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# Climate change and biodiversity in the Arctic—Nordic perspectives

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**1** This paper is based upon a presentation given on United Nations Environment Programme (UNEP) World Environment Day, 5 June 2007, as part of the Nordic Perspectives session of the climate change conference Melting Ice—A Hot Topic?

The broad aims of this paper are to define biodiversity and ecosystem services, to set the biodiversity of the Arctic terrestrial realm into its global context, and, through the use of case studies, to illustrate how environmental change can influence biodiversity and ecosystems, and to explore what the implications of these changes might be. A comprehensive treatment of the topic is well beyond the scope of both the presentation and this paper, but the reader is directed to the CAFF (2001) and ACIA (2005) reports for reviews and synthesis.

## Biodiversity and ecosystem services

Biodiversity is defined as

The variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems. (Article 2, *Convention on biological diversity* 1992)

**2** This presentation focuses upon terrestrial biodiversity, but a key point to emphasize in the definition is that biodiversity includes “diversity within species” and “of ecosystems”. So biodiversity cannot be used interchangeably with “species richness” (or numbers of species). In the Arctic the diversity within species can be very great, and CAFF (2001: 49) notes that “genetic, morphological and behavioural diversity may be especially significant components of biodiversity”; this assumes even greater significance in the Arctic, where species richness is often

low compared with communities and ecosystems from temperate and tropical environments.

Biodiversity is fundamental to the provision of “ecosystem services”, and these are defined by the Food and Agriculture Organization (FAO) as

The conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. Examples include provision of clean water, maintenance of liveable climates (carbon sequestration), pollination of crops and native vegetation, and fulfilment of people’s cultural, spiritual, intellectual needs. (FAO 2005)

Note that the term “ecosystem services” is anthropocentric, and refers to services to humankind. So, in essence, when we talk of ecosystem services this is a utilitarian view of life on Earth, but it does provide a basic foundation for an assessment of the value of biodiversity to people, and as such has some worth. In the context of the Arctic terrestrial realm, ecosystem services that are straightforward to recognize include (i) the provision of food and fodder (e.g. for reindeer herders and their animals in the Nordic and Russian contexts), (ii) fuel and fibre (the latter including animal and plant products), (iii) a sense of cultural and spiritual identity, (iv) the maintenance of fundamental ecosystem services (such as photosynthesis, decomposition and nutrient recycling), (v) a clear link to the global climate system and biogeochemical cycles, (vi) the provision of genetic resources and (vii) a clear link with service industries such as the tourism sector. In relation to (v), the Arctic is profoundly important in the global energy budget (with snow cover, and the forest–tundra ecotone, assuming great importance in terms of albedo and surface roughness effects). In terms of genetic resources (vi), cold-adapted organisms (particularly micro-organisms) are likely to have major potential for

development of therapeutic or pharmaceutical products, and soils and sediments undoubtedly represent major reservoirs of genetic diversity in the Arctic terrestrial realm (as indicated by the work of Torsvik et al. 2002).

Arctic terrestrial biodiversity in context

Set against this background of the role of biodiversity for ecosystem services in the Arctic, and emphasizing the point that biodiversity includes within-species and among-ecosystem diversity, a tacit generalization can be made that biodiversity is low in the Arctic (at least among higher plants and vertebrates: see Table 1). The results of Rannie (1986), Chernov (1989, 1995) and Matveyeva & Chernov (2000) show a clear inverse relationship, for example, between mean July temperature and the biodiversity of vascular plant species, nesting birds, ground beetles and day butterflies across transects in Canada and Russia. The logical conclusion from this is that warming should increase biodiversity (at least in the long term). But this is likely to be a gross oversimplification, particularly bearing in mind the predicted rapid rates of climate change (especially for the arctic landmasses), and the other drivers of change superimposed upon climate; this is an issue that will be raised again in due course. Some specialist “Arctic” species may, however, be lost (e.g. of the plants, some “euarctic” components, currently widespread in the northern part of the Arctic tundra zone, and hyperarctic species of the northern tundra, polar deserts and semi-deserts, may be especially vulnerable; see Cal-

**Table 1** Biodiversity estimates in terms of species richness (numbers of species) within selected groups for the Arctic terrestrial realm north of the latitudinal treeline, and their percentage of the terrestrial total globally. Modified from CAFF (2001) and ACIA (2004). “Other groups” includes amphibians and reptiles (seven species), centipedes (10 species), terrestrial molluscs (three species), oligochaetes (earthworms and enchytraeid worms; 70 species) and nematodes (ca. 500 species).

