

TERRESTRIAL ECOSYSTEMS ON SVALBARD: HETEROGENEITY, COMPLEXITY AND FRAGILITY FROM AN ARCTIC ISLAND PERSPECTIVE

Ingibjörg S. Jónsdóttir

ABSTRACT

Svalbard is an archipelago at the north-western edge of the Barents Sea. Despite its extreme northerly position, the climate is relatively mild in the western part of the archipelago. This is due to the warm North Atlantic Current reaching Spitsbergen, the largest island, causing temperatures there to frequently fluctuate around freezing, even in winter. Svalbard ecosystems share some attributes typical of islands. However, in spite of the limited land area there is large heterogeneity among ecosystems on different spatial scales: three out of five Arctic bioclimatic subzones occur in the archipelago, stretching from extremely low productive polar deserts to relatively productive tundra. Plant community data presented in this paper demonstrate that plant communities in mesic (zonal) habitats are well differentiated among the different bioclimatic subzones. Within a subzone, strong community differentiation occurs between mesic and ridge habitats in the two warmest zones, but not in the coldest, the polar desert. Relative to 'mainlands', species diversity is low on Svalbard and terrestrial food webs are simple, with strong links to marine food webs. However, fully accounting for the invertebrate components of the food webs reveals a considerable complexity that may contribute to ecosystem robustness. Fragility of the terrestrial ecosystems on Svalbard is discussed in terms of island characteristics. It is concluded that these ecosystems are robust in terms of temporal variation in herbivore populations and climate, but are fragile in terms of human disturbance. Their fragility in terms of climate change is still an open question that needs more thorough evaluation.

I.S. Jónsdóttir
(e-mail: isj@unis.no),
University Centre in
Svalbard, UNIS, P.O.
Box 156, 9171
Longyearbyen,
Norway.

INTRODUCTION

Svalbard is an archipelago situated in the High Arctic at the north-western edge of the Barents Sea at 74–81°N and 10–30°E (Fig. 1). Its total land area is roughly 60,000km², of which 60% is presently covered by glaciers. In spite of this extreme northerly position, Svalbard shares some features common to the Atlantic islands. First of all, the climate over parts of the archipelago is relatively oceanic. The warm North Atlantic Current reaches the west coast of Spitsbergen, the largest island, resulting in a relatively mild climate in the western and central parts of the archipelago (Fig. 2), while cold Barents Sea waters impact on the east coast and the southernmost tip of Spitsbergen. A second island feature is the interaction between marine and terrestrial ecosystems, given the proportionally large coastal area. A third feature is that the terrestrial flora and fauna of Svalbard lack some elements that are common on Arctic 'mainlands'. As a consequence, although terrestrial ecosystems on Svalbard are in many ways typical of the High Arctic, they are composed of biological communities that are unique to Svalbard.

The Arctic is by definition a treeless landscape that is often referred to as one entity composed of tundra ecosystems that are simple and fragile due to the harsh climate and low energy budget. In reality, the Arctic spans more than a three-fold difference in growing season length and a ten-fold difference in mean July temperatures—a heterogeneity that has long been recognised by people living, working or travelling in the Arctic. Furthermore, the simplicity of Arctic ecosystems in general, and Svalbard ecosystems in particular, has recently been questioned after fully accounting for the invertebrate component of Arctic food webs (Hodkinson and Coulson 2004). Finally, Arctic ecosystems often experience extreme variability in climate and other conditions on different time scales (among years, seasons, days), especially those on islands with oceanic climates where freeze–thaw cycles are frequent (Fig. 2). Because of this, they should be regarded as rather robust in some aspects at least. Therefore, it is necessary to specify more carefully in which sense Arctic ecosystems are fragile and if ecosystem robustness versus fragility is different on islands compared to the 'mainland'.

I will begin this paper with a brief account of the terrestrial ecosystems on Svalbard, emphasising their heterogeneity and complexity. I will then address the sense in which ecosystems on Svalbard can be regarded as fragile and examine the extent to which fragility can be related to the island characteristics of the archipelago.

HETEROGENEITY AMONG SVALBARD ECOSYSTEMS

REGIONAL HETEROGENEITY

On a large, geographic scale, the heterogeneity of Arctic ecosystems can be described in relation to climatic and vegetation characteristics. There have been different schools of thought about how to further divide the Arctic bioclimatic zone into subzones, but recently a consensus was reached where five subzones were recognised, being A–E, with A the coldest and E the warmest subzones (referred to as ‘zones’ hereafter). This subdivision provided a framework for both the Pan Arctic Flora Project (Elvebakk *et al.* 1999) and the Circumpolar Arctic Vegetation Mapping project (CAVM Team 2003) and this framework will also be applied in this paper. In spite of the comparatively limited land area of the Svalbard archipelago, it encompasses the three coldest zones: A, B and C. Elvebakk (1997) termed them for Svalbard as Arctic polar desert, northern Arctic tundra and middle Arctic tundra. The strong influence of the warm ocean currents on the terrestrial ecosystems is obvious from the irregular shift between the different zones (Fig. 1). Habitats in the landscape that are intermediate in terms of snow cover in winter and active layer depth and soil moisture in summer reflect the general climatic conditions and can be referred to as zonal (Elvebakk 1999; CAVM Team 2003). On Svalbard, the vegetation cover and soil organic matter in zonal habitats are greatest in zone C, the middle Arctic tundra, and are lowest in zone A, the polar desert (Table 1).

