Wild and semi-domestic herds of *Rangifer* (caribou or reindeer) are almost omnipresent in Arctic tundra. Rangifer management is an important issue, as the herds exert a number of important controls on the Arctic terrestrial ecosystem through their effects on vegetation and carnivore populations, as well as providing essential ecosystem goods to indigenous people. Photo: Susan Morse.

Chapter 12

Terrestrial Ecosystems

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Contents

> ❯❯ It has progressively become warmer. I recall that only in our traditional area did the trees occur, but when I returned there via plane last year, a lot more of the tundra was inundated with trees, small mind you, but they have moved north and east. The area we used to inhabit has been overgrown with vegetation, mainly shrubs and small trees. It has become almost like a mini-forest where we used to have our main camp. We visited the site in 2000 and it was almost unrecognizable due to all of the growth that occurred during our absence. I think this is due to a shorter spring, a longer summer and longer frost free falls.
>
> Utok; Elders Conference on Climate Change 2001.

SUMMARY

The Arctic tundra biome is geographically restricted to a strip around the margins of the Arctic Ocean. A key force determining the tundra biome's zonal structure is the bottom-up effect of decreased vegetation productivity and complexity with increasing latitude. Accordingly, there are trends of decreasing diversity within and among trophic guilds of consumers with increasing latitudes. Low food web complexity in the northern parts of the biome is also due to island biogeographic features, as large parts of the high Arctic are located on islands. Similarly, a substantial proportion of the high biodiversity of low Arctic zones stems from 'spillover effects' from sub-Arctic ecosystems. Historic processes have also contributed to shaping the current large-scale regional provinces in terms of Arctic species communities. At sub-regional scales the terrestrial Arctic harbors diverse mosaics of communities that are structured by gradients and disturbances in climate, substrate, hydrology and cryosphere that form unique patterns of within — and among — community diversity. Hot spots of high regional diversity are currently found in some old, topographically and geologically complex regions.

The architecture of tundra food webs is modulated by inter-specific interactions within and between trophic levels. Herbivores can regionally exert strong top-down controls on tundra vegetation, whereas predators often control small mammal herbivores and the reproductive success of ground nesting birds. Multi-annual, cascading bottom-up and top-down interaction cycles mediated by lemming populations are crucial for the maintenance of terrestrial Arctic biodiversity in many tundra ecosystems. Functional traits of plants in interactions with below-ground microbial communities and herbivores maintain essential roles in the regulation of the global climate system through controls on fluxes of greenhouse gasses (GHG) and heat fluxes between the earth surface and the atmosphere. Changes to the composition of terrestrial biodiversity may determine whether the Arctic will become a source or a sink for GHGs in a warming climate.

Climate is historically and currently the most important driver of change of Arctic terrestrial ecosystems, through alteration of coastal sea ice, glaciers, snow and permafrost, changed seasonality and extreme events. At present, a second emerging driver is an increased footprint of human presence within the Arctic. Currently, the most profound ecosystem impacts include (1) increased plant biomass due to growth of tall woody plants that cause lower albedo and possibly enhance GHG emissions and thereby accentuating the Arctic amplification of climate change, (2) collapsed cycles of lemmings and emergent outbreaks of insect herbivores and plant pathogens with cascading impacts on food webs and ecosystem functioning, and (3) increasing abundance of boreal and human commensal species impacting Arctic endemics as predators or competitors.

Recommended actions to conserve Arctic terrestrial ecosystems under the impacts of climatic change and other anthropogenic stressors include conservation of topographically diverse areas with landscape-scale 'buffer-capacity' to maintain cold refuges in a warmer climate and of remote high Arctic islands that are the most physically protected from species invasions from the south and human presence. Prudent management of Arctic herbivores such as reindeer *Rangifer tarandus*, using their capacity for shaping vegetation on landscape scales, may be considered for counteracting encroachment of tall woody vegetation that otherwise will eliminate tundra habitats, while avoiding the negative impacts of herbivore overabundance that have been documented in some regions.

A key message from the present assessment is that essential attributes of terrestrial Arctic biodiversity, some of which have global repercussions, are ultimately dependent on how interactions within ecological communities and trophic webs are impacted by rapidly changing external drivers. Consequently, research, monitoring and management ought to be properly ecosystem-based. Because ecosystems are structurally and functionally heterogeneous across the tundra biome and may also be subjected to external drivers of different strengths, new ecosystem-based observatories that include state-of-the art research, often combined with adaptive management, should be widely distributed across the circumpolar Arctic. Model-based predictions about how Arctic species and ecosystems will respond to the substantial climate change currently projected for the Arctic have limited powers to accommodate surprises in terms of novel climates and ecosystems that may rapidly emerge. New efforts urgently need to be deployed to enable well-designed real-time observations as a basis for empirically based documentation and understanding of cause-effect relationships of future ecosystem changes in the terrestrial Arctic.

12.1. INTRODUCTION

The Arctic tundra biome is characterized by low-growing vegetation composed of low shrubs, sedges, grasses, forbs, lichens and mosses (bryophytes) that grow beyond the northern climatic limit of trees (see Section 2 in Meltofte *et al.*, Introduction for this assessment's definition of the Arctic). A polar view of the biome from space reveals that the continental portion of the Arctic tundra occupies a thin strip of land between the Arctic Ocean and the boreal forest (Fig. 12.1). Eighty percent of the lowland portion of the Arctic lies within 100 km of seasonally ice-covered seas. The biome essentially owes its existence to cold sea breezes that keep the temperatures during the growing season below that required for tree growth. One fifth of the total coastline of the world, or about 177,000 km, occurs in the Arctic, a biome that comprises only about 5% of the Earth's terrestrial surface. Three main aspects of the extensive Arctic coastlines make the tundra biome extremely vulnerable to

climate warming: (1) the strong climatic influence of the nearby sea ice, (2) narrow bioclimate zonation associated with these coastlines, and (3) extensive lowland plains near most of the Arctic coast (CAVM Team 2003).

In terms of climate, the Arctic tundra can be viewed as a strongly oceanic-influenced biome, but one that varies considerably in the degree of maritime expressions of cloudiness, fog, humidity and equitable temperatures, because the Arctic Ocean is covered by ice to a varying extent during the winter and summer. The longevity of the ice near the coast in summer strongly affects summer land temperatures and local continentality of the climate as well as the diversity of organisms and total productivity of the land (Bhatt *et al.* 2010). Steep temperature gradients occur inland from these coastlines resulting in extraordinarily long and narrow ecological transition zones with several bioclimate subzones compressed near the coast. Permafrost strongly affects the ecosystems of most of the biome, but is not a condition that defines the biome, as permafrost also extends far into the boreal forest in continental areas of Siberia and North America. On the other hand, there are portions of coastal tundra with no or only discontinuous permafrost (Callaghan *et al.* 2004a, AMAP 2011).

The integrity of terrestrial Arctic ecosystems, as shaped by biotic and abiotic processes, is ultimately conditional on low primary productivity resulting from short and cool summers that restrict plant growth and metabolic activity of other poikilothermic[1] organisms, such as bacteria, fungi and invertebrates. The low productivity at the base of trophic chains restricts secondary productivity and the complexity of food webs and decomposer webs. Tundra food webs are usually composed of only three major trophic levels: plants, herbivores and predators (Krebs *et al.* 2003, Ims & Fuglei 2005). The structure of decomposer webs, in which cryptic microbial communities and soil faunas play a central role, is considerably less known (Callaghan *et al.* 2004b), but may be more complex than the more conspicuous food webs composed of green plants and macroscopic animals (see Hodkinson, Chapter 7). Terrestrial food webs also include fewer trophic levels than, for instance, aquatic ecosystems in the Arctic (Wrona & Reist, Chapter 13, Michel, Chapter 14), although high Arctic limnic systems may be as simple as their terrestrial counterparts (van der Wal & Hessen 2009, Wrona & Reist, Chapter 13).

Although Arctic tundra ecosystems have a simple trophic structure, often with relatively low species richness within each trophic level, other structural features of biodiversity can be remarkably complex. Spatial variability in temperature, winds, precipitation, hydrology, cryosphere and soil chemistry creates gradients and complex mosaics of abiotic conditions that shape the composition of species assemblages (i.e. ecological communities) at multiple spatial scales. For this reason, a spatially hierarchical approach to characterize biodiversity patterns in

terms of differences in species assemblages as functions of abiotic controlling factors from local to circumpolar scales appears to be particularly applicable to Arctic tundra. In terms of ecosystem functions, and the biotic and abiotic processes that shape these functions, tundra ecosystems are no less diverse than other ecosystems. Some of the ecosystem functions are crucial for the livelihood of local people, such as locally produced food, while others have essential roles in the global climate system, such as controls of exchange of heat and GHG.

In this chapter we start with a review of present knowledge of how natural abiotic and biotic factors shape biodiversity in terms of ecosystem structure, processes and functions within the tundra biome (Section 12.2). This provides the background for assessing past and present trends in terrestrial Arctic biodiversity, and the drivers of such trends (Section 12.3). Towards the end of the chapter we provide a synthesis of the assessment's key findings (Section 12.4) before we conclude with a set of recommendations on how policy makers, managers and ecosystem scientists could act on these findings (Section 12.5).

12.2. ECOSYSTEM STRUCTURE, PROCESSES AND FUNCTIONS

Ecosystem structure (Section 12.2.1) concerns the contemporary distributions (i.e. spatial pattern) of biodiversity at various levels of biological organization as they are shaped by abiotic factors at a range of spatial scales. *Ecosystem processes and functions* (Section 12.2.2) concerns the biotic processes that shape biodiversity in conjunction with abiotic conditions. Our aim is to present the key patterns, processes and their determinants that are necessary to appreciate the present status and ongoing trends of terrestrial Arctic biodiversity (Section 12.3). Our account is biased towards the most studied parts of the ecosystem for which trend information is available; notably the vegetation and vertebrate animals that form the most conspicuous components of the ecological communities and food webs. As pointed out elsewhere in this volume (Hodkinson, Chapter 7, Dahlberg & Bültmann, Chapter 10, Lovejoy, Chapter 11) there is a strong need for long-term research to document status and trends in biodiversity of other compartments of the tundra ecosystem, notably microbial and invertebrate communities and decomposer webs.