Group	Arctic species numbers	Arctic % of total
Insects	3300	0.4
Mites	700	1.9
Springtails	400	6.0
Spiders	300	1.7
Birds	240	2.9
Mammals	75	1.7
Other groups	600	—
Fungi	2500	2.3
Lichens	2000	11.0
Flowering plants	1735	0.7
Algae	1200	3.3
Mosses	600	4.1
Liverworts	250	2.5
Ferns	62	0.6
Conifers	12	1.6

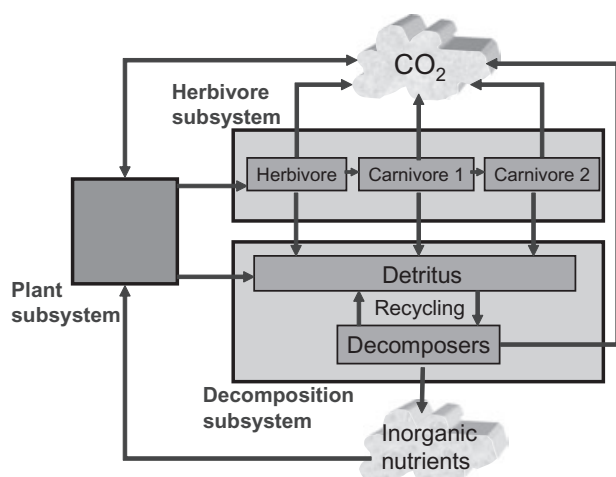
laghan et al. 2005). This partly reflects the likely northern shift in life zones, and an overall contraction of the tundra biome. Plants, animals and microorganisms are also likely to respond differentially to change (because of contrasting life histories, generation times and dispersal mechanisms), resulting in the advent of “novel” communities for which there are no contemporary analogues.

Although interspecific diversity is generally low in the Arctic, some taxa are proportionally well-represented in the Arctic terrestrial biota (Table 1): in particular in the cryptogams (spore-producing plants; specifically the algae, lichens and mosses) and soil invertebrates such as the collembola (springtails) (CAFF 2001; ACIA 2005). The diversity of soil microorganisms in Norwegian tundra and Arctic desert (Svalbard) soils also compares favourably with arable and pasture soils (Torsvik et al. 2002). Indeed for Arctic terrestrial ecosystems the soil is undoubtedly the largest reservoir of biodiversity and genetic capital, although this situation is unlikely to be unique among terrestrial ecosystems. Soil biodiversity is, in ecosystem terms, as important as plant biodiversity, and in terms of energy flows and material recycling, there are internal recycling processes (where decomposer organisms themselves die, and are decomposed in turn by others) which confer a complexity to the decomposer subsystem that is frequently overlooked in discussions of biodiversity and environmental change (Fig. 1).

Environmental change in the Arctic is multifaceted

Environmental change in the Arctic is multifaceted, and organisms respond both directly and indirectly to these changes. Climate change is just one of several environmental change “drivers”, alongside the ongoing changes in atmospheric composition themselves (e.g. increasing CO<sub>2</sub> concentrations; increasing deposition of airborne N- and S-containing contaminants; and stratospheric ozone depletion resulting in greater UVB fluxes at the surface), and direct anthropogenic disturbance (e.g. for transport infrastructure, fossil fuel and mineral extraction, forestry, tourism and hydropower generation).

Because environmental changes of contrasting rate, magnitude and geographical extent are all occurring simultaneously in the Arctic, and organisms will respond differentially to these changes, there are serious challenges involved in attempting to predict how biodiversity, communities and ecosystems will respond to change. And we cannot always rely with confidence on the lessons of history (“the past as a key to the future”; see Adams & Woodward 1992) because changes are occurring for which there are no analogues in the palaeoenvironmental or palaeoecological records.



**Fig. 1** A general model of a terrestrial ecosystem. The three component subsystems (plant, herbivore and decomposer) are shown, together with their component parts. The major transfers of material are denoted by arrows, whereas organic matter pools are shown within rectangles, and inorganic pools are shown within "clouds". Note, in particular, that a key raw material for photosynthesis [carbon dioxide ( $\text{CO}_2$ )] is returned to the atmosphere principally by the decomposer organisms (this is certainly the case in the Arctic), and that "mineral" nutrients are also made available to plants by the decomposers (although there is growing evidence that plants may "bypass" this process and take up amino acids, for example, directly from the soil, or via mycorrhizas). Note, also, the internal recycling within the decomposition subsystem: this is an aspect of internal biocomplexity that is not matched directly within the plant and herbivore subsystems. Furthermore, we know very little indeed of soil biodiversity in most arctic terrestrial ecosystems, in spite of the significance of the decomposition subsystem to ecosystem processes and properties (including carbon sequestration in soil organic matter and permafrost). Figure redrawn from Swift et al. (1979).