Almost the whole of Svalbard was covered by ice during the last ice age, which left a landscape with, in principle, no soil or vegetation as the glaciers retreated (Hjelle 1993; Brochmann *et al.* 2003). It takes a long time for soils to develop in Arctic climates, and today a range of different rocks are still exposed on Svalbard, which adds considerably to the heterogeneity among terrestrial ecosystems. Bedrock type may affect both drainage and soil chemistry, and consequently plant nutrient availability and the decomposition rate of dead organic matter. The potential effect of bedrock on plant communities was demonstrated in a survey of pH preferences of

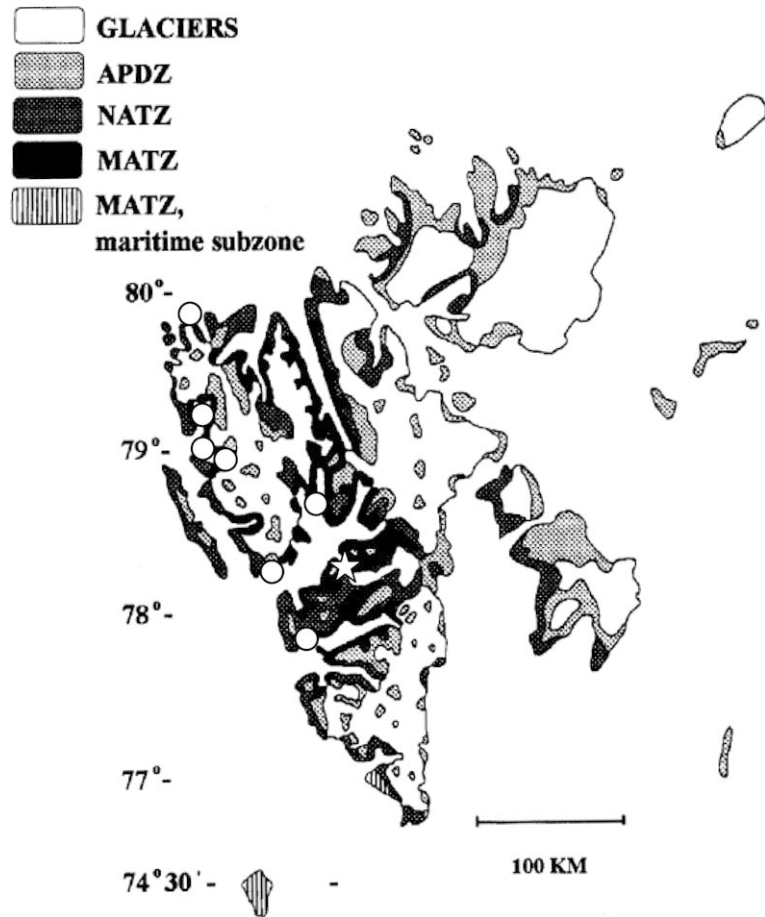


Fig. 1—The bioclimatic subzones of Svalbard. APDZ (Arctic polar desert)=subzone A; NATZ (northern Arctic tundra)=subzone B; MATZ (middle Arctic tundra)=subzone C. The star indicates the location of Svalbard Airport, Longyearbyen, the circles indicate the locations of the sites for the plant community study presented in Fig. 3. Reproduced from Elvebakk (1997) with permission from Elsevier.

eighty species of vascular plants and cryptogams on fourteen different rock substrata on Svalbard (Elvebakk 1982). Accordingly, pH was found to have a strong effect in studies on plant community differentiation and diversity on Svalbard (Jónsdóttir 2002). A similar dominating effect of pH on species diversity has been demonstrated for Low-Arctic plant communities in Alaska (Gough *et al.* 2000).

LANDSCAPE HETEROGENEITY

On a landscape scale, a mosaic of different ecosystems develops in response to sharp environmental gradients, often over short distances, created by variations in topography and uneven snow distribution in winter. Snow is blown off ridges and accumulated in depressions, leaving the ridges exposed to extreme temperatures and strong desiccating winds, but providing protection from