12.2.1. Ecosystem structure

Vegetation is the main structuring element of terrestrial ecosystems. Plant community types (e.g. plant associations) constitute the basis of classification of terrestrial biota at the scales of communities, ecosystems and biomes. Indeed, mapping of plant community types and investigations made to understand the environmental factors shaping their composition and spatial distribution have a long scientific tradition (Daniëls *et al.*, Chapter 9). Moreover, a comprehensive hierarchic approach has been

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1 An organism whose internal temperature varies considerably.
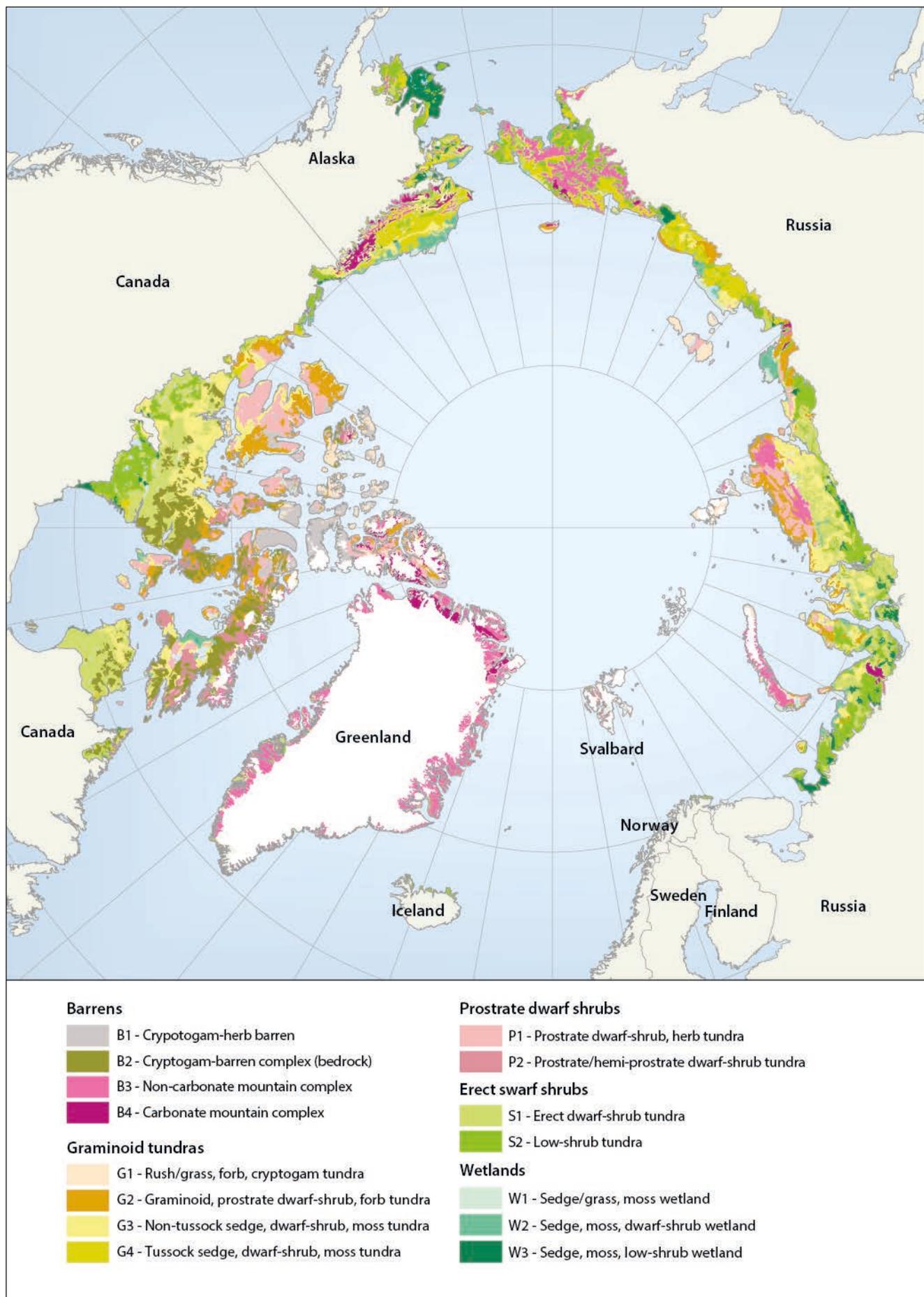
Figure 12.1. Circumpolar Arctic Vegetation Map (Walker *et al.* 2005).

developed to describe, explain and map the structure of Arctic vegetation at macro- (global), meso- (regional) and micro- (local) scales by analyzing the variation of plant communities with respect to climate, biogeographic history, topography and parent material (Cantlon 1961, Walker & Walker 1991, Walker 2000). This is the organizing principle behind the Circumpolar Arctic Vegetation Map (Fig. 12.1; CAVM Team 2003, Walker *et al.* 2005).

Here we expand on the CAVM scheme to describe ecosystem structure more comprehensively. We do this by incorporating animal communities and the perspective of food webs. The latter perspective has provided an important theoretical framework to tundra ecosystem science in terms of describing and predicting ecosystem properties (Oksanen *et al.* 1981, Ims & Fuglei 2005, Legagneux *et al.* 2012) as well as for documenting recent trends (Post *et al.* 2009). The structure of food webs depends to a large extent on the vegetation, due to bottom-up trophic processes. Moreover, higher trophic levels are subject to many of the same multi-scale abiotic controls as plants. However, there are also some obstacles to directly linking the CAVM scheme to communities of other taxa. First, while there is a widely used methodological approach for classification of vegetation (the Braun-Blanquet approach; Westhoff & van der Maarel 1978), equivalent approaches are largely missing for other taxa (e.g. animal and microbial communities). Furthermore, while Arctic plant communities are relatively well described (Daniëls *et al.*, Chapter 9), there are still large differences between animal taxa in the degree to which taxonomy is known and species distributions and assemblages (communities or guilds) are described (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7). Microorganisms are very poorly known compared with all other Arctic species (Lovejoy, Chapter 11), although they are critically important for ecosystem function (Section 12.2.2.2). A recent global synthesis indicates that soil microbial biomass dramatically exceeds total faunal biomass at the ecosystem scale (Fierer *et al.* 2009). Finally, owing to different types of controls and the spatial and temporal scaling of processes that affect different taxa and trophic levels, the hierarchical scheme for describing vegetation structure (i.e. the CAVM) may not always fit with the spatial structure and temporal dynamics of other ecosystem compartments (e.g. taxa or trophic levels). Descriptions of animal and microbial communities are also often missing at some of the spatial scales that vegetation ecologists examine due to methodological and logistical reasons. Thus our description of vegetation structure with respect to certain spatial scales and/or to some abiotic controls cannot always be accompanied by equivalent accounts on other ecosystem compartments.

Following the spatially hierarchical framework of CAVM we start with a description of how circumpolar-scale bioclimatic factors determine the latitudinal zonation of tundra ecosystems and how other large-scale climate gradients as well as historical contingencies create cross-zonal, longitudinal patterns of biodiversity. Next we proceed to regional- and landscape-level structures and explain how they are influenced at several scales by factors such as topography and substrate chemistry. Finally, we identify locations that stand out as 'hot spots' of diversity at various spatial scales (Daniëls *et al.*, Chapter 9) where certain combinations of present-day and historical factors coincide to create conditions that favor exceptionally high biodiversity.

12.2.1.1. Circumpolar-scale variation

Latitudinal zonation of vegetation structure, species composition and richness

At the circumpolar scale, summer temperature is the overriding environmental factor controlling the structure and productivity of *zonal* Arctic vegetation, which is the natural vegetation that develops under the prevailing Arctic climate on moderately drained fine-grained soils with moderate exposure to wind and snow (Vysotsky 1909, Alexandrova 1971, Elvebakk 1999, Razzhivin 1999, CAVM Team 2003). The changes in species diversity, plant productivity and structure of the vegetation along the Arctic climate gradient form the basis of all zonal approaches to subdivide the Arctic (Young 1971, Yurtsev *et al.* 1978, Alexandrova 1980, Edlund 1990, Bazilevich *et al.* 1997, Chernov & Matveyeva 1997, Matveyeva 1998, Elvebakk 1999, Walker *et al.* 2005). A remote-sensing approach that uses land-surface temperatures derived from satellite data provides a detailed picture of the distribution of summer temperatures and the amount of warmth available for plant growth that reflects the bioclimate zones of the CAVM (Box 12.1; Raynolds & Walker 2009).

The 10 °C difference in positive mean July air temperatures along the Arctic climate gradient (from 0-3 °C to 10-12 °C) corresponds to important differences in the total amount of summer warmth available for plant growth and results in major structural differences in plant canopies that are the basis for the delineation of the five latitudinal bioclimate subzones (A-E) of the CAVM (Tab. 12.1 and Fig. 9.1 in Daniëls *et al.*, Chapter 9), where A-C corresponds to the high Arctic and D and E to the low Arctic in North America (Bliss 1997). The corresponding changes in the vertical structure of zonal vegetation range from very small plants < 2 cm tall in a single discontinuous moss layer in subzone A to complex canopies with 2-3 layers that include shrubs exceeding 80 cm tall in subzone E. Likewise, the horizontal structure changes from < 5% cover of vascular plants in subzone A to 80-100% cover in subzone E (Chernov & Matveyeva 1997). The plant growth forms that compose the zonal plant cover also change. Subzone A is dominated by mosses, lichens, liverworts, algae, bacteria and a few small cushion forbs, rushes and grasses; whereas subzone E has complex plant canopies composed of a mixture of dwarf and low deciduous and evergreen shrubs, sedges, grasses, forbs, mosses and lichens. There is also a general trend of increasing shrub abundance and height along the north to south temperature gradient (Tab. 12.1).

Subzone A lacks all woody plants (see Daniëls *et al.*, Chapter 9). Subzones B and C are dominated by creeping prostrate dwarf shrubs (e.g. mountain avens *Dryas* spp., prostrate willows *Salix* spp.) and in parts of subzone C the hemi-prostrate shrub Arctic white heather *Cassiope tetragona* is abundant. In subzone D, dwarf erect shrubs less than 40 cm tall are common (e.g. many species of willow *Salix* spp., dwarf birch *Betula nana/exilis*, crowberry *Empetrum nigrum* and bilberry *Vaccinium uliginosum*). Finally, in subzone E, low shrubs over 40 cm tall are common on most zonal sites, whereas drainages with warm soils and abundant water and nutrients can have tall shrubs over 2 m tall. In most flat regions, the transition from tundra to forest is not a sharp line but a gradual transition along a forest-tundra ecotone with open tundra landscapes over broad areas, often with widely spaced trees or patches of fragmented forest, particularly along streams, grading to continuous forest (Scheffer *et al.* 2012). Trees (e.g. balsam poplar *Populus balsamifera* in Alaska and chosenia *Chosenia arbutifolia* in Chukotka) occur even north of the tundra boundary in small protected enclaves on south facing slopes or near perennial springs (Murray 1980, Bockheim *et al.* 2003, Breen 2010).

The reduced height and number of layers of the vegetation canopy in northern subzones has a critical effect on many species of animals. For example, all the birds and insects directly associated with shrubs disappear from zonal sites at the transition between subzones E and D. Farther north they are present only in warm extra-zonal and intra-zonal habitats, mainly shrubby areas along streams and south facing slopes (Chernov 1995). Clear latitudinal zonation is most evident along the continental portions of Arctic Eurasia and North America. The very large Canadian Arctic Archipelago and more mountainous terrain in Alaska, Greenland and Svalbard makes the zonation more complex in these areas (Bliss 1997), but nonetheless the bioclimate subzone approach developed in Eurasia can be applied to both continents as well as Arctic islands (e.g. Edlund 1983, Edlund & Alt 1989, Elvebakk 1999, Walker *et al.* 2008) and in Arctic mountains (Sieg & Daniëls 2005, Sieg *et al.* 2006).