### But what are the effects of warming?

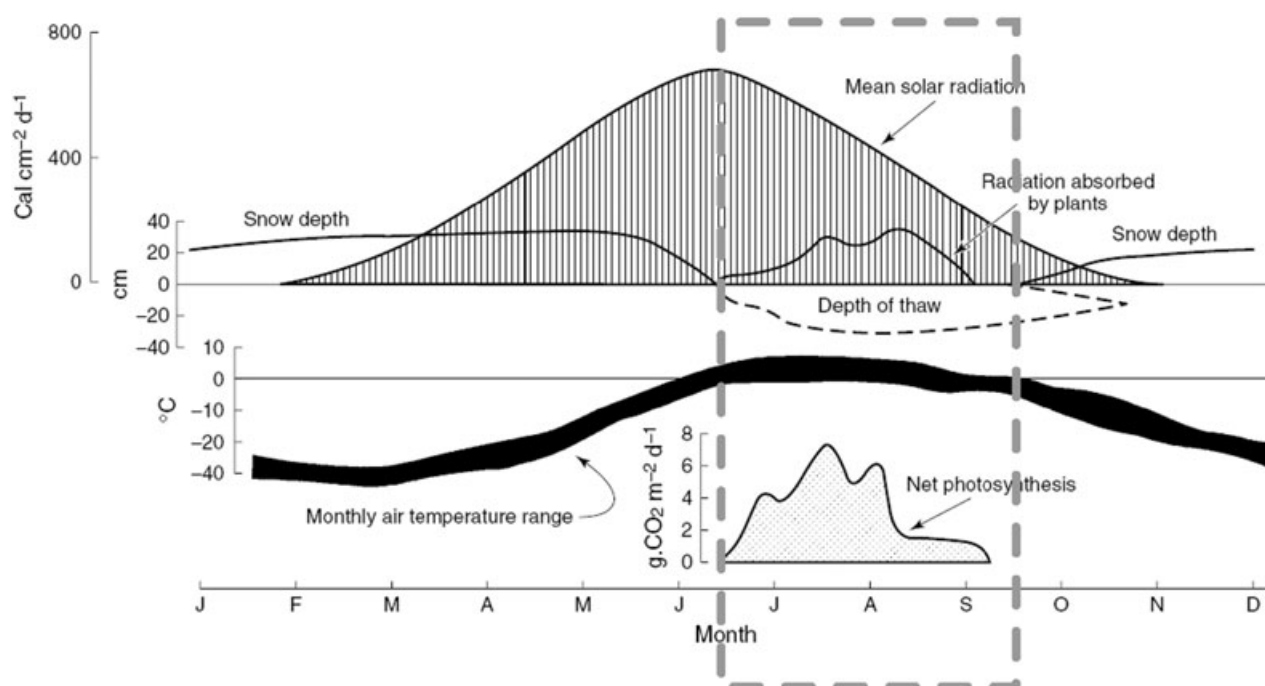
However, setting this issue aside, even in the case of climate warming it is by no means straightforward to predict the impacts on terrestrial ecosystems. In an Arctic context, landscape heterogeneity and the role of the cryosphere are potentially significant "modifiers" of the effects of warming on ecosystems. Figure 2, for example, shows the potential for earlier snowmelt in tundra regions to have a major impact on plant phenology and photosynthesis resulting from the availability of substantial fluxes of photosynthetically active radiation (PAR) around the summer solstice (when solar elevations are high). Later autumn freeze-up may also result in delayed plant senescence.

But earlier snowmelt may also have negative, or counterintuitive, consequences. In complex landscapes, where snow is redistributed from wind-exposed areas to hollows and depressions, early snowmelt may cause a reduction of habitat heterogeneity caused by the loss of snowbeds.