TERRESTRIAL ECOSYSTEMS ON SVALBARD

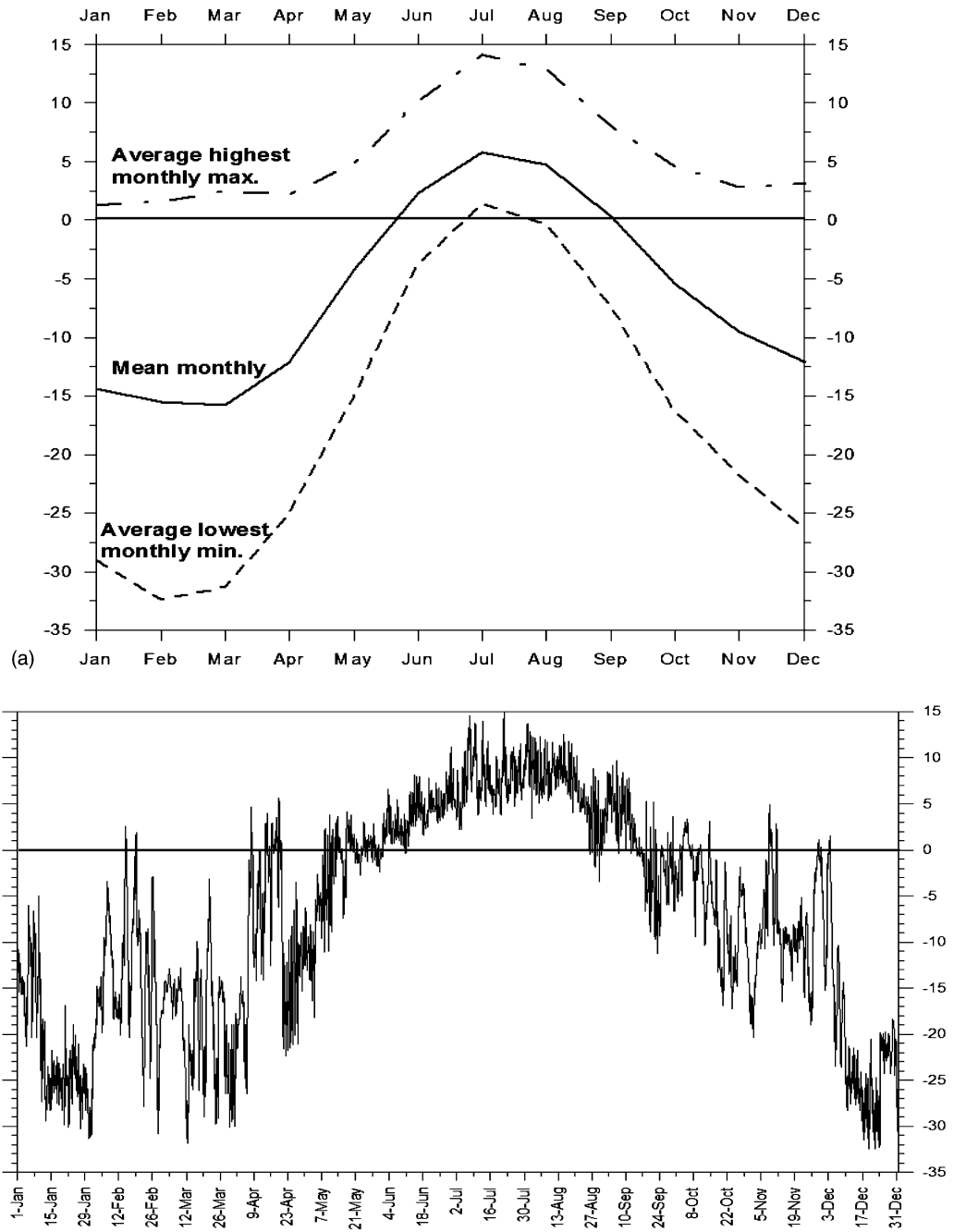


Fig. 2— Air temperature on Svalbard within bioclimatic subzone C, the middle Arctic tundra. a) Annual and monthly variation indicated by monthly mean temperatures (1912–1996) and average lowest and highest monthly means (1976–1996) at Svalbard Airport, Longyearbyen, (based on Førland *et al.* 1997) showing that the difference between the highest and lowest monthly mean in December–March is about 25°C; b) Daily variation in air temperatures in 2002–2003 in Adventdalen, c. 10km east of Longyearbyen showing frequent freeze–thaw cycles in autumn, winter and spring (from Christiansen 2005).

adverse winter weather in hollows and depressions. Unevenly distributed snow also strongly affects conditions during the growing season. There may be more than one-month difference in the onset of the growing season between ridges and adjacent late-melting snow beds, a considerable difference in relation to the already short summer seasons on

Svalbard. The depth of the active layer (the proportion of the soil that thaws on top of the permafrost) and soil temperatures in summer are greater on ridges than in other habitats due to the early onset of the season and scarce vegetation cover, consisting mainly of scattered rosette or cushion-forming plants in association with

cryptogams. Soils contain little organic matter and are well drained, frequently causing severe water deficits in summer. In contrast to the ridge habitats, soil moisture is much greater in the zonal habitat and other less exposed habitats (due to melt of snowdrifts and run-offs) and the vegetation cover is more extensive, and soil organic matter content higher. In snow beds, where the snow melts very late, plant community types and vegetation cover vary depending on how much the growing season is reduced on average. Wetlands develop in areas where there is continuous water seepage, such as below snow beds or where the water table is high throughout the season due to a shallow active layer on top of the permafrost. The vegetation cover in wetlands is usually complete and dominated by mosses and graminoids.

Other environmental gradients come into play close to the coast. Salinity gradients become apparent in sheltered seashores and river deltas where salt marshes may develop. Where suitable habitats for breeding seabird colonies occur, usually in steep cliffs and talus slopes, sharp nutrient gradients develop below due to bird manuring. The enhanced nutrient availability greatly affects plant community composition and increases productivity and soil organic matter. These 'hot spots', created by biotic agents (the seabirds) can be regarded as natural experiments demonstrating how limiting nutrients are for biological production in Arctic terrestrial ecosystems.

Other biotic agents, such as herbivores, can also influence ecosystem heterogeneity in the tundra,

and different herbivore types will have different impacts with effects that vary temporally and spatially (Jefferies *et al.* 1994). This issue will be addressed in the section on ecosystem fragility.