A north to south gradient of increasing plant diversity with temperature has been documented in several Arctic studies (Young 1971, Rannie 1986, Chernov 1989, Daniëls *et al.*, Chapter 9). Similar patterns are observed for animal diversity. Species diversity decreases with decreasing temperature and increasing latitude in most groups, including birds, ground beetles and butterflies (Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7). Latitudinal patterns of diversity differ strongly between groups of animals, however. In general, the decline in diversity is more pronounced in animals than in plants, but in some specialized groups, such as shorebirds and sawflies on willows, there are opposite local

Box 12.1. Use of remote sensing to map circumpolar patterns of sea ice, land temperatures and above-ground plant biomass

Sensors aboard Earth-orbiting satellites gather data that are used for mapping changing patterns of sea-ice distribution, land-surface temperatures and productivity of vegetation (Bhatt *et al.* 2010). Circumpolar maps of sea ice concentration use Special Sensor Microwave Imager (SSM/I) data (Comiso & Nishio 2008) and Advanced Very High Resolution Radiometer (AVHRR) radiometric surface temperature data.

Maps of the summer land-surface temperature also use the AVHRR surface temperature data with enhanced cloud masking and calibration with in situ ground temperatures (Comiso 2003). The summer warmth index (SWI) is the sum of average May-September monthly surface temperatures above freezing within each pixel, and can be closely related to the bioclimate subzones portrayed in Fig. 9.1 in Daniëls *et al.*, Chapter 9.

The Normalized Difference Vegetation Index (NDVI) is the most common satellite-derived index used to monitor global-scale vegetation productivity. The index is derived from the difference in reflectivity of the land surface in the near-infrared (NIR) band where vegetation reflects strongly, and the red (R) band where vegetation absorbs strongly for photosynthesis. The difference is divided by the sum of reflectances in the same two bands to normalize for differing illumination conditions (NDVI = (NIR-R)/(NIR+R)). The NDVI is interpreted as the photosynthetic capacity of the vegetation (Tucker & Sellers 1986) or its 'greenness' and has been shown to be correlated with ground measurements of biomass, leaf-area index (LAI), intercepted photosynthetically active radiation (IPAR), carbon dioxide flux and other measures of tundra photosynthetic activity (Stow *et al.* 1993). The Global Inventory Modeling and Mapping Studies (GIMMS) data set (now updated to the GIMMS3g), is the most widely used global NDVI data set. The GIMMS3g NDVI is derived from imagery obtained from the AVHRR onboard the NOAA satellite series 7, 9, 11, 14, 16, 17 and 18. This NDVI data set has been corrected for sensor and orbital calibration, view geometry, volcanic aerosols and other artifacts in the data. The data are temporal composites of the maximum NDVI value for two halves of each month, which minimizes the effects of cloud cover. The data set has been used for monitoring trends in vegetation change and biophysical properties of the vegetation in many biomes (Tucker & Sellers 1986, Paruelo *et al.* 1997, Li *et al.* 2002, Fensholt *et al.* 2009) including the tundra biome (Jia *et al.* 2003, Goetz *et al.* 2005, Verbyla 2008, Bhatt *et al.* 2010, Macias-Fauria *et al.* 2012, Xu *et al.* 2013). A circumpolar map of aboveground phytomass has been prepared using the correlation between zonal aboveground biomass and NDVI along two transects in North America and Eurasia (Box 12.1 Fig. 1; Reynolds *et al.* 2012).
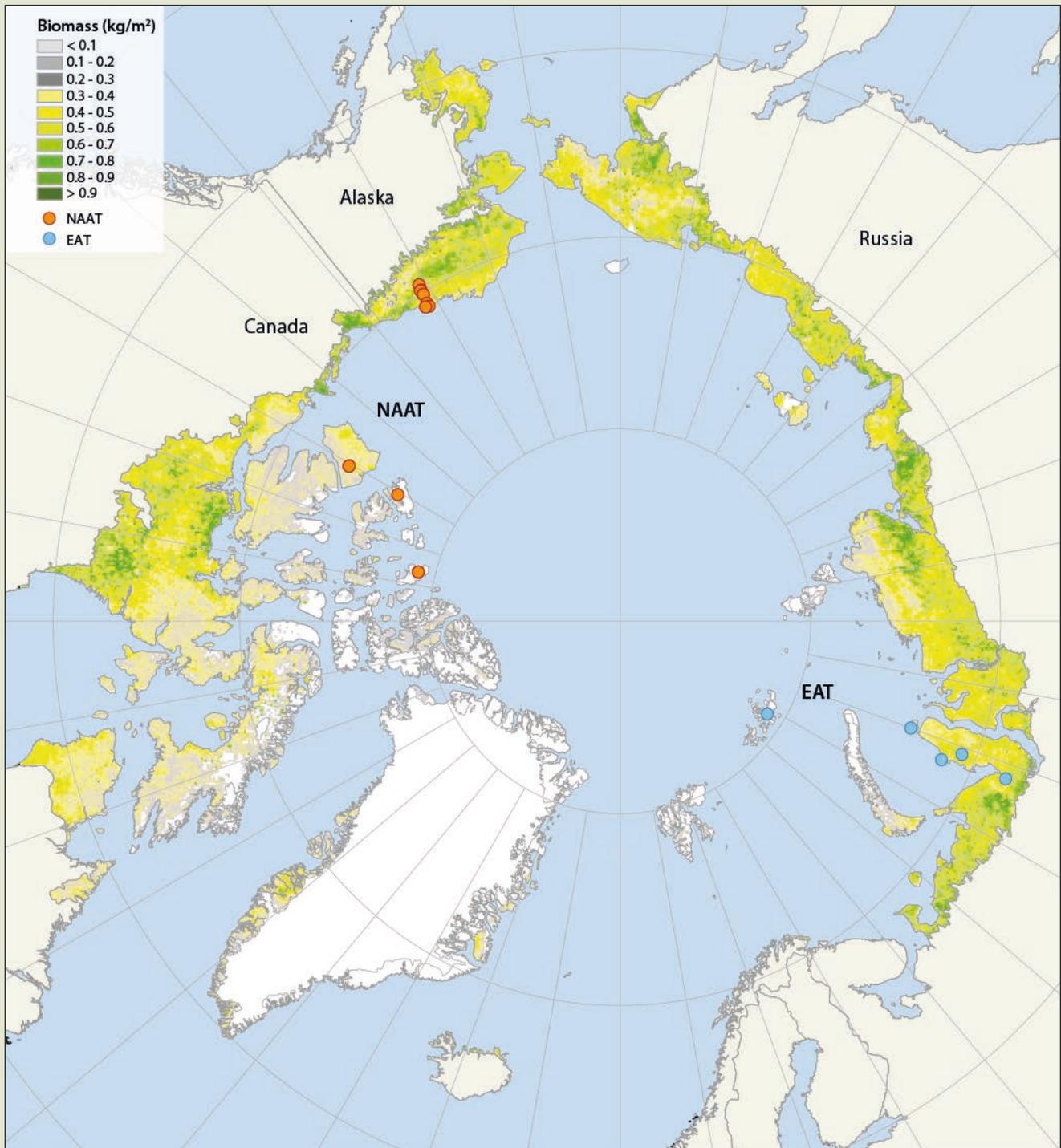
Box 12.1 Figure 1. Aboveground phytomass in the Arctic in 2010, mapped using the relationship between phytomass and NDVI developed through field sampling of zonal sites along the North America and Eurasia Arctic Transects (NAAT, red dots, and EAT, blue dots). From Raynolds *et al.* (2012).

Table 12.1. Vegetation properties in each bioclimate subzone. Adapted from CAVM Team (2003). Vertical and horizontal vegetation structure based on Chernov & Matveyeva (1997).

Sub-zone	Mean July temp. (°C)[1]	Summer warmth index (thawing °C mo)[2]	Vertical structure of plant cover[3]	Horizontal structure of plant cover[4]	Major plant functional types[5]	Total above-ground zonal phy-tomass (g/m^2)[6]	Number of vascular plant species in local floras[7]
A	0-3	< 6	Often barren or with biological soil crusts. In favorable microsites, 1 lichen or moss layer < 2 cm tall, very scattered vascular plants hardly exceeding the moss layer	< 5% cover of vascular plants, up to 40% cover by mosses and lichens	b, g, r, cf, of, ol, c	66-154	< 50
B	3-5	6-9	2 layers, moss layer 1-3 cm thick and herbaceous layer, 5-10 cm tall, prostrate dwarf shrubs 5 cm tall	5-25% cover of vascular plants, up to 60% cover of cryptogams	npds, dpds, b, ns, cf, of, ol	145-388	50-100
C	5-7	9-12	2 layers, moss layer 3-5 cm thick and herbaceous layer 5-10 cm tall, prostrate and hemi-prostrate dwarf shrubs < 15 cm tall	5-50% cover of vascular plants, open patchy vegetation	npds, dpds, b, ns, cf, of, ol, ehds* (*in acidic areas)	297-508	75-150
D	7-9	12-20	2 layers, moss layer 5-10 cm thick and herbaceous and dwarf- shrub layer 10-40 cm tall	50-80% cover of vascular plants, interrupted closed vegetation	ns, nb, npds, dpds, deds, neds, cf, of, ol, b	313-563	125-250
E	9-12	20-35	2-3 layers, moss layer 5-10 m thick, herbaceous/dwarf-shrub layer 20-50 cm tall, sometimes with low-shrub layer to 80 cm	80-100% cover of vascular plants, closed canopy	dls, ts*, ns, deds, neds, sb, nb, rl, ol (*in Beringia)	740-749	200-500

1) Based on Edlund (1996) and Matveyeva (1998).

2) Sum of mean monthly temperatures greater than 0°; modified from Young (1971).

3) Based on Chernov & Matveyeva (1997).

4) Based on Chernov & Matveyeva (1997).

5) Codes for plant functional types: b = barren; c = cryptogam; cf = cushion of rosette forb; deds = deciduous erect dwarf shrub; dls = deciduous low shrub; dpds = deciduous prostrate dwarf shrub; g = grass; ehds = evergreen hemiprostrate dwarf shrub; nb = nonsphagnoid bryophyte; neds = nondeciduous erect dwarf shrub; npds = nondeciduous prostrate dwarf shrub; ns = nontussock sedge; of = other forb; ol = other lichen; r = rush; rl = reindeer lichen; sb = sphagnoid bryophyte; ts = tussock sedge. Underlined plant functional types are dominant.

