensities in northern latitudes, compared to the present. The warmer summer months enabled trees to extend their ranges further northwards than at present; positive feedback resulting from the contrasting albedo of forest compared to tundra (71, 72) probably enhanced this extension of the forest (73). Boreal forest trees expanded their ranges at rates of between 0.2 and 2 km yr⁻¹ (74, 75). They exhibited individualistic responses with respect to their distributions, and abundance patterns in response to climatic patterns that differed from those of today. Milder winters and more winter precipitation in western Siberia at that time, for example, allowed *Picea abies* (Norway spruce) to dominate in areas where *Abies sibirica* (Siberian fir) and *Pinus sibirica* (Siberian stone pine) subsequently have become important forest components during the later Holocene (59, 72, 76). Throughout northern Russia the Arctic treeline already had advanced more or less to the position of the present Arctic coastline by ca. 10 200 years ago, although the lower sea level at that time meant that a narrow strip of tundra, up to 150 km wide at most, persisted to the north of this (61). Subsequently, as sea level continued to rise during the early Holocene, the extent of tundra reached a minimum that persisted for several millennia. For tundra species, including tundra-breeding birds, the early Holocene thus seems likely to have been a time of particular stress. This stress may, however, have been in part relieved by enhanced productivity in these areas, compared to modern tundra ecosystems, as a consequence of the warmer summers and their higher insolation intensity.

In glaciated areas of the Arctic, such as northern Fennoscand-

dia and much of Arctic Canada, peatlands became extensive only after the mid-Holocene (77, 78) in response to the general pattern of climatic change towards cooler and regionally moister summer conditions. The same cooling trend led to the southward retreat of the Arctic treeline, which reached more or less its present location in most regions by ca. 4500 years ago (61). The consequent increase in extent of tundra probably relieved the stress experienced by tundra organisms during the early Holocene, although the cooler, less productive conditions, and the increasing extent of seasonally waterlogged tundra peat lands, may have offset this at least in part. Whereas at least in some regions the early Holocene was a time of permafrost decay and thermokarst development (79), the extent of permafrost has increased once again in many areas during the later Holocene (78, 80).

LATE-QUATERNARY HISTORY OF HUMANS IN THE ARCTIC RELATED TO ECOSYSTEMS

Recently discovered evidence (81) shows that Paleolithic "hunter-gatherers" were present ca. 40 000 years BP as far north as 66° 34'N in Russia, East of the Fennoscandian ice sheet and well before the last glacial maximum. Although it seems likely that humans did not range so far north during the glacial maximum, it is clear that they expanded rapidly into the Arctic once again during the deglaciation.

Humans entered North America *via* the Beringian 'land bridge' and along its southern coast ca. 14 000–13 500 years BP (82). These so-called Clovis hunters were hunter-gatherers who had developed sophisticated ways of working stone to produce very fine spear- and arrowheads. Over the next few millennia they expanded their range and population rapidly, occupying most of the North American continent. As they did so their prey apparently included many of the large vertebrate species that soon were to become extinct. The extent to which human hunting may have been principally responsible for these extinctions is a matter of continuing debate, but recent simulations for North America indicate that this possibility cannot be excluded for that region (83). These extinctions coincide, however, with an envi-

ronmental change that caused the area of the biome with which the large Arctic vertebrates were associated to be reduced to an extent that apparently was unprecedented during previous glacial-interglacial cycles (84). Thus, it is more probable that the hunting pressure exerted by humans was at most an additional contributory factor leading to the extinctions, rather than their primary cause.

In Eurasia, Paleolithic hunter-gatherers shifted their range northwards into the Arctic, as did their large vertebrate prey. To the south they were replaced by Mesolithic peoples who occupied the expanding forests. By the early Holocene these Mesolithic peoples had expanded well into the Arctic (85) where they probably gave rise to the indigenous peoples that in many cases continued to practice a nomadic hunter-gatherer way of life until the recent past or even up to the present day in some regions (1). The arrival of later immigrants has had major impacts upon the indigenous peoples and their way of life. In turn, land-use and natural-resource exploitation by the immigrants, as well as the changes that they have brought about in the way of life of the indigenous peoples, have had negative impacts upon many Arctic ecosystems. These impacts may in some cases have increased the vulnerability of these ecosystems to the pressures that they now face from climate change and increased exposure to UV-B.