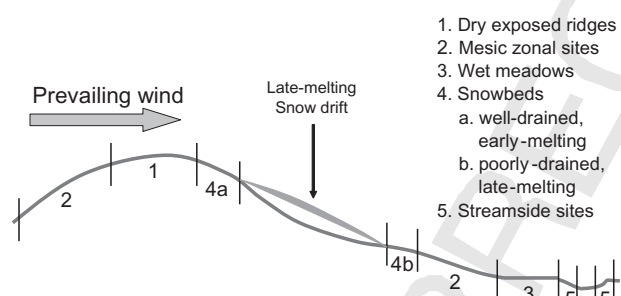
Snowbed "specialists" (e.g. the moss *Kiaeria starkei*) may not be able to survive the change in physical environmental conditions, or increased competition. Furthermore, earlier melting of snowbeds may also have negative consequences for herbivores if it means that the availability of high-quality forage (associated with new growth) is temporally "compressed" earlier into the summer; in this respect, complex landscapes, with a mosaic of vegetation communities and late-melting snowbeds, might offer newly-emerged high-quality food for herbivores throughout a growing season (Fig. 3) (Björk & Molau 2007).

The effects of experimental warming on both Arctic and alpine tundra ecosystems has been investigated by the team of scientists from ITEX (the International Tundra Experiment). This experiment was launched, in concept, in 1990, and soon after was established at 28 sites in the tundra biome. The broad geographical coverage and international participation were seen as important components of the original set-up, in recognition that plants in contrasting parts of their geographical range might respond differently to the same change in temperature (Fig. 4). Initially, ITEX focused upon the phenological and growth responses of a set of broadly circumpolar Arctic and alpine vascular plant species (see e.g. Fig. 5) to experimental warming [achieved by using small hexagonal open-topped chambers (OTCs)], designed to simulate the greenhouse effect. The OTCs generally produced a near-surface warming of around 1–3°C above the ambient temperatures for control (unwarmed) plots. After several years (up to four) of the experiment, the data from 13 of the sites was subjected to meta-analysis to test whether any generalizations could be made regarding geographical contrasts in responses to warming, as well as contrasts relating to plant functional type (e.g. deciduous vs evergreen dwarf shrubs, forbs and graminoids). This meta-analysis (Arft et al. 1999) demonstrated the sensitivity of tundra plants to warming, and identified differential responses among contrasting growth forms and among contrasting regions (High Arctic; Low Arctic; alpine). With regards to the current presentation, however, the subsequent ITEX work on community (as opposed to individual plant) responses to warming (Walker et al. 2006) provides data to suggest that some plant growth forms (specifically lichens and bryophytes) do badly in warmer conditions. This may be the result of shading by plant functional types that respond particularly vigorously to warming (e.g. deciduous dwarf shrubs such as the dwarf birch *Betula nana*), or to competition for nutrients, or to factors such as surface drying (a possible artefact of the OTCs). Diversity and evenness indices all decreased significantly with warming, and the results strongly suggest that biodiversity might decrease (at least





**Fig. 2** Schematic diagram of the annual pattern of environmental variables and net photosynthesis at Barrow, Alaska. Barrow has a climate classified as just within the High Arctic zone. The period of net photosynthesis is highlighted by the dashed box. Notice how snow cover lasts through until June, at a time when solar radiation inputs are at a peak and are soon to decline. Earlier snowmelt is likely to increase phytomass and accelerate plant reproductive phenology. Later senescence may result from later autumn freeze-up, although light may be limiting, and senescence may be triggered by changes in light quality.

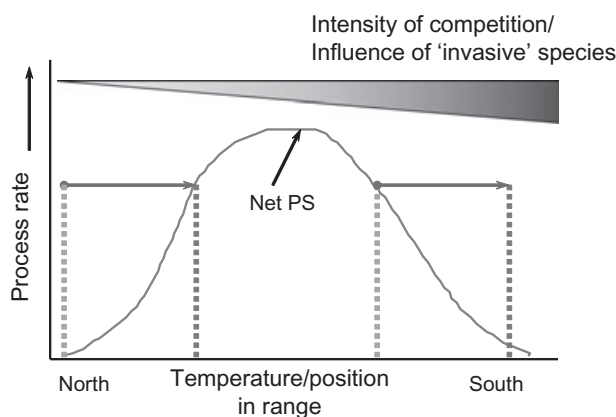


**Fig. 3** A schematic diagram showing a mesotopographic gradient for the Arctic that includes five habitats: dry, mesic (zonal), wetland, snowbed and streamside vegetation. The landscape heterogeneity here, associated with the presence of a snowbed, increases habitat diversity and thus biodiversity. Asynchronous melting of snowbeds through the thaw period maintains the availability of newly-emerged high-quality food for herbivores over space and time. Earlier thawing of snowbeds has the potential to reduce habitat diversity. Redrawn from Walker (2000).

observation that lichens are adversely affected by experimental manipulations simulating climate change impacts (including the addition of mineral nutrients to simulate more rapid decomposition processes) has also been observed by Cornelissen et al. (2001), so this result seems robust and consistent.