6) Based on Appendix S3 in Walker *et al.* (2012). Range of values for zonal sites along the North America Arctic Transect (NAAT) and Eurasia Arctic Transect (EAT). The values represent landscape-level biomass associated with mapped 100 m^2 areas along the NAAT and 2,500 m^2 areas along the EAT. Numbers are extrapolated from clip-harvest samples of vegetation types within each mapped area. The values are the mean total standing crop of dead and live plant material within and above the top layer of live green moss.

7) Based mainly on Young (1971).

trends related to habitat and food resource availability (Callaghan *et al.* 2004b). For soil micro-organisms there are no consistent trends in community composition with latitude or altitude (Neufeld & Mohn 2005, Fierer & Jackson 2006, Bjorbaekmo *et al.* 2010, Fierer *et al.* 2011, but see Geml *et al.* 2009 and Timling *et al.* 2012).

Specialization for specific microhabitats decreases also at higher latitudes. In the southern tundra subzones, many more species occur in intra-zonal habitats (habitats where conditions differ from what is typical for the zonal sites, due to, for instance, topography or microclimate), occupying relatively small and isolated sites, than in zonal habitats. The latter contain only a small proportion of the regional flora and fauna. An important consequence of the decrease in number of species with latitude is an increase in dominance. At high latitudes, ecologically plastic species may become 'super-dominant': they occupy a wide range of habitats and have in general a large effect on ecosystem processes (Callaghan *et al.* 2013).

Plant aboveground biomass on zonal sites increases from about 50-150 g per m^2 in subzone A to about 750 g per m^2 in subzone E (Tab. 12.1). Similarly, annual produc-tion increases from about 1 g C per m^2 per year in polar desert environments of subzone A to about 90-135 g C per m^2 in low Arctic tussock tundra and low-shrub tundra of subzone E (Oechel & Billings 1992, Bazilevich *et al.* 1997). There is, however, considerable regional variation. A recent study measured aboveground biomass of zonal vegetation in all five bioclimate subzones along two transects in Russia and North America, respectively (Walker 2010, Walker *et al.* 2011a, Walker *et al.* 2012). Differences were observed in the growth-form composition of the biomass along the two transects (Fig. 12.2). For example, the North America transect had greater amounts of lichens and evergreen shrubs, and greater total biomass in subzones D and E. Also the North America transect had lower biomass in subzone C compared with that in Russia, and Russia had much lower biomass in subzones A and E. The differences were attributed to variations in precipitation (a drier climate at the Banks Island subzone C location of North America, a much colder and snowier climate at the Franz Josef Land subzone A location in Russia), and to different disturbance regimes, particularly greater amounts of reindeer *Rangifer tarandus* grazing along most of the Eurasia transect (Walker 2010).
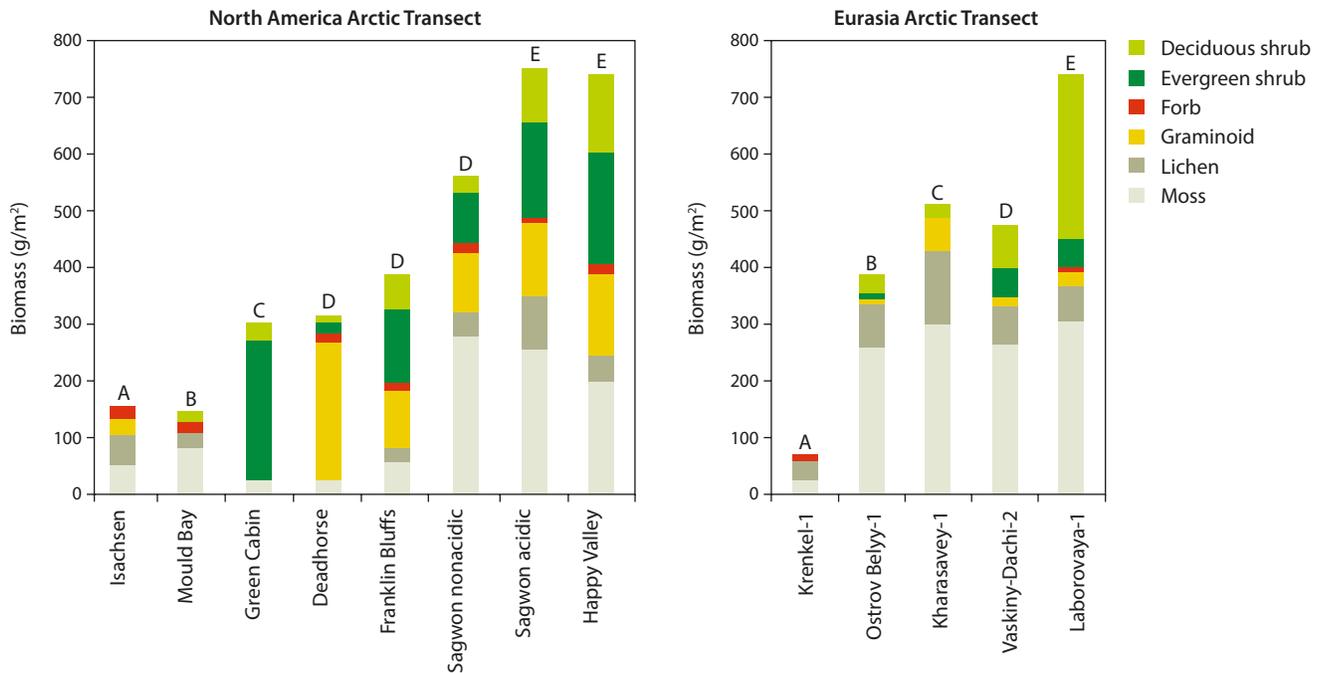
Figure 12.2. Total aboveground biomass of zonal vegetation for representative sites along the North America Arctic Transect and Eurasia Arctic Transect, respectively. Values exclude biomass of dead moss, dead lichen, detached dead and biological soil crusts. Bioclimate sub-zones (A-E) are shown above each bar, and the study sites are marked on Box 12.1 Fig. 1 (from Walker *et al.* 2012).

One of the clearest conclusions from latitudinal studies in Russia and North America is the special nature of both margins of the tundra zone. In the north, subzone A covers a very small area (2% of the Arctic), and mean July temperatures hovering near freezing are likely to make it extraordinarily sensitive to climate change (Walker *et al.* 2008). It truly exists at the margin where even a small summer warming will cause a shift toward vegetation with structure and function characteristic of more southerly subzones. Furthermore, subzone A is situated where some of the largest temperature changes can be expected because it only exists in regions where the summer-long presence of sea ice keeps air temperatures near freezing. At the extraordinarily long forest tundra boundary along the southern extreme of the tundra zone, changes in temperature, primarily summer temperatures, will probably also cause major transitions in ecosystem structure and function. These transitions are likely to be slower in some areas because of natural buffering in tundra soil temperature caused by deep peat, and faster in others because of disturbances caused by thawing permafrost, but everywhere occurring over immense areas associated with the tundra-forest boundary transitions in both North America and Eurasia.

In addition to latitudinal zonation, the Pan-Arctic Flora (Elven *et al.* 2011) divides the Arctic into 21 floristic regions circumscribed by common features independent of the general thermic south-north gradient (Daniëls *et al.*, Chapter 9). These features reflect a combination of glacial history, continental vs. oceanic climate and other historical biogeographic influences. The effect of glacial history and landscape age can be seen using vegetation mapping and remote sensing studies. At a circumpolar scale, Arctic areas show distinctive increases in bio-

mass during the first several thousand years following deglaciation (Raynolds & Walker 2009). Landscape age accounts for 34% of the circumpolar variation in productivity as indicated by the Normalized Difference Vegetation Index (NDVI) (Raynolds & Walker 2009) – landscapes older than 20,000 years in subzones B to E have higher NDVI values (Box 12.1) and greater vegetation cover.

Latitudinal zonation of food webs
The best studied terrestrial trophic systems in the Arctic are the plant-based food webs where vertebrates usually dominate the higher trophic levels both in terms of biomass and consumption (Batzli *et al.* 1980, Krebs *et al.* 2003, Callaghan *et al.* 2004b). These vertebrates can be classified into *guilds* of species with similar trophic positions. For instance, a particularly important guild of herbivores is formed by small rodents that are associated with a specialized guild of rodent predators (Batzli *et al.* 1980, Ims & Fuglei 2005). As a result of the general trend of decreasing diversity of Arctic organisms with increasing latitude, guilds lose species and become fewer and the food webs get simpler farther north (Callaghan *et al.* 2004b). Whereas in bioclimate subzone E most guilds are typically composed of several species often with fairly even abundances, single super-dominant species that are truly 'Arctic' are features of more northerly subzones. Examples of such super-dominant species are lemmings among the vertebrates (*Lemmus* or *Dicrostonyx* spp.) or springtails among invertebrates (e.g. *Folsomia* spp.). In bioclimate subzones A and B entire guilds are missing in certain areas, resulting in greatly simplified food webs (Fig. 12.3). Note that this may also be due to dispersal barriers as these high Arctic food webs are often located and studied on islands.
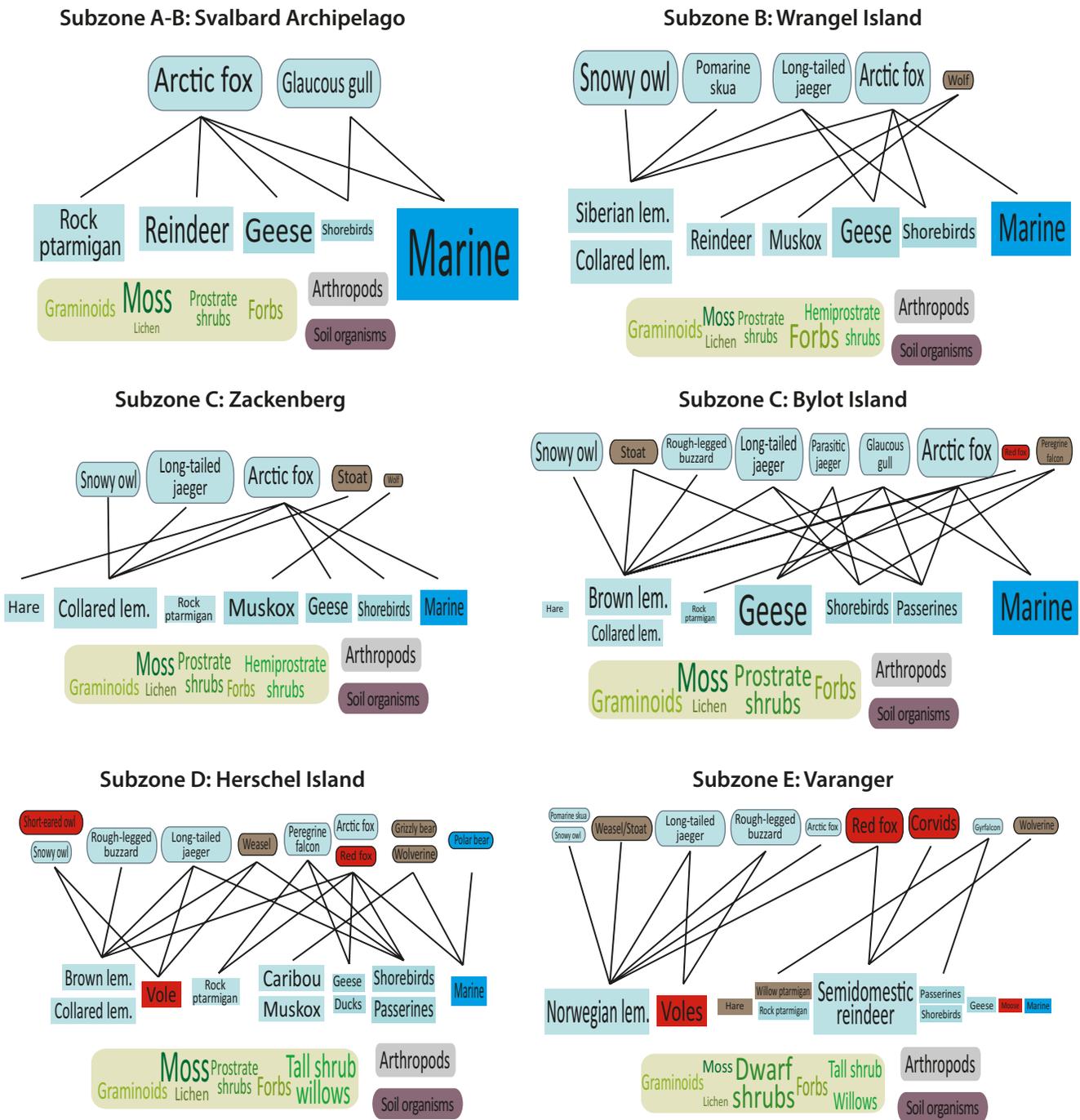
Figure 12.3. Conceptual models for the plant based vertebrate food webs typical for the five Arctic bioclimate subzones represented at six research sites. The graphs illustrate main hypotheses about relative importance of components and trophic links in the food webs taking into account current knowledge about the ecosystem at the respective sites. For vertebrates, mainly boreal species are shown in red, wide-spread boreal and Arctic species in brown and typically Arctic species in pale blue. Only major trophic relationships are represented by lines (based on Chernov & Matveyeva 1997, Matveyeva 1998, Krebs *et al.* 2003, ACIA 2005, Gauthier & Berteaux 2011 and Ims *et al.* 2013).