CASE STUDY: PLANT COMMUNITY
DIFFERENTIATION WITHIN AND ACROSS
ZONES

The degree of plant community differentiation between exposed ridge and zonal habitats within seven different localities on Svalbard (Fig. 1), representing three bioclimatic zones, was analysed during the second week in July 2003 by using the point intercept method. At each locality, six 50cm × 50cm plots were randomly placed in each habitat and all vascular and cryptogam plant species that were hit by 25 evenly distributed points across each plot were recorded. By using the software PC-ORD, the community data were ordinated by a Detrended Correspondence Analysis (McCune and Mefford 1999). Within zone B and C, plant communities were well differentiated between ridge and zonal habitats along the first two axes, but not within zone A (Fig. 3). While the plant communities of zonal habitats were well differentiated across the three bioclimatic zones, the ridge communities of all zones were much more similar to each other. Interestingly, the ridge communities of zones A and B showed similarity to the zonal community of the polar desert (zone A). This reflects the fact that microclimatic conditions in ridge habitats of the different zones resemble the conditions in the polar desert zone.

Table 1—Characteristics of the bioclimatic subzones on Svalbard. Based on Elvebakk (1999) and Jónsdóttir (pers. obs.).

Subzone	Zonal vegetation	Character species	Mean July temperature (°C)	Length of the growing season (months)	Soil organic content in zonal habitats (% loss on ignition)*
A Polar deserts	Scattered rosette herbs and cryptogams Vegetation cover 2–10%	<i>Papaver dahlianum</i> , <i>Saxifraga</i> spp, <i>Draba</i> spp	1–2.5	1–1.5	0–5
B Northern Arctic tundra	Prostrate dwarf shrubs and cryptogams Vegetation cover > 50%	<i>Salix polaris</i> , prostrate forms of <i>Saxifraga oppositifolia</i>	2.5–4	1.5–2.5	5–25
C Middle Arctic tundra	Erect dwarf shrubs, unless too alkaline	<i>Cassiope tetragona</i> dominates on acidic to neutral substrates <i>Dryas octopetala</i> more abundant on alkaline substrate	4–6	2.5–3	10–30

*Jónsdóttir, unpublished data.

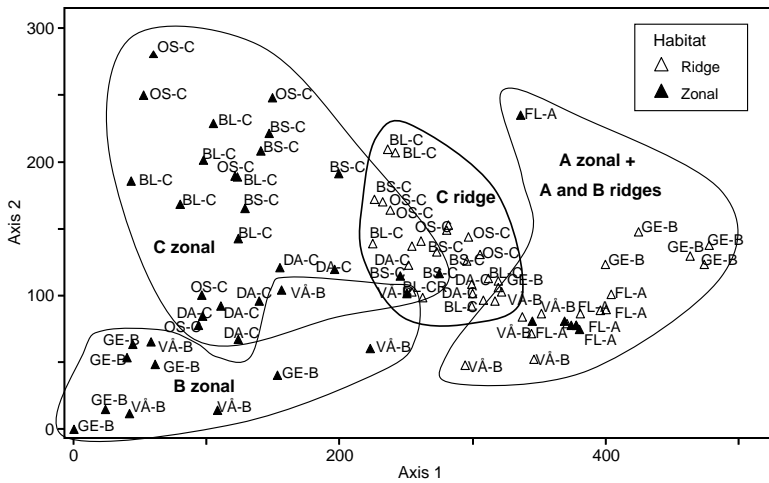


Fig. 3—Ordination of zonal and ridge plant communities along the first two ordination axes in a Detrended Correspondence Analysis. The first two letters of plot labels denote location name (OS = Ossian Sars; BL = Blomesletta; DA = Daudmannsøyra; BS = Blomstrandshalvøya; GE = Generalfjella; VÅ = Vårsolbukta; FL = Flathuken). The third letter denotes the bioclimatic zone for that location. Filled symbol: zonal habitat, open symbol: ridge habitat. The total variance ('inertia') of the species data = 7.315; the eigenvalue of axis 1 = 0.686; the eigenvalue of axis 2 = 0.362.

FLOW OF ENERGY AND MATTER

The ultimate aim of ecosystem studies is to understand how ecosystem processes affect the flow of energy and matter. Tundra soils have been functioning as a carbon sink for thousands of years due to slow decomposition rates, thereby accumulating large amounts of organic matter (Oechel and Billings 1992). Present-day carbon balances have been widely studied in low Arctic regions where vegetation cover is more extensive and soil organic matter is higher than in Svalbard. These studies indicate a potential switch in tundra soils in response to climate warming from carbon sinks to carbon source (Oechel *et al.* 2000).