FUTURE CHANGE IN THE CONTEXT OF LATE-QUATERNARY CHANGES

The potential changes for the next century can be put into context by comparing their rates and magnitudes to those estimated for the changes documented by paleoecological and other evidence from the late-Quaternary (Table 1).

It is apparent from Table 1 that the potential future changes have several characteristics that pose a particular threat to the biota and ecosystems of the Arctic. Firstly, the climatic changes of the next century (1) are likely to be comparable in magnitude to the changes seen between full glacial conditions and present conditions, and larger than the maximum changes seen during

Table 1. Summary comparison for key aspects of potential future environmental changes in the context of changes in the late-Quaternary.

Phenomenon	Late-Quaternary	Potential Future
Sea-level	ca. 120 m lower at last glacial maximum increased at maximum rate of ca. 24 mm yr ⁻¹ (82)	0.09–0.88 m higher in ca. 100 yr; 3–10 m higher in 1000 yr; increase at rate of 1–9 mm yr ⁻¹ (83)
Climate	<p><i>mean annual temperature:</i> full glacial – global mean ca. 5°C lower; regionally in the Arctic 10–13°C lower Holocene – global mean < 1°C higher at maximum; regionally in the Arctic similar to present</p> <p><i>winter temperature:</i> full glacial > 15°C cooler regionally Holocene ca. 2–4°C warmer regionally at maximum</p> <p><i>rate of change:</i> mean annual temperature increase – globally ≤ 1°C per millennium; regionally > 5°C in a century</p>	<p><i>mean annual temperature:</i> 2100 – global mean 1.5–5.8°C higher; regionally in the Arctic 2.1–8.1°C higher (83)</p> <p><i>winter temperature:</i> 2100: 4–10°C higher regionally (83)</p> <p><i>rate of change:</i> mean annual temperature increase – globally 1.5–5.8°C per century; regionally 2.1–8.1°C in a century (83)</p>
Ecosystem responses	<p><i>treeline displacement:</i> full glacial > 1000 km southward Holocene 50–200 km northward at maximum (84)</p> <p><i>range margin displacement rates:</i> early Holocene rates of 0.2–2 km yr⁻¹ estimated for trees from pollen data (72)</p>	<p><i>treeline displacement:</i> 2100 – >500 km northward Anthropogenic disturbance, however, may result in an opposite response (71)</p> <p><i>range margin displacement rates:</i> potential rates during 21st century of 5–10 km yr⁻¹ estimated from species-climate response models (85)</p>
Area of tundra	full glacial: 197% (ranging from 168 to 237%) of present. Holocene: 81% (ranging from 76 to 84%) of present at minimum	2100–51% of present (J. Kaplan, pers. comm.; see 86)
UV-B radiation	No long-term trend known. Due to solar variability, levels of DNA-active UV-B wavelengths may have varied by up to 27% with a period of ~150 years (39)	In addition to the continuing internal cycles of the sun, anthropogenic cooling of the stratosphere may delay recovery of the ozone layer.

the Holocene. Secondly, the global increase in mean annual temperature is expected to occur at rates that are higher than the rate of global warming during the last deglaciation; even regionally the rate of warming is likely to match the most rapid regional warming of the late-Quaternary. Thirdly, as a consequence of this climate change, and the accompanying rise in sea level, tundra extent is likely to be less than at any time during the late-Quaternary. Fourthly, global mean temperatures and mean annual temperatures in the Arctic will reach levels unprecedented in the late-Quaternary; this will result in a further rapid reduction in the extent of permafrost, with associated thermokarst development in areas of permafrost decay leading to potentially severe erosion and degradation of many Arctic peatlands (72). When climate projections are combined with human activities and their consequences (including enhanced levels of UV-B, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation), the future will be without a past analogue and will pose unprecedented challenges to Arctic ecosystems and biota that evolved in response to global cooling throughout the last 5 million years or so (the late-Tertiary and Quaternary periods), a period similar to that during which our own species evolved.

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