The following overview of the structural characteristics of the consumer guilds of tundra food webs according to the CAVM scheme for vegetation subzones will primarily be based on information provided by previous large-scale syntheses such as those provided by the IBP (Chernov & Matveyeva 1997, Matveyeva 1998), ACIA (2005) and the IPY-project Arctic WOLVES (Gauthier & Berteaux 2011). Moreover, we will draw on information from research stations and programs spread over most Arctic subzones.

The most complex and species-rich food webs are found in the low Arctic. Ecosystems of subzone E are characterized by a relatively high abundance of boreal species at all trophic levels. The small rodent guild is composed of several species of voles, in addition to the typical Arctic lemmings (Fig. 12.3). Medium-sized herbivores include ptarmigan *Lagopus* spp., hare *Lepus* spp., Arctic ground squirrel *Spermophilus parryii* and geese, whose numbers vary considerably between different geographic regions. The main large herbivore is the caribou/rein-

deer, although Eurasian elk/moose *Alces alces/americanus* regularly enters the low Arctic in summer, where tall shrubs are abundant. Indeed, the presence of tall shrubs as food or structural habitat is a key factor behind the relatively high species diversity and food web complexity in subzone E. Endemic Arctic predators such as the Arctic fox *Vulpes lagopus* or the long-tailed jaeger *Stercorarius longicaudus* are common, as well as the small rodent specialists weasel *Mustela nivalis* and stoat *M. erminea*, but the most specialized lemming predators such as the snowy owl *Bubo scandiaca* or pomarine jaeger *Stercorarius pomarinus* are mostly lacking. At the same time, widespread predators with strongholds in southerly biomes such as the red fox *Vulpes vulpes*, eagles and corvids may also be common (Killengreen *et al.* 2012). Large predators such as the wolf *Canis lupus*, wolverine *Gulo gulo* and brown bear *Ursus arctos* are less numerous in the tundra than in the boreal forest, and in regions with domestic reindeer their numbers are often under strict anthropogenic control (Reid *et al.*, Chapter 3). In subzone D, Arctic species become more dominant than boreal ones. Thus lemmings dominate the small rodent guild, although voles are present, and typical Arctic predators such as snowy owls can breed there in years with high lemming peaks.

The high Arctic is characterized by endemic tundra food webs in the sense that they are dominated by species whose distribution ranges are restricted to the Arctic tundra biome. Small rodents are represented by one or two species of lemmings, which are distributed as far north as vascular plants are present (Reid *et al.*, Chapter 3). Several species of medium-sized herbivores occur, but are fewer and less abundant than in the low Arctic. Geese, however, can form large colonies, such as the lesser snow goose *Chen c. caerulescens* on Bylot Island (Gauthier *et al.* 2011). Reindeer/caribou are widespread although often at low densities, and muskox *Ovibos moschatus* are present locally. The predator guild is dominated by Arctic species such as Arctic fox, snowy owl and jaegers. Some widespread species, however, still occur. The stoat is an important lemming predator in high Arctic Greenland as far north as Nearctic collared lemmings *Dicrostonyx groenlandicus* are present (Born & Böcher 2001). Large predators such as wolves are rare or absent. Most areas in subzone A and B are located on islands, where fewer vertebrate species are present (presumably due partly to dispersal barriers), and the tundra food web is simplified compared with mainland sites at the same latitude (e.g. on Taimyr Peninsula; Ebbinge & Mazurov 2007). Thus, ptarmigans, hares and small mustelids are absent from Wrangel Island in subzone B (Menyushina *et al.* 2012). In the high Arctic archipelago of Svalbard, which is mostly situated in subzone A, resident terrestrial herbivores are represented only by reindeer and rock ptarmigan *Lagopus muta*. Geese are important in summer. Predators are few, as there is no subsistence for the predator guild that is dependent on lemmings. The main terrestrial predator is the Arctic fox for which marine subsidies constitute important resources (Eide *et al.* 2012).

12.2.1.2. Regional- to local-scale variation

Factors that affect vegetation patterns at regional scales include major substrate differences such as major glaciations, large sand sheets, marine incursions and major topographic variations related to mountains (Cantlon 1961, Walker 2000). At the landscape scale, variations related to smaller hillslope gradients, snow gradients and variations within smaller watersheds become apparent. At local scales, variation in plant communities is caused by such factors as different bedrock types, local drainage conditions, periglacial landforms and small-scale disturbance.

Altitudinal zonation and hill-slope toposequences
Topography affects diversity at several scales. Mountain ranges have elevation belts that correspond somewhat to the latitudinal bioclimate subzones. Theoretically, elevation belts are thermally equivalent to the latitudinal zonation and can be determined by the adiabatic lapse rate of -6 °C per 1,000 m elevation with about 333 m steps between the belts (CAVM Team 2003). Studies of alpine vegetation in the Arctic are not numerous (e.g. Jedrzejek *et al.* 2013), but the launch of the Global Observation Research Initiative in Alpine Environments (GLORIA) protocols for analyzing changes in species distribution on high mountain peaks (Pauli *et al.* 2004, Grabherr *et al.* 2010) represents significant progress. GLORIA is organized around the principle that the alpine zonation of many mountain ranges will change because of elevated temperatures. Active GLORIA monitoring sites are located near the Arctic research stations at Toolik Lake, low Arctic Alaska, and Zackenberg, high Arctic NE Greenland.

On a smaller scale, predictable changes in vegetation and soils that occur along hill slopes provide a convenient conceptual means to describe variation in most landscapes (Milne 1935, Billings 1973, de Molenaar 1987, Birkeland 1999). A conceptual framework consisting of five hill-slope positions typically found in hilly Arctic terrain is shown in the upper section of Fig. 12.4 (CAVM Team 2003). The approach provides a way to visualize the common variation in vegetation structure and composition that is attributable mainly to variations in water moving down slope over long periods of time. The changes in plant-community structure along typical toposequences in each Arctic bioclimate subzone are described by Elvebakk (1999; see lower section of Fig. 12.4).

A unique aspect of Arctic and alpine toposequences is the role of snow, which has complex consequences for vegetation patterns and ecosystem processes (Gjærevoll 1956, Billings & Bliss 1959, de Molenaar 1987, Walker *et al.* 1993, Walker *et al.* 2001a). The accumulation of snow can decouple the surface almost completely from air temperatures, resulting in much milder winters beneath the snowpack but correspondingly shorter growing seasons (Scott *et al.* 1993, Zhang 2005). Late snow beds (Bjork & Molau 2007) also influence soil moisture as well as the supply and seasonal availability of nutrients (Fahnestock *et al.* 2000).

1. Dry exposed ridges
2. Mesic zonal sites
3. Wet grassland
4. Snow beds
   a. well-drained, early-melting
   b. poorly-drained, late-melting
5. Streamside sites
   a. stabilized floodplains
   b. active floodplains

1

2   4a

Prevailing wind

4b

Semi-permanent
snow drift

2

3   5a 5b 5a

Subzone A

Scattered rosette
herbs (*Papaver* ssp.)

Scattered herbs
like *Phipsia algida*
and *Cerastium regelii*

Pleurocarp mosses,
but no real mires

Open ridge
vegetation

Zonal
vegetation   Snow-bed
vegetation

Vegetation on wet sites

Open gravel, frost boils,
<5% vegetation

Partial moss cover,
no peat layer

Subzone B

Prostrate dwarf-shrubs
(*Dryas* ssp.)

Prostrate dwarf-shrubs
(*Salix* ssp.) and herbs

Herbs like
Saxifraga spp.
and *Oxyria digyna*

Mires of
pleurocarp mosses,
Carex spp. and *Dupontia fisheri*

Open ridge
vegetation

Zonal
vegetation

Snow-bed
vegetation

Vegetation of
wet sites

Discontinuous
vegetation

Mires with moderate
peat layer

Subzone C

Prostrate dwarf-shrubs
(*Dryas* ssp.)

The dwarf-shrub
Cassiope tetragona

Herbs like
Saxifraga spp. and *Oxyria digyna*
plus weakly southern species
like *Trisetum spicatum*

Open ridge
vegetation

Zonal vegetation

Mires of pleurocarp
mosses and *Carex* spp.

Snow-bed
vegetation

Vegetation of wet sites

Discontinuous
vegetation

Continuous vegetation

Subzone D

Prostrate dwarf-shrubs
(*Dryas* ssp.)