So far, there are only a few studies on carbon balances on Svalbard. Wüthrich *et al.* (1999) measured CO_2 fluxes in different plant communities within a watershed on the west coast of Spitsbergen (zone B) in the early to mid-summer season during the rainy summer of 1996. They found great differences between communities, and the CO_2 balance was negative (i.e. net loss of carbon) in almost all of them, even during daytime, except for a *Racomitrium lanuginosum* moss community that covered only 0.6% of the area. Calculations of CO_2 fluxes for the whole catchment showed a negative carbon balance of $-0.58 \text{ g C m}^{-2} \text{ d}^{-1}$. Lloyd (2001) found that a semi-polar desert in Ny-Ålesund (=ridge community in zone B–C) was an overall sink for carbon in 1995 and a carbon source in 1996. Such a

temporal carbon imbalance is probably frequent in Svalbard ecosystems due to temporal variations in radiation. The long-term effects on the ecosystem carbon stocks may depend on whether they are counterbalanced in years with higher radiation. These two studies demonstrate the importance of ecosystem types and annual variation, and indicate how delicate the long-term carbon balance on Svalbard might be (Wüthrich *et al.* 1999; Lloyd 2001). Studies from other High Arctic areas of more continental climates than on Svalbard indicate an overall positive carbon balance across different vegetation types (Christensen *et al.* 2000; Welker *et al.* 2004) and that a warmer climate may increase net ecosystem exchange of CO_2 especially in dry and mesic tundra (Welker *et al.* 2004).

The majority of nitrogen and other plant nutrients in tundra ecosystems are stored in soil organic matter, and nutrient release primarily depends on soil processes, although above-ground herbivores may also have significant impact in some areas. The input of nitrogen through biological nitrogen fixation is generally low in comparison with other biomes, but of considerable significance in these nutrient-limited ecosystems. Nitrogen input to tundra ecosystems both on Svalbard and elsewhere through N-fixation by cyanobacteria, either free-living or in loose symbiosis with vascular plants, varies greatly depending on habitat (Chapin and Bledsoe 1992; Zielke *et al.* 2002). To understand the variation in the flow of C and N in Arctic ecosystems it is necessary to account for the organisms involved in the different ecosystem compartments as well as their interactions. In other words, such an understanding calls for a detailed knowledge of food webs.

COMPLEXITY OF SVALBARD ECOSYSTEMS

Arctic ecosystems are less diverse in terms of species number than ecosystems of other biomes and, based on this low diversity, they are assumed to be simple. In recent years it has frequently been suggested that the low species diversity may be compensated for by high intra-specific diversity, i.e. either high genetic diversity within populations or high degree of ecotype differentiation (e.g., Crawford 1997; Wookey 2002), but there are as yet too few studies available for this to be confirmed generally. Furthermore, it has been suggested that high genetic diversity within individuals of many Arctic plants, i.e. high polyploidy levels, might compensate for low species diversity and thus buffer against environmental change (Brochmann *et al.* 2004), but the functional significance of such

intra-individual genetic variation remains to be evaluated.

Although the vascular plant flora of Svalbard is small, the cryptogam flora (including bryophytes, fungi and lichens) consists of a comparatively high number of species for a High Arctic region (Table 2). In contrast, the terrestrial fauna of Svalbard, especially the vertebrate fauna, is smaller than in many other Arctic regions covering the same bioclimatic zones. This is most likely an effect of the geographic isolation of the archipelago (Table 2). However, comparisons of the diversity of different regional floras and faunas are complicated by their sensitivity to the size of the regions and the variable cover of glaciers.

Some flora and fauna elements that are widespread and common elsewhere in the Arctic are absent on Svalbard or only found on a few isolated localities; as for instance the rhizomatous sedges *Carex stans* and species belonging to the *C. bigelowii* complex often dominant in plant communities in mesic to wet habitats in Arctic tundra. Likewise, the Arctic willow (*Salix arctica*), a prostrate deciduous shrub, common in mesic to dry habitats in the circumpolar High Arctic, is replaced by the much smaller *Salix polaris* on Svalbard. Both the rhizomatous sedges and the Arctic willow are important forage plants for a range of herbivores, especially lemmings, that are a missing faunal element on Svalbard. Lemmings, with their highly cyclic populations (3–4 year cycles), are assumed to be keystone species in Arctic tundra ecosystems, forcing other animal populations and even plants into cyclicity (Danell *et al.* 1999; Turchin *et al.* 2000). On Svalbard, however, there are no lemmings and observed population fluctuations in plants and animals are thus more likely to be directly related to climatic fluctuations than in regions where lemmings are present. Furthermore, the absence of lemmings is the most likely explanation for the small number of predatory bird species on Svalbard. Species that specialise in small rodents to a variable degree, such as the snowy owl (*Nyctea scandiaca*) and different species of raptors (Wiklund *et al.* 1999), are either totally absent or, like the long-tailed skua (*Stercorarius longicaudus*) and the pomarine skua (*Stercorarius pomarinus*), present in only small numbers.

NOT SO SIMPLE AFTER ALL?

Because some key floral and faunal elements are missing, Svalbard ecosystems are expected to be even simpler than in other Arctic regions (Summerhayes and Elton 1923). When viewing the part of the terrestrial summer food web for Svalbard that only involves vertebrate consumers, it indeed looks simple: three trophic levels with low

diversity of both herbivores and predators (Fig. 4). Since many of the species are migratory (waders, snow bunting, geese), the winter food web is even simpler. However, the vertebrate-based food web is tightly linked with a much more complex invertebrate- and microbial-based food web, involving several trophic levels (Hodkinson and Coulson 2004) in spite of the relatively impoverished invertebrate fauna (Table 2). The most diverse part of the invertebrate-based food web includes the soil-dwelling fauna, such as nematodes, enchytraeids, collembolans and mites. The significance of these organism groups is inevitable: their interactions with plants and micro-organisms play an important role in the most rate-limiting processes in cold terrestrial ecosystems, i.e. the decomposition and mineralisation of organic matter and, consequently, the ecosystem flow of C and N (Bardgett *et al.* 2002).