So, the effects of climate warming on tundra ecosystems are by no means straightforward to predict, and a criticism that has been levelled at programmes such as ITEX is that it might have placed too much weight on summer warming effects (whereas the general circulation models of the Earth's climate suggest that winter warming will be of much greater magnitude in the polar regions). Warmer winters in a cold environment might be expected to be beneficial for the biota, but again there are data from the Arctic suggesting the converse. Aanes et al. (2000) and Yoccoz & Imms (1999) have data from Svalbard showing that both Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and sibling voles (*Microtus rossiaemeridionalis*) have undergone population crashes during winters with freezing rain. This is likely to result from the formation of ice layers in the snowpack (which reindeer cannot penetrate for foraging), or the collapse of the subnivean space beneath the snowpack. Such examples are not restricted to Svalbard. Indeed in the Nordic

in the short term) in response to warming. The other notable results were that tundra plant communities exhibited detectable responses to warming over time periods of only three to four years, and the significant "winners" were the deciduous shrubs, with increases both in percentage cover and in height (Fig. 7). The



**Fig. 4** This schematic diagram illustrates the performance of a plant species [in terms of net primary productivity (NPP)] across a gradient of temperature (which could be expressed as mean temperatures over a growing season, or as some other metric of thermal energy availability, e.g. growing degree days, or in the case of tundra plants thawing degree days, representing accumulated “thermal time”). Increasing temperature in tundra ecosystems will co-vary with other abiotic factors (e.g. precipitation or depth of the active layer) and also with biotic factors, such as intensity of competition or herbivory. Intensity of competition (e.g. for light or soil nutrients) is likely to increase from the extreme polar deserts and alpine fellfields to the more closed tundras of the Low Arctic and mid to low alpine (perhaps leading to a skewed NPP curve, with values dropping more steeply at the warmer end of the distribution as a result of competition interactions). Note that, according to this scheme, a given temperature increase ( $\Delta T$ ) could produce quite different outcomes depending on where in the species’ range the warming occurs. Thus, warming at the colder end of the distribution could markedly improve plant performance, whereas towards the warmer end of the distribution increased respiratory demands, or intensity of competition, could reduce NPP to the extent that the species dies out, or is forced out, of the community.

context, milder winters with increased incidence of freezing and thawing cycles may have serious implications for summer pasture systems with perennial grasses (Fig. 8), as well as for natural ecosystems (see, for example, Robinson et al. 1998).

### The Arctic is not isolated

In contrast to the views of many people living in industrialized regions to the south, the Arctic is not isolated biologically, climatically or socio-economically. Migratory animals provide clear examples of the linkages between the Arctic and lower latitudes, and strong climatic teleconnections (e.g. between the North Atlantic Oscillation, Arctic Oscillation and the El Niño–Southern Oscillation) are evident, as are their biological consequences (e.g. Aanes et al. 2002; Post & Forchhammer 2004; Forchhammer et al. 2005). Events and policy outside the Arctic often have a clear impact within the Arctic, even if this was unintentional. The European Union FRAGILE