Dominance of
dwarf-shrubs other
than *Cassiope*
(*Betula nana* sl., *Empetrum*,
Vaccinium, *Salix*)

Open ridge
vegetation

Zonal vegetation

Thermophiloous herbs
like *Sibbaldia* and
Potentilla crantzii

Mires of pleurocarp
mosses in admixture
with *Sphagnum* spp.
Carex dominance

Snow-bed
vegetation

Thick peat

Discontinuous
vegetation

Continuous vegetation

Subzone E

Prostrate dwarf shrubs
and rosette plants
Loiseleuria procumbens,
Diapensia lapponica

Shrubs (*Salix*, *Betula*, *Alnus*)
and in the Amphi-Beringian
area tussock tundra of
Eriophorum vaginatum

Open ridge
vegetation

Zonal
vegetation

Numerous herbs
and forbs like
Alchemilla spp. and
Epilobium angustifolium

Development
of hummocky bogs
with *Sphagnum*
dominance

Snow-bed
vegetation

Thick ombrogenous peat

Discontinuous
vegetation

Continuous vegetation
with partly podzol
development

Figure 12.4.
Upper section: Conceptual toposequence used for the Circumpolar Arctic Vegetation Map (Walker *et al.* 2005).
Below: Generalized toposequences for vegetation in the five Arctic bioclimate subzones (adapted from Elvebakk 1999).

Snow beds are a key habitat for important tundra herbivores. Lemmings spend the winter under the insulating snow layer, which provides relatively mild and stable conditions necessary for winter breeding (Reid *et al.* 2012). The availability of stable snow cover seems to be a prerequisite for the characteristic lemming outbreaks (Ims *et al.* 2011) — a key biotic process in shaping tundra food webs and maintaining Arctic biodiversity (Section 12.2.2.1).

Soil pH
Local pH boundaries and gradients are associated with different bedrock types, loess, riparian systems, toposequences along slopes, cryoturbated soils and glaciated landscapes of different age. Soil pH boundaries are particularly noticeable in Arctic and alpine systems because of contrasting near-surface bedrock, extensive loess and coastal marine deposits, and have large consequences for

plant community structure and diversity (Edlund 1983, Walker *et al.* 1994). A complex set of soil and ecosystem properties are affected by soil pH, including calcium and phosphorus availability, soil temperature, active layer thickness, photosynthesis, respiration, decomposition rates and fluxes of trace gases together with energy and water (Sjörs 1959, Walker 1985, Bockheim *et al.* 1998, Walker *et al.* 1998).

Soil types and climate are intimately linked. Acidic soils are more common in the southern bioclimate subzones, particularly subzone E, because of accumulations of organic matter in warmer climates, whereas near-surface mineral soils with higher soil pH are more common in the colder regions. However, this is not universally true because sandy soils or acidic bedrock areas in the far North can have acidic soil. Likewise, areas in subzone E

with calcareous bedrock, recent glacial till, loess, river alluvium or recent disturbances will often have nonacidic soils. In general, the nonacidic zonal soils have higher species diversity, greater heat flux, warmer and drier soils, deeper active layers, are less of a carbon (C) sink, and are a smaller source of methane (CH_4) to the atmosphere (Walker *et al.* 1998). This has implications both for biodiversity but also for phytomass and functional composition (Epstein *et al.* 2008). Also, soil bacterial community composition and diversity in the Arctic is structured according to local variation in soil pH (Chu *et al.* 2010). Many of the physico-chemical factors structuring communities and ecosystems in the Arctic are, however, strongly related, so assigning direct causality is frequently hampered by confounding co-varying factors.

Glacial history
The effects of past glaciation are clearly expressed in terms of regional plant community diversity (i.e. beta-diversity), which tends to decrease with increasing landscape age. The differences in plant beta-diversity seen on glacial surfaces of contrasting age are also strongly linked to differences in soil pH and soil moisture. These differences often decline over long periods of time as landscapes become paludified[2], and soils become leached and wetter due to the presence of near-surface permafrost.

For example, at Toolik Lake, low Arctic Alaska, distinctly different vegetation types and biomass are found on glacial surfaces differing by more than 100,000 years in age. The oldest surfaces (Sagavanirktok-age, more than 125,000 years since deglaciation) have a dominance of acidic tussock tundra. In contrast, the much younger Itkillik II surfaces (about 11,500 years since deglaciation) have more irregular terrain and more diverse landscapes and vegetation with more lakes, drier vegetation, a dominance of nonacidic tundra and higher percentages of snow-bed vegetation. The diversity of plant communities tends to decrease as time, erosion and vegetation succession proceed (Walker 1995). Many features such as small ponds and diverse glacial landforms become rounded or are eliminated; and large areas become covered by the dominant zonal vegetation (Walker *et al.* 1994). Similar patterns have been shown with vegetation of glacial sequences covering shorter time periods (Zollitsch 1969, Reiners *et al.* 1971, Matthews 1992).

The older landscapes near Toolik Lake and throughout northern Alaska also have higher NDVI and greater amounts of standing biomass (Munger *et al.* 2008, Walker & Maier 2008) and higher production of CH_4 (Shippert *et al.* 1995). This is due in part to the relative proportions of dry, moist and wet vegetation types on different-age surfaces. Generally, drier vegetation with lower NDVI is dominant on younger surfaces. The biomass of the *Sphagno-Eriophoretum vaginati* (bog moss-tussock cotton grass association), which grows on the older surfaces, is about 25% greater than its counterpart in

younger areas, the *Dryado integrifoliae-Caricetum bigelowii* (entire leaf mountain aven-Bigelow's sedge association). These types also have contrasting key ecosystem properties with respect to differences in soil pH. *Dryado integrifoliae-Caricetum bigelowii*, the zonal vegetation type for subzone D, occurs on moist nonacidic calcareous soils (mean soil pH 6.3) and has the highest species richness of any association sampled near Toolik Lake – 56 species (26 vascular-plant species, 16 bryophytes and 14 lichens) per 20 m^2 plot. Several of these species have Beringian or western North American distributions. This is substantially higher than the diversity of the corresponding plant association that occurs on moist acidic soils in the same region (*Sphagno-Eriophoretum vaginati*; mean soil pH 4.6) and has an average of 39 species (15 vascular plants, 14 bryophytes and 10 lichens; Walker *et al.* 1994). The younger Itkillik surfaces also had a stronger NDVI increase during the period of the Landsat satellite record, perhaps due to the somewhat warmer soils, more abundant disturbances caused by non-sorted circles and other periglacial processes, and more gaps in the vegetation canopy (Raynolds *et al.* 2013).

Disturbance
Natural ecosystem disturbances occur in a hierarchy of spatial and temporal scales from daily needle-ice formation in soils at sub-meter scales to the major glaciations that cover much of whole continents (Walker 1996). Many natural disturbances in Arctic regions are related to the presence of permafrost including the growth and erosion of ice-wedges, thermokarst (e.g. Jorgenson *et al.* 2006), thaw lake drainage, differential frost heave, and mass movements due to thawing permafrost (e.g. Kokelj *et al.* 2009). Many natural disturbances are good analogs of disturbances caused by humans (anthropogenic disturbances are dealt with in Section 12.3.2). The successional processes following disturbances are strong modifiers of diversity, structure and phytomass (Bliss 1997, Callaghan *et al.* 2004a, 2004b). Walker *et al.* (2009) observed that many of the greenest landscapes on the Yamal Peninsula, Russia, are associated with landslides and drainage networks resulting from ongoing rapid permafrost degradation (Fig. 12.5). On older, stabilized slopes there are successional shifts in community composition, for example from pioneer vegetation through grass and forb-dominated communities to willow shrubs. Other disturbances are related to erosion caused by wind, snow or flooding water. The role of wildfires in low Arctic shrub tundra is also increasingly being recognized (Racine *et al.* 2004, Higuera *et al.* 2008). Tundra wildfires have recently scorched thousands of square kilometers in particularly warm and dry summers. Such fires initiate a cascade of processes including release of C to the atmosphere, changed vegetation successional path-ways, thawing permafrost and thermokarst (Mack *et al.* 2011, Rocha & Shaver 2011a, 2011b).

Extreme herbivore abundance owing to erratic or cyclic population outbreaks are also 'pulse events' that may cause considerable physical disturbance to the substrate and the vegetation. Examples are cyclic rodent peak

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2 Paludification is a common process by which peatlands in the boreal and Arctic zone are formed.

Figure 12.5. Exposed ground-ice thawing along the Se-yakha River within the low Arctic Bovanenkovo gas field in Yamal, Russia. A great deal of terrain within the tundra zone in W Siberia supporting oil and gas infrastructure is underlain by ice-rich permafrost. This surface of marine clay was exposed in the late 1980s and a graminoid cover has regenerated naturally in the intervening decades, but subsidence was still occurring in 2005. See Kumpula *et al.* (2011, 2012) for details. Photo: B.C. Forbes.

Figure 12.6. Patterned-ground area in the high Arctic coastal tundra at Barrow, Alaska. These low center polygons (one with standing water) are about 10-30 m across and delineated by ice wedges that are formed by thermal contraction of the ground surface. Photo: George Burba/shutterstock.com

years (Batzli *et al.* 1980) or insect pest outbreaks at the southern margin of the tundra (Jepsen *et al.* 2013, Karlsen *et al.* 2013). Besides the effect of grazing (dealt with in Section 12.2.2), the disturbance effect of such herbivores includes digging of burrows by rodents, grubbing for plant rhizomes and roots by geese, trampling by herds of large ungulates and release of nutrients.

Disturbance and succession are intertwined concepts; the study of one must inevitably consider the other. Disturbance initiates succession, influences its subsequent trajectory and can determine its rate, endpoint and duration through subsequent intervention (Walker 1999). The spatial extent and the frequency of disturbances can be expected to increase in the near future with increased human presence and exploitation, combined with thawing permafrost in a warming climate.

Patterned ground features, which are typical for Arctic landscapes that are underlain by permafrost, represent natural disturbances at small scales (Fig. 12.6). Most often these features are caused by a combination of seasonal frost cracking (whereby the ground contracts during winter and cracks into polygons of varying dimensions) and differential frost heave (whereby ice forms in soils and causes it to heave more in some areas than in others). Small, medium and large non-sorted polygons, non-sorted circles (frost boils) and earth hummocks are typical forms (Washburn 1980). These patterns have intrigued geomorphologists and permafrost scientists for decades and have recently been studied by biologists because of their importance notably to local biodiversity and net fluxes of GHG (Kade *et al.* 2005, Ping 2008, Vonlanthen *et al.* 2008).