Terrestrial and limnic invertebrates are an important food source for the omnivorous snow bunting (*Plectrophenax nivalis*), as well as for the waders breeding on the tundra. Another link between the vertebrate and invertebrate food webs is through parasites. For instance, the Svalbard reindeer does not have any true predators, but recent studies of the Svalbard reindeer suggest that parasitic nematodes have a strong impact on reindeer populations (Albon *et al.* 2002) and in that respect they function as predators. In summary, when the

Table 2—Number of species in different organism groups recorded in terrestrial and freshwater ecosystems of Svalbard.

Organism group	Number of species
Flora ^a	
Vascular plant species	173
Bryophytes	373
Lichens	597
Algae and cyanobacteria	766
Fungi	566
Fauna ^b	
Invertebrates	937 ^c
Birds (breeding)	33 ^d
Mammals	3 ^e

a: Elvebakk and Prestrud 1996.

b: Prestrud *et al.* 2004.

c: Includes some accidental migrants.

d: Of these, 13 species are true seabirds, only affecting terrestrial ecosystems indirectly through manuring at their breeding sites.

e: Includes the polar bear, a predominantly marine mammal, but occasionally an efficient egg predator.

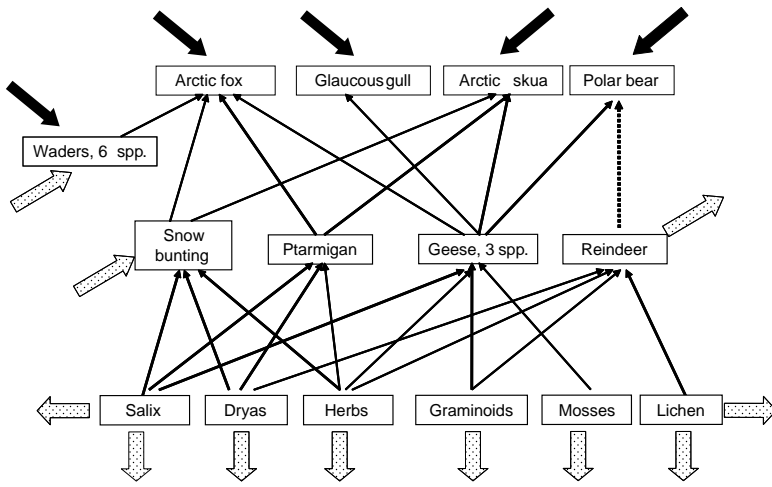


Fig. 4— Vertebrate-based food web on Svalbard. Dotted arrows indicate entries to or from the invertebrate-based food web. Black arrows indicate entries from the marine food web. *Salix* is predominately represented by *S. polaris* and *Dryas* by *D. octopetala*, while several species are included in each of the plant groups Herbs, Graminoids, Mosses and Lichens.

invertebrates are fully accounted for, a surprisingly high level of complexity is revealed in Arctic food webs, even within the island ecosystems of Svalbard (Hodkinson and Coulson 2004).

THE MARINE LINK

Typically, in most islands there are strong links between terrestrial and marine ecosystems and in this respect Svalbard is no exception (Fig. 4). Waders, feeding on both terrestrial and marine invertebrates, are prey for terrestrial predators, such as the Arctic fox (*Alopex lagopus*). The Arctic fox also preys on seabirds, and these make up an important proportion of its diet on Svalbard, especially in coastal populations (Prestrud 1993). The diet of the glaucous gull (*Larus hyperboreus*) and the Arctic skua (*Stercorarius parasiticus*) is mainly of marine origin, even though they are efficient predators on goose eggs and chicks (especially the glaucous gull) (Mehlum 1989). The same can be said about the polar bear (*Ursus maritimus*), a frequent and significant nest predator for geese and other birds (Clausen *et al.* 1999).

It is reasonable to suspect that Arctic terrestrial food web-links to marine ecosystems become stronger in the absence of lemmings, a key food item to many predators. Accordingly, the link between terrestrial and marine food webs is probably stronger on Svalbard than in other Arctic island ecosystems, such as those in the Canadian archipelago, where both lemmings and lemming predators are present, even on the most barren islands (Krebs *et al.* 2003).

FRAGILITY OF SVALBARD ECOSYSTEMS

It is frequently claimed in official policy documents for conservation and management that Arctic ecosystems are fragile due to their simplicity, extreme physical environment and low productivity, implying vulnerability to disturbance or change in the environment. Arctic organisms have adapted to the extreme temporal variation both in terms of seasonality and annual variation in the physical environment. For instance, many plants and animals have an extended life history (longevity) that increases the probability of successful breeding in favourable years. Such adaptations may increase ecosystem robustness to environmental changes, but may also increase fragility in terms of disturbance. Potential ecosystem threats are various mechanical disturbances, overgrazing and climate change.