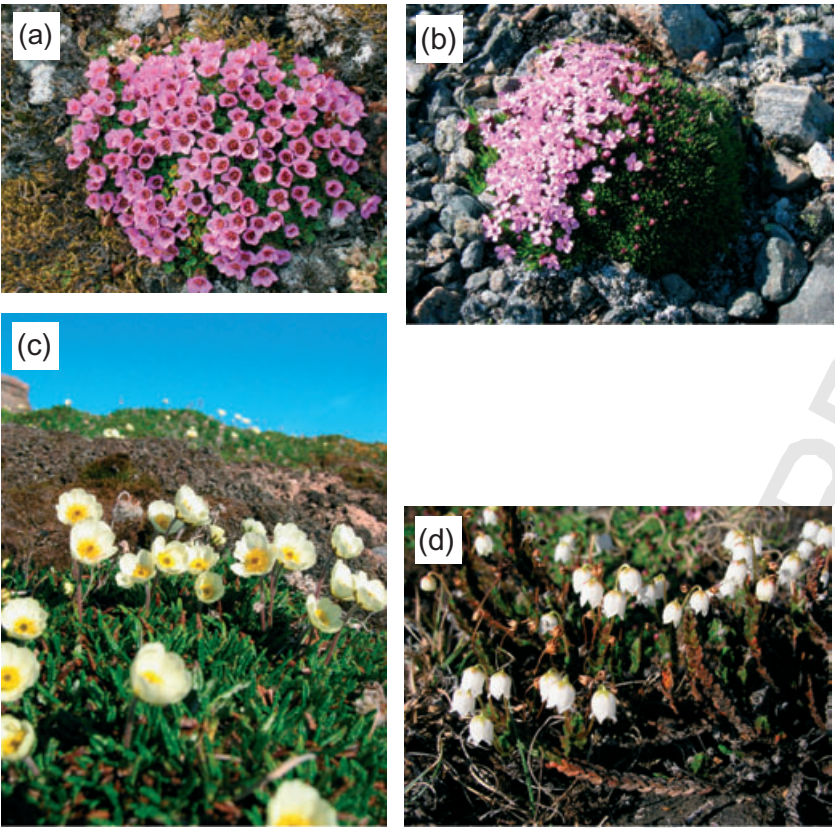
project (Fragility of Arctic goose habitat: impacts of land use, conservation, and elevated temperature) highlights this, as does the example of snow geese in North America. The numbers of several species of goose that breed in Svalbard in the summer, but that migrate to western Europe to overwinter, have increased dramatically in the last 40 years [with a 30-fold increase in barnacle geese (*Branta leucopsis*) and a fourfold increase in pink-footed geese (*Anser brachyrhynchus*)]. Changes in land use and hunting practice in the overwintering areas (both linked with socio-economic and/or political decisions) have resulted in rapid increases in winter survivorship, whereas earlier melt-out in the breeding areas may be responsible for increased breeding success (Cooper et al. 2004). Research to determine the impacts of the increased grazing intensity and climate change on the vegetation communities and ecosystem processes of the breeding areas in Svalbard is ongoing. This interplay between climate change drivers and socio-economic/political drivers of change demonstrates clearly the linkages between climate, wildlife and society, and these linkages extend across thousands of kilometres.

### Conclusions

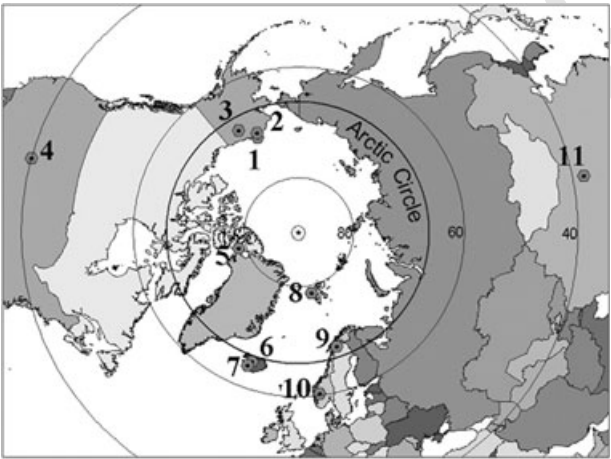
- The Arctic biota has been subject to dramatic environmental change during the last 2.5 million years, but ongoing and predicted change is rapid and very different.
- Conventional wisdom suggests that biodiversity should increase with warming in the medium to long term, but the tundra biome is increasingly “compressed” between the Boreal zone and the Arctic Ocean.
- Many species and habitats in the Arctic are potentially highly vulnerable to change.
- Rates of change are so rapid that “novel” assemblages of organisms will develop, and we know very little of how these will function, or of the possible role of “invasive” species.
- Like it or not, the Arctic and its organisms and communities are set to provide an early detection system of the impacts of environmental change on planet Earth.