12.2.1.3. Hot spots of diversity

In addition to the diversity gradients and patterns described above, sites with locally high biodiversity are observed. Such diversity 'hot spots' are often literally hotter, but topography, continentality and historical factors affect the occurrence of extra-zonal Arctic hot spots (Daniëls *et al.*, Chapter 9). Thermal hot spots are often characterized by the presence of anomalously tall shrubs or trees. Alders *Alnus* spp. and tall willows are present in the warmer parts of the low Arctic, occurring mainly on sites where soil conditions permit more luxuriant growth, such as on warm south-facing slopes or along streams and drainages. The tall shrub thickets they form represent hot spots of productivity and diversity, and are important structural elements in the tundra landscape. They provide shelter and food for many animal species such as willow ptarmigan *Lagopus lagopus*, many passerine birds, insects and hares (den Herder *et al.* 2004, Henden *et al.* 2011a, Ehrich *et al.* 2012, Ims & Henden 2012). The presence of balsam poplar, a species with higher thermal requirements than the tall shrubs, is a strong indicator of floristic hot spots because this species often forms small boreal enclaves that occur near springs in limestone bedrock areas or on thermally warm valleys and slopes in the low Arctic (Bockheim *et al.* 2003,

Breen 2010). The presence of trees and tall shrubs does not, however, necessarily indicate an area of high plant species diversity. Yet, for some animal taxa like passerine birds, they certainly do (Henden *et al.* 2013), although the high diversity is mostly attributed to the presence of species with their strongholds in the boreal forest (Sokolov *et al.* 2012).

For the diversity of Asiatic and steppe-tundra plant endemics, continentality is more important than temperature. Many of these species evolved in Beringia, where extensive glacier-free areas isolated from oceanic influences during the Pleistocene permitted the evolution of a rich cryo-xerophytic (steppe tundra) flora (Hultén 1937, Hopkins *et al.* 1982, Yurtsev 1982). They were adapted to warm summers, very cold winters, dry year-round climate, warm (in summer) well-drained mineral-rich soils, high disturbance regimes related to the abundant animals, and continual deposition of loess from the floodplains of rivers that were carrying high silt loads from the glacial meltwaters (Guthrie 1982, Yurtsev 1982). At present, these steppe-tundra plants are mostly found in sites that are at a considerable distance from marine influences and also have warm extra-zonal climates, where they form distinct assemblages of xerophytic species.

Locations that have a mix of warm summer soils due to extra-zonal conditions and azonal site factors, such as the occurrence of warm springs, or favorable geology, such as calcareous bedrock, are likely to enhance the probability of high regional species diversity (gamma diversity). Such areas are more common within regions of high habitat diversity (beta diversity), such as mountainous areas with a variety of bedrock types or different-age glacial surfaces, different slope exposures and snow regimes, and large river floodplains with different-age terraces, sand dunes and abandoned channels and meanders. Gamma diversity is furthermore enhanced if the location is in a biogeographic region with high species diversity, such as Beringia. Areas with high plant diversity are also likely to have high diversity of other taxa. For example, pingos (ice-cored mounds up to 50 m high) in northern Alaska are often hot spots of floristic and faunal diversity within 'seas' of wet tundra because of the large variety of microhabitats concentrated within a small area (Walker 1990).

12.2.2. Ecosystem processes and functions

The abiotic factors reviewed in Section 12.2.1 set broad constraints on species distribution ranges and thus site-specific community composition and species diversity. Such abiotic factors also constrain functional attributes of the biota such as plant growth forms, their phytomass and primary productivity, as well as the multitude of interactions among ecosystem components (producers, consumers, decomposers and pathogens). In this section we first review current knowledge about how interactions between species within food webs, in conjunction with abiotic factors, contribute to shaping biodiversity

patterns in time and space in tundra ecosystems (Section 12.2.2.1), and second, how functional ecosystem properties mainly at the level of broader compartments of terrestrial Arctic biodiversity feed back to the abiotic environment through physico-chemical processes (Section 12.2.2.2). Although obviously linked, the two issues belong largely to separate sub-disciplines within ecosystem science. Food web ecology deals mostly with trophic linkages between macroscopic producer (plants) and consumer (herbivore and predators) species and typically above-ground processes, while functional ecosystem scientists typically deal with linkages between above-ground and below-ground processes, between macro-organism and microbial communities and processes within the decomposer web. However, as separation of the two sub-disciplines is unhelpful for understanding how tundra ecosystems respond to specific drivers of change, we also discuss how trophic interactions are linked to ecosystem functions in terms of physico-chemical processes (Section 12.2.2.3).

Much of the current research on tundra ecosystems is aimed at understanding the impacts of climate change. Research approaches include modeling, field experiments, comparisons across spatial climatic gradients, and time-series analyses. In the present section we review research that provides an understanding of how tundra ecosystems are shaped by climate and are expected to respond to climate change (e.g. by means of modeling, experiments, comparative studies), while research that demonstrates historical, recent and current trends (e.g. by means of time-series analysis) is reviewed in Section 12.3.

12.2.2.1. Food web interactions

Theoretical framework
There has been a vigorous debate about the relative roles of producers and consumers in controlling the structure and functioning of food webs in different climate settings (Turkington 2009). A prominent theoretical framework, specifically addressing tundra ecosystems, is provided by the Exploitation Ecosystem Hypothesis (EEH; Oksanen et al. 1981, Oksanen & Oksanen 2000). EEH focuses on the high energetic costs of maintenance of endothermic animals, and this sets a 'bottom-up' constraint on the number of trophic levels (plants → herbivores → carnivores) that can be maintained along climatic gradients of decreasing primary productivity. Low Arctic climatic zones are predicted to be productive enough to hold all three trophic levels, where predators in turn can provide a 'top-down' control on the abundance of herbivores to the extent that plant communities are little affected by herbivores. In low productivity (or 'harsh') high Arctic environments it is predicted that tri-trophic dynamics are reduced to simple two-level systems (plants → herbivores). In such a situation heavy winter grazing pressure will restrict the above-ground accumulation of biomass and effectively exclude erect woody plants (Oksanen & Oksanen 2000). When released from predator control, herbivores are also predicted to be able to homogenize plant biomass
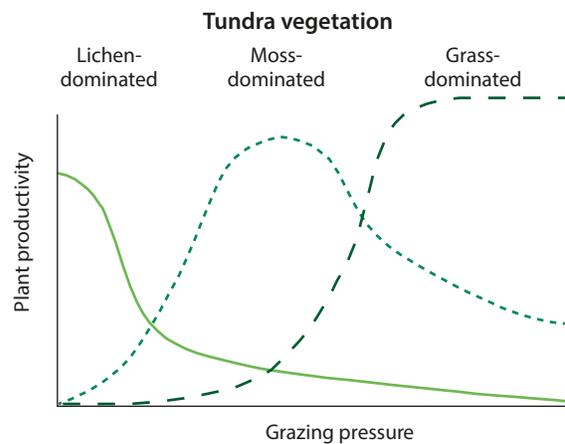
Figure 12.7. Predicted transitions between tundra vegetation states with increased grazing impact (from van der Wal 2006).

across environmental gradients at the landscape scale, and moreover to be able to bring about gross transitions between alternative tundra vegetation states (Fig. 12.7). Finally, models of both two-trophic and three-trophic level systems show that they are liable to strong multi-annual cyclic fluctuations in interaction strength and biomass (Turchin et al. 2000, Ims & Fuglei 2005). One major limitation of the EEH, however, is that it does not include the typical spatial subsidies that tundra ecosystems are often subject to. Below, we review empirical studies of plant-herbivore and predator-prey interaction in light of the predictions from the EEH.

Plant-herbivore interactions
Reindeer/caribou, geese and small rodents are three guilds of herbivores in tundra ecosystems (cf. Fig. 12.3) that are particularly important both in terms of their broad geographic distribution (across bioclimatic sub-zones and longitudinal eco-regions) and strong impact on vegetation. These keystone herbivores are, however, also fundamentally different in their modes of herbivory (food preferences, grazing/browsing/grubbing behavior), mobility (migratory or resident) and population dynamics (including sensitivity to predation and climatic variability), so there is justification for considering their impacts on the vegetation separately.

Herbivore exclusion experiments in northern Fennoscandia have identified the partial effects of reindeer and small rodents (voles and lemmings) on functionally important shrubs. In this region, reindeer are semi-domestic and have an abnormally high abundance (partly owing to strong anthropogenic control of large predators), whereas the small rodents exhibit distinct 4-5 year population cycles. In low Arctic riparian grasslands, reindeer and small rodents had strong complementary effects on the growth of tall willow recruits, indicating that herbivore community structure matters for the dynamics of tall willow thickets (Ravolainen et al. 2011). While the reindeer impose a more constant pressure ('press effect') on the vegetation (Kitti et al. 2009), the impact of small rodents is a typical 'pulse effect' associated with cyclic peak abun-

Figure 12.8. Thick layer of litter on snow in late June, composed mainly of clipped vegetation mixed with soil and lemming feces, resulting from intense activity of Norwegian lemming *Lemmus lemmus* during a peak-density winter on Varanger Peninsula. This litter, which some Arctic indigenous people term 'lemming hay' (Chernov & Matveyeva 1997), is often flushed by melt water in spring and may appear on the top of remaining snow patches. Photo: R.A. Ims.

dances (Fig. 12.8). Indeed, the pulsed effects of lemming population cycles on dwarf-shrub biomass were strong enough to be picked up as a signal in NDVI (Olofsson *et al.* 2012). Because experimental studies were undertaken during an 'exceptionally warm' decade, it was also possible to identify an interaction between climatic and herbivore effects: while the shrub biomass within herbivore exclosures accumulated strongly in the heath habitat over the > 10 year period in which the experiments were conducted, this was not the case for the open control plots (Olofsson *et al.* 2009). This indicates that there is a significant potential for ungulates and rodents to control biomass of shrubs even in a warming Arctic (see also Post & Pedersen 2008, Post *et al.* 2009, Wookey *et al.* 2009). Aside from direct effects on biomass, ungulate herbivores may also promote diversity within the plant community and prevent reduction of this diversity by warming-induced increases in the dominance of dwarf shrubs (Post 2013a). Reindeer may, however, have little impact on established thickets of very tall shrubs (above the 'browsing line') (Forbes *et al.* 2010).

Other non-mammalian herbivores may contribute to controlling the growth of shrubs. Tape *et al.* (2010), for example, provided evidence of substantial impacts of willow ptarmigan on shrub growth and shoot patterns. While insect folivores are usually considered to be unimportant compared with vertebrates in Arctic tundra (Callaghan *et*

al. 2004b), recent studies have demonstrated impacts of lepidopteran population outbreaks on deciduous shrubs that, at least occasionally and locally, can outpace the impact of vertebrate folivores (Post & Pedersen 2008, Jepsen *et al.* 2013). The role of boreal and Arctic insects in controlling woody vegetation may become substantially more important in a warming climate, because of their often non-linear responses to increasing temperature (Hagen *et al.* 2008, Jepsen *et al.* 2011).