DISTURBANCES

Mechanical disturbance may indeed change the character of the ecosystems and even damage them, depending on its severity and extent. Natural disturbances such as cryoturbation, solifluction, rock- and landslides and sedimentation by dust storms and flooding, all of which are frequent events in High Arctic areas with sparse vegetation cover, have a significant impact on ecosystem dynamics, but only occasionally do they reach such intensities as to cause damage to ecosystems over a larger area (Crawford 1997). In contrast, human disturbances of various kinds may have damaging effects on Arctic ecosystems. Even a relatively mild disturbance, such as vehicle tracks, can potentially be visible in the tundra for tens or even hundreds of years. This is because of the slow re-colonisation and growth rates of the aboveground organisms, the plants, and the changes in the delicate soil structure caused by the tracks, with severe consequences for soil organisms and soil processes (Forbes *et al.* 1999). If we do not accept human disturbance as part of the natural physical environment, such disturbance must be regarded as damage. The relationship between recovery rate to an original state (resilience) and ecosystem complexity is still debated. Accordingly, the vulnerability of the relatively simple island ecosystems on Svalbard is not fully explored.

HERBIVORY

As in other biomes, herbivore impact on tundra ecosystems depends on the frequency and intensity of grazing, but we might expect a lower threshold for damage by overgrazing in the Arctic (i.e. more fragile ecosystems) than elsewhere. Populations of various vertebrate herbivores fluctuate greatly from

year to year, causing temporal variation in grazing pressure. In addition to grazing, herbivores also affect the ecosystem through activities such as manuring and trampling. However, ecosystem damage by overgrazing is a rare phenomenon in the Arctic, indicating that Arctic ecosystems are not fragile in this respect, but robust to temporal variation in herbivore populations (Jefferies *et al.* 1994).

On Svalbard, reindeer populations fluctuate irregularly in response to climate (Solberg *et al.* 2001). The animals roam over relatively large distances in the landscape and consume only a small proportion of the primary production at each spot, although some vegetation types are favoured over others. Their impact on the ecosystem is probably greatest through trampling (Cooper *et al.* 2001) and manuring (van der Wal *et al.* 2004) leading to structural changes in both soil and plant communities. Foraging by migratory geese is more concentrated in time and space and their impact through grazing, trampling and manuring is thus much greater than by reindeer at a single spot. The non-migratory Svalbard ptarmigan (*Lagopus mutus hyperboreus*) is spread in space and probably has only a low ecosystem impact.

Even though there are not any studies available that fully assess the impact of invertebrate herbivores on tundra vegetation, it is generally believed to be low and true outbreaks (i.e. sudden population increases) are rare (Jefferies *et al.* 1994). On Svalbard the herbivore invertebrate fauna is small. The largest and most conspicuous insect herbivore in the Arctic, the woolly-bear caterpillar (*Gynaephora groenlandica*), is absent, and other moth species are most likely only sporadic migrants. In some areas where conditions are favourable, herbivorous invertebrates may occasionally rise to considerable densities, as was demonstrated in warming experiments at two different localities on Svalbard. Populations of the aphid *Acyrtosyphon svalbardicum*, endemic to Svalbard and monophagous on the mountain avens (*Dryas octopetala*), increased in response to warming by 1–3°C in the first season both in Ny-Ålesund (Strathdee *et al.* 1995) and Endalen close to Longyearbyen (Dollery *et al.*, in press). Only at one of these localities, Endalen, did the experiment continue over more than one season and in contrast with the initial response, the number of aphids was significantly lower in the warmed plots than the controls in the second season of warming (Dollery *et al.*, in press). In the second season mites that prey on aphids were at larger numbers in the warmed plots than the controls indicating a possible top-down suppression of the aphid population under warming (Fig. 5). These results suggest that the High Arctic island food web on Svalbard is complex enough to mitigate a sudden

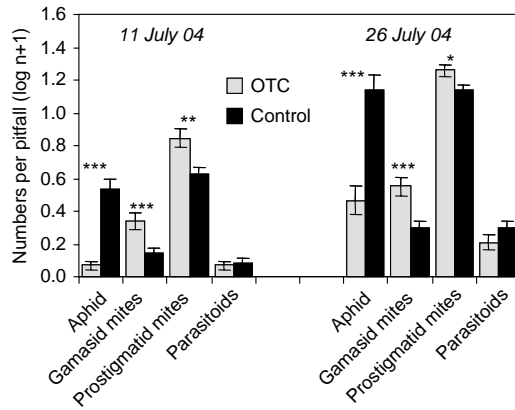


Fig. 5—The effect of two seasons of experimental warming on the abundance of the aphid *Acyrtosyphon svalbardicum*, two predatory mite species and a parasitoid in a *Dryas* heath in bioclimatic subzone C on Svalbard (number per pitfall trap \pm SE). OTC = open top chambers. Significant differences: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Reproduced from Dollery *et al.* (in press.) with permission from Ecography.

increase in herbivorous insects when 'favourable' conditions arise, thus preventing outbreaks.

The few examples of overgrazing and subsequent habitat destruction in tundra ecosystems are usually directly or indirectly linked with human interference (Jefferies *et al.* 1994). The introduction of a few caribou (*Rangifer tarandus*) to St Mathew Island in the Bering Sea led to an exponential population increase and subsequent destruction of the lichen vegetation and soil exposure (Klein 1987). A similar example of overgrazing is documented from Svalbard where fifteen Svalbard reindeer (*Rangifer tarandus platyrhynchus*) were experimentally introduced to an area previously not accessible to them (Aanes *et al.* 2000). Here also the population increased exponentially, destroying extensive lichen communities that were replaced by barren areas.