### Acknowledgements

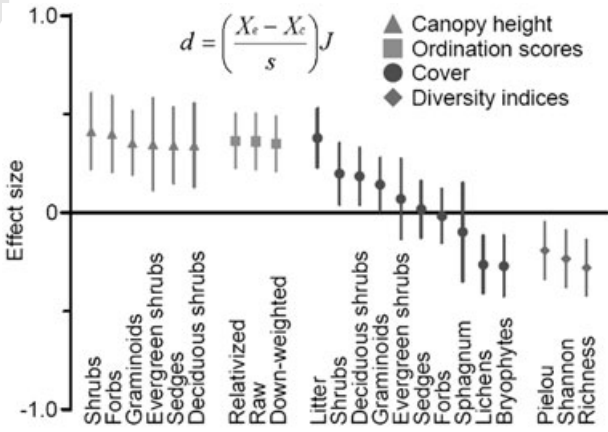
Many thanks to the Norwegian Polar Institute, the Nordic Council of Ministers and the United Nations Environment Programme for the opportunity to speak on World Environment Day. I would also like to thank my colleagues in the International Tundra Experiment (ITEX) and the Circum-Arctic Terrestrial Biodiversity Initiative (CAT-B; supported by the International Arctic Science Committee) for their insights, enthusiasm and support over the years.



**Fig. 5** Some of the vascular plant species studied as part of ITEX (Arft et al. 1999; Walker et al. 2007). (a) *Saxifraga oppositifolia* (purple saxifrage), (b) *Silene acaulis* (moss campion), (c) *Dryas octopetala* ssp. *octopetala* (mountain aven) and (d) *Cassiope tetragona* (Arctic bell heather).



**Fig. 6** ITEX sites contributing to the Walker et al. (2006) meta-analysis of plant community responses to experimental warming. (From Walker et al. 2006; reprinted with permission from the authors and Macmillan Magazines.)



**Fig. 7** Response of tundra plant community variables to experimental warming in ITEX. The symbols represent the mean effect size based on the meta-statistic “Hedges *D*” (the normalized difference between experimental and control means adjusted for sample size), and the lines give 95% confidence intervals. The effect sizes for canopy height, ordination scores and diversity indices were all considered “moderate” by meta-analysis convention. Note the general increase in height of vascular plants (triangles), the significant increases in shrubs, deciduous shrubs and litter cover, and the decreases in both lichen and bryophyte cover (circles) and diversity indices (diamonds). (From Walker et al. 2006; reprinted with permission from the authors and Macmillan Magazines.)





**Fig. 8** Environs of the Agricultural Research Institute research station near Akureyri, north Iceland, with ice-layer formation in the foreground. Damage to perennial grasses resulting from anoxia beneath the ice cover can be very severe during “mild” winters. (Photograph by permission of Bjarni E. Guðmundsson.)