Evidence for vegetation-state shifts from moss-rich tundra heaths to more productive grasslands caused by reindeer grazing, according to the framework of Van der Wal (2006; see Fig. 12.7), comes from sites in high Arctic Svalbard (van der Wal & Brooker 2004) and sub-Arctic northern Fennoscandia (Olofsson *et al.* 2004). However, Bråthen *et al.* (2007) suspected that the finding regarding semi-domestic reindeer in northern Fennoscandia (Olofsson *et al.* 2004) was confounded by local effects of trampling close to fences separating herding districts (see Forbes *et al.* (2009) for similar local effects close to Nenets camp sites). Using a spatially extensive sampling design, Bråthen *et al.* (2007) found that abundant reindeer on the contrary depressed biomass of palatable grasses. However, in accordance with the EEH they noted that abundant semi-domestic reindeer were able to homogenize biomass of palatable forage plants across landscape-scale productivity gradients. Although
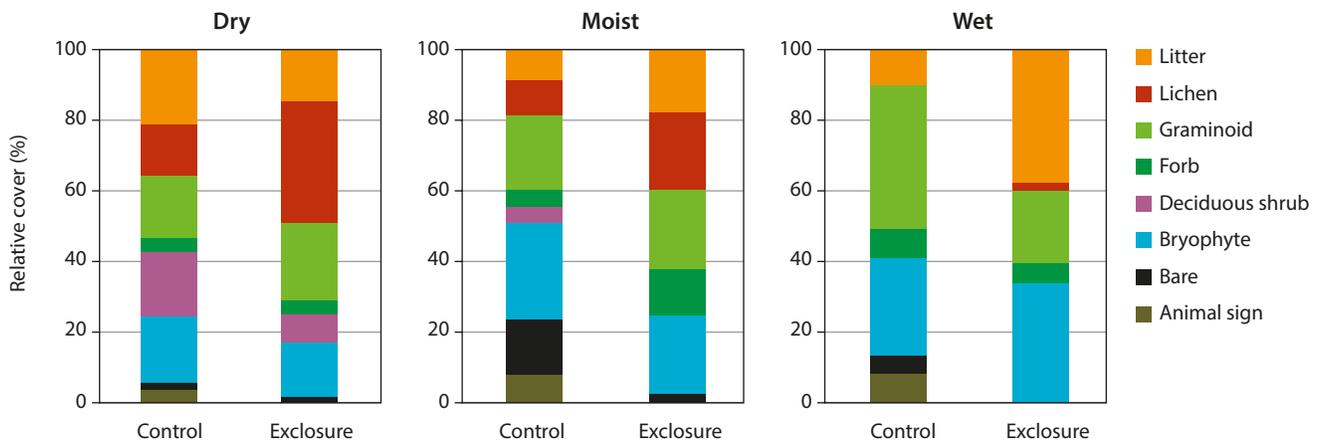
Figure 12.9. Long-term effects of lemming grazing on tundra vegetation composition. The plots show the mean relative cover of plant functional types and animal signs in control plots and exclosures from which lemmings had been excluded over 50 years in three tundra types on the Arctic coastal plain near Barrow, high Arctic Alaska, in 2010 (from Johnson *et al.* 2011).

abundant reindeer are known to be able to deplete their lichen resources on winter pastures (Johansen & Karlsen 2005) to the extent that this may cause population crashes and economically unsustainable management (Hausner *et al.* 2011), there is at present little evidence to substantiate use of terms such as 'habitat degradation' or 'ecological disasters' (e.g. as suggested by Moen & Danell 2003) to characterize reindeer-caribou grazing systems (van der Wal 2006).

A relatively high resilience of Arctic vegetation to herbivory is expected (van der Wal 2006, Oksanen *et al.* 2008), both owing to the fact that some Arctic plants are adapted to tolerate high levels of grazing (e.g palatable grasses; Zimov 2005), while others are generally unpalatable and thus resistant to herbivores. One typical grazing-resistant species is the black crowberry *Empetrum nigrum* that often dominates low Arctic tundra heath vegetation and has a retarding effect on ecosystem productivity (Bråthen *et al.* 2010). Crowberry does not appear to respond to changed abundance of vertebrate herbivores (Bråthen *et al.* 2007, Ravolainen *et al.* 2010), but may be severely impacted by emergent climate change-induced outbreaks of insects and pathogens (see Section 12.2.2.3). Conversely, grasses with high concentrations of silica – considered to be a defense against herbivory – decreased rapidly in response to experimental exclusion of mammalian herbivores, indicating that herbivores maintain their dominance (Ravolainen *et al.* 2011). Herbivory may also facilitate certain Arctic vegetation types. Arctic steppes are promoted by trampling and grazing by large mammalian herbivores (Zimov *et al.* 1995, Zimov 2005), while intense pulsed lemming grazing on mosses in snow beds (Virtanen 2000, Virtanen *et al.* 2002a) appears to stimulate growth of vascular plants and to promote higher species richness in such habitats (Oksanen *et al.* 2008). Examining the vegetation in 50-year-old lemming exclosures near Barrow in high Arctic Alaska also suggested that sustained lemming activity promotes growth of vascular plants in some habitats at the expense of lichen (Johnson *et al.* 2011; Fig. 12.9). However,

other Arctic habitats appear to have little resilience to certain forms of herbivory. A prime example of apparently irreversible habitat degradation caused by herbivore overabundance is the locally devastating impact of lesser snow goose populations in salt marshes in northern Canada (Jefferies *et al.* 2006). Grubbing for underground plant roots and rhizomes by geese is also a form of herbivory that has been found to have locally destructive effects on other types of Arctic vegetation, such as wet tundra, as well as drier tundra on Svalbard (van der Wal *et al.* 2007, Pedersen *et al.* 2013).

Explicit consideration of spatial scale is important in any studies concerned with trophic interactions (Post *et al.* 2009), because resource availability varies in space (habitat heterogeneity, patch dynamics) and time (successional processes, seasons). Jefferies (1999) emphasized that herbivores, because of their mobility, can exploit high quality forage, in a landscape context, when and where it occurs. Marell *et al.* (2006) studied nutrient dynamics of reindeer forage species across regional and local snowmelt regimes and found that the greatest spatial and temporal variability in nutrient concentrations occurred early in the thaw period, at the time of highest nutrient requirements by reindeer (including calves). Landscape-level heterogeneity in forage availability may decline in the future with earlier and faster melt-out of snow beds and snow patches (Bjork & Molau 2007, Post *et al.* 2008) leading to mismatched timing of herbivore reproduction relative to peak quality of their forage plants (Miller-Rushing *et al.* 2010).

Predator-prey interactions
Contrary to the predictions of the EEH, empirical evidence reveals that predators play an important role for the functioning of even high Arctic tundra food webs (Gauthier *et al.* 2011). Predators are present nearly everywhere in the terrestrial Arctic (Krebs *et al.* 2003). The guild of small- or meso-sized predators has been shown to depress lemming populations (Reid *et al.* 1995, Wilson *et al.* 1999), and it has been suggested that

specialist predators can drive the lemming cycle (see below). Applying a mass balance model to data from 12 sites located throughout the Canadian Arctic, Krebs *et al.* (2003) provided evidence that top-down regulation is more prevalent than bottom-up regulation, at least for small herbivores. This approach was further developed by Legagneux *et al.* (2012), who show that on Bylot Island only < 10% of the annual primary production is consumed by herbivores, whereas up to 100% of the herbivore production can be consumed by predators. Predator populations, which are larger than expected based on local terrestrial primary production, can be maintained mainly because of subsidies from marine ecosystems (Leroux & Loreau 2008, Gauthier *et al.* 2011). Marine resources are important for Arctic fox populations in many areas (Roth 2003, Eide *et al.* 2012, Tarroux *et al.* 2012), illustrating the 'coastal' aspect of the Arctic tundra biome. Inuit residents of Pond Inlet on Baffin Island, Nunavut report Arctic fox movements on the sea ice, particularly in spring when seals have new-born pups (Gagnon & Berteaux 2009). Allochthonous resources subsidizing predators can also originate from southern ecosystems. Geese and other birds breeding in the tundra in large numbers every summer, and whose eggs and chicks are heavily predated by tundra preda-

tors, are prominent examples (Gauthier *et al.* 2004, Jefferies & Drent 2006). For the large Arctic herbivores (reindeer and muskoxen), regulation by predators within the Arctic region has not been reported and seems improbable given the very low densities of large predators such as wolves (Reid *et al.*, Chapter 3).

Despite the fact that keystone predators have not been explicitly described from Arctic tundra ecosystems, predators may have indirect effects on vegetation primarily though their effect on small rodents. The characteristic small rodent cycles (voles and lemmings; Reid *et al.*, Chapter 3) have been attributed to many hypothetical causes, but currently the main focus is on trophic interactions. According to classical models, specialist predators are dynamically strongly coupled to their prey. In particular, year-round resident specialist predators can cause population cycles in their small rodent prey, whereas generalist or nomadic predators stabilize the prey's population dynamics (Hanski *et al.* 1991, Hanski *et al.* 2001). In the Arctic, small mustelids are resident specialist predators (Andersson & Erlinge 1977) and have been attributed a keystone role in generating the small rodent cycles (Hanski *et al.* 1991, Gilg *et al.* 2003; see Box 12.2).

Box 12.2. Lemming cycles in the unique food web of Wrangel Island

Wrangel Island is situated 140 km north of the Chukotka peninsula in bioclimate subzone B (Russia; 70.8° N, 179° W). Biodiversity on Wrangel is uniquely high for the Arctic (e.g. Daniëls *et al.*, Chapter 9 for plants), due to both historical stability (it has not been glaciated during at least two last major glaciations, was part of the extensive Beringian land area, and was not fully flooded by ocean transgressions; Bauch *et al.* 2001, Stauch & Gualtieri 2008) and the high diversity of landscapes. The Wrangel Island State Nature Reserve was established in 1976 and covers the whole island together with surrounding sea areas.

Systematic research on the island's fauna and flora started in 1970-1980. Since 1990, systematic monitoring of key species has been carried out by the scientific staff of the reserve using standard protocols. Two lemming species (Wrangel Island collared lemming *Dicrostonyx vinogradovi* and Wrangel Island brown lemming *Lemmus portenkoi*) are present together with a predator guild typical for this bioclimatic

subzone, with the notable exception of small mustelids (stoat and least weasel). Despite the lack of small mustelids, the lemming populations exhibit cyclic fluctuations. The period of the cycle was 5-7-years in 1970-1980 (Chernyavsky & Tkachev 1982). During the last decades, however, the cycles have been less pronounced, with more years with intermediate abundances and periods increasing to 8-9 years (Box 12.2 Fig. 1; Menyushina *et al.* 2012). Changes in snow conditions and repeated ground icing in winter are most likely causing these changes.

Box 12.2 Figure 1. Qualitative time series of lemming dynamics on Wrangel Island using an index ranging from 0 to 6. This series depicts the dynamics of both species together and combines information from all available sources of data (cf. Menyushina *et al.* 2012). The yellow boxes mark years where there were discrepancies between the different sources.