Another example of the severe consequences of human interference was seen in salt marshes along the coasts of Hudson Bay, the breeding grounds of the lesser snow goose (*Chencaerulescens caerulescens*) in low Arctic Canada. The goose populations have increased dramatically during the last few decades in response to changes in conservation measures and land use in the over-wintering areas, causing overgrazing in the salt marshes and ecosystem damage (Jefferies *et al.* 2004). Although goose populations breeding on Svalbard have showed a similar increase to those in Canada, especially the barnacle goose (*Branta leucopsis*) and the pink-footed goose (*Anser brachyrhynchus*), (Owen and Black 1999; Madsen *et al.* 1999) there are still no signs of over-exploitation or ecosystem degradation on Svalbard. There may be several reasons: species-specific foraging

differences between Svalbard breeding geese and Canadian geese; habitat shifts throughout the season by Svalbard breeding geese; the existence of areas still available on Svalbard for geese to expand into; and a greater robustness of Svalbard ecosystems. If, however, the goose populations continue to increase, the risk of damage potentially increases. Warmer climates might mitigate such damage, depending on other aspects of climate change (see below). The FRAGILE project (Fragility of Arctic Goose habitat: Impact of Land use, conservation and Elevated temperatures: www.fragile-eu.net) aims at identifying thresholds for damage by geese on Svalbard in response to a climate-warming scenario.

CLIMATE CHANGE

In recent years, the fragility of Arctic ecosystems has been discussed in relation to climate change. Although ecosystem *damage* is unlikely to occur as a direct response to climate change, any long-term changes in the climate will inevitably *change* the existing ecosystems. The geographic location of Svalbard, at the northernmost reach of the North Atlantic Current, makes Svalbard more susceptible to climate changes than many other areas. Svalbard ecosystems are adapted to extreme fluctuations in climate on different temporal scales (Fig. 1) and can thus be regarded as rather robust. Ecosystem changes will thus occur only if the long-term energy balance or hydrology is changed. A major 'threat' to existing ecosystems under warmer conditions would be an expansion of species that are at their northern distribution limits on Svalbard today or an invasion of new species. The degree of change may depend on ecosystem diversity and complexity, an issue that remains to be fully evaluated.

Although there is no evidence for less diverse ecosystems being more vulnerable to invasive species than diverse ecosystems, rather the opposite (e.g. Myers and Bazely 2003), island ecosystems seem to be rather sensitive to species invasion. In a warmer climate, conditions may improve in the Arctic for species from other bioclimatic zones and the sparse vegetation cover in the High Arctic may provide many opportunities for establishment of new plant species. Potentially, Svalbard ecosystems may thus be extremely vulnerable to invasive species. On the other hand, the unique light conditions at such high latitudes (i.e. low light intensity combined with midnight sun in summer, and no light in winter) might hinder the establishment of plant species adapted to conditions at lower latitudes. Light levels may change in response to change in cloudiness, but the photoperiod cannot be changed. In the context of invasive species, it is of interest to consider the

significance of bird cliffs and other 'hot spots' in fostering species that are ready to expand if climate improves. An example is the temperate sibling vole (*Microtus rossiaemridionalis*) that was accidentally introduced in the 1960s to a Russian mining village close to a seabird colony. Ever since, the population has thrived in the high productive vegetation below the bird cliffs, but has not yet successfully expanded to other areas on Svalbard (Henttonen *et al.* 2001).

One aspect of climate change in the Arctic that can be expected to be harmful for both individual species and whole ecosystems is increased frequency of freeze–thaw cycles. In this respect island ecosystems and coastal ecosystems affected by warm ocean currents in general may be more robust than continental systems because they are already adapted to frequent freeze–thaw cycles in spring and autumn (Fig. 1). A more severe threat might be the delayed onset of winter. For most plants on Svalbard, the growing season ends in mid- to late August and after that the level of photosynthetically active radiation decreases fast. If high temperatures are maintained long after cessation of growth, plant and soil respiration may also be maintained at high rates, thus disrupting the carbon balance of individual plant species and eventually the whole ecosystem.

CONCLUSION

High Arctic terrestrial ecosystems in general, and Svalbard ecosystems in particular, are robust in terms of temporal variation in herbivore populations and climate, but are fragile in terms of human disturbance and other human interference. Fragility in terms of climate change is still not resolved and needs more thorough study and evaluation. Some of the island characteristics contribute to a resilience of the terrestrial ecosystems on Svalbard. The Svalbard flora and fauna have evolved a high degree of tolerance to extreme climatic variability, including the otherwise harmful freeze–thaw cycles in spring and autumn. Other characteristics that can be attributed to islands are low species diversity and ecosystem complexity relative to 'mainland' ecosystems, which would make them more vulnerable to human disturbance and long-term climate change. Such vulnerability may either be mitigated or enlarged by the strong link to marine ecosystems that is typical of islands and coasts. The marine link enhances the complexity of the food webs, which might enhance ecosystem robustness to change. At the same time the marine link may facilitate establishment of introduced species.

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