## References

- Aanes R., Sæther B.-E. & Øritsland N.A. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* 23, 437–443.
- Aanes R., Sæther B.-E., Smith F.M., Cooper E.J., Wookey P.A. & Øritsland N.A. 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a High-Arctic ecosystem. *Ecology Letters* 5, 445–453.
- ACIA (Arctic Impact Climate Assessment) 2005. *Arctic Climate Impact Assessment—scientific report*. Cambridge: Cambridge University Press.
- Adams J.M. & Woodward F.I. 1992. The past as a key to the future—the use of paleoenvironmental understanding to predict the effects of man on the biosphere. *Advances in Ecological Research* 22, 257–314.
- Björk R.G. & Molau U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic and Alpine Research* 39, 34–43.
- CAFF (Conservation of Arctic Flora and Fauna) 2001. *Arctic flora and fauna: status and conservation*. Helsinki: Edita.
- Callaghan T.V., Björn L.O., Chapin F.S. III, Chernov Y., Christensen T.R., Huntley B., Ims R., Johansson M., Riedlinger D.J., Jonasson S., Matveyeva N., Oechel W., Panikov N. & Shaver G. 2005. Arctic tundra and polar desert ecosystems. In ACIA [C. Symon et al. (eds.)]: *Arctic Climate Impact Assessment—scientific report*. Pp 243–352. Cambridge: Cambridge University Press.
- Convention on biological biodiversity 1992. Accessed on the internet at <http://www.cbd.int/convention/convention.shtml> on 25 June 2007.
- Cooper E., Jónsdóttir I.S., Chaput D., Kuijper D., Loonen M., Pahud A., Sjögersten S., Ubels R., van der Wal R., Woodin D. & Huiskes A. 2004. Climate change and goose grazing on Svalbard's tundra. ACIA International Symposium on Climate Change in the Arctic. 9–12 November, Reykjavik, Iceland.
- Cornelissen J.H.C., Callaghan T.V., Alatalo J.M., Michelsen A., Graglia E., Hartley A.E., Hik D.S., Hobbie S.E., Press M.C., Robinson C.H., Henry G.H.R., Shaver G.R., Phoenix G.K., Jones D.G., Jonasson S., Chapin F.S., Molau U., Neill C., Lee J.A., Melillo J.M., Sveinbjörnsson B. & Aerts R. 2001. Global change and Arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89, 984–994.
- FAO (Food and Agriculture Organization) 2005. Ecosystem services. Accessed on the internet at [http://www.fao.org/ag/wfe2005/glossary\\_en.htm](http://www.fao.org/ag/wfe2005/glossary_en.htm) on 25 June 2007.
- Forchhammer M.C., Post E., Berg T.B.G., Høye T.T. & Schmidt N.M. 2005. Local-scale and short-term herbivore–plant spatial dynamics reflect influences of large-scale climate. *Ecology* 86, 2644–2651.
- Post E. & Forchhammer M.C. 2004. Spatial synchrony of local populations has increased in association with the recent Northern Hemisphere climate trend. *Proceedings of the National Academy of Sciences (PNAS)* 101, 9286–9290.
- Robinson C.H., Wookey P.A., Lee J.A., Callaghan T.V. & Press M.C. 1998. Plant community responses to simulated environmental change at a High Arctic polar semi-desert. *Ecology* 79, 856–866.
- Sturm M., Racine C. & Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature* 411, 546–547.
- Swift M.J., Heal O.W. & Anderson J.M. 1979. *Decomposition in terrestrial ecosystems*. Oxford: Blackwell Scientific Publications.
- Torsvik V.L., Øvreås L. & Frede Thingstad T. 2002. Prokaryotic diversity—magnitude, dynamics and controlling factors. *Science* 296, 1064–1066.
- Walker D.A. 2000. Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* 6, 19–34.
- Walker D.A., Epstein H.E., Jia G.J., Balser A., Copass C., Edwards E.J., Gould W.A., Hollingsworth J., Knudson J., Maier H.A., Moody A. & Reynolds M.K. 2003. Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research, Atmospheres* 108 (D2), Art. No. 8169.
- Walker M.D., Wahren C.H., Hollister R.D., Henry G.H.R., Ahlquist L.E., Alatalo J.M., Bret-Harte M.S., Calef M.P., Callaghan T.V., Carroll A.B., Epstein H.E., Jónsdóttir I.S., Klein J.A., Magnússon B., Molau U., Oberbauer S.F., Rewa S.P., Robinson C.H., Shaver G.R., Suding K.N., Thompson C.C., Tolvanen A., Totland Ø., Turner P.L., Tweedie C.E., Webber P.J. & Wookey P.A. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences (PNAS)* 103, 1342–1346.
- Yoccoz N.G. & Imms R.A. 1999. Demography of small mammals in cold regions: the importance of environmental variability. In A. Hofgaard et al. (eds.) : *Animal responses to global change in the North*. *Ecological Bulletin* 47, 137–144.

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<i>Instruction to printer</i>	<i>Textual mark</i>	<i>Marginal mark</i>
Leave unchanged	... under matter to remain	Ⓟ
Insert in text the matter indicated in the margin	⧵	New matter followed by ⧵ or ⧵ <sup>Ⓢ</sup>
Delete	/ through single character, rule or underline or ⎯⎯⎯ through all characters to be deleted	⧻ or ⧻ <sup>Ⓢ</sup>
Substitute character or substitute part of one or more word(s)	/ through letter or ⎯⎯⎯ through characters	new character / or new characters /
Change to italics	— under matter to be changed	↵
Change to capitals	≡ under matter to be changed	≡
Change to small capitals	≡ under matter to be changed	≡
Change to bold type	~ under matter to be changed	~
Change to bold italic	≈ under matter to be changed	≈
Change to lower case	Encircle matter to be changed	≡
Change italic to upright type	(As above)	⧻
Change bold to non-bold type	(As above)	⧻
Insert 'superior' character	/ through character or ⧵ where required	Y or Y under character e.g. Y or Y
Insert 'inferior' character	(As above)	⧵ over character e.g. ⧵
Insert full stop	(As above)	⊙
Insert comma	(As above)	,
Insert single quotation marks	(As above)	Y or Y and/or Y or Y
Insert double quotation marks	(As above)	Y or Y and/or Y or Y
Insert hyphen	(As above)	⎯
Start new paragraph	┐	┐
No new paragraph	┐	┐
Transpose	┐	┐
Close up	linking ○ characters	○
Insert or substitute space between characters or words	/ through character or ⧵ where required	Y
Reduce space between characters or words		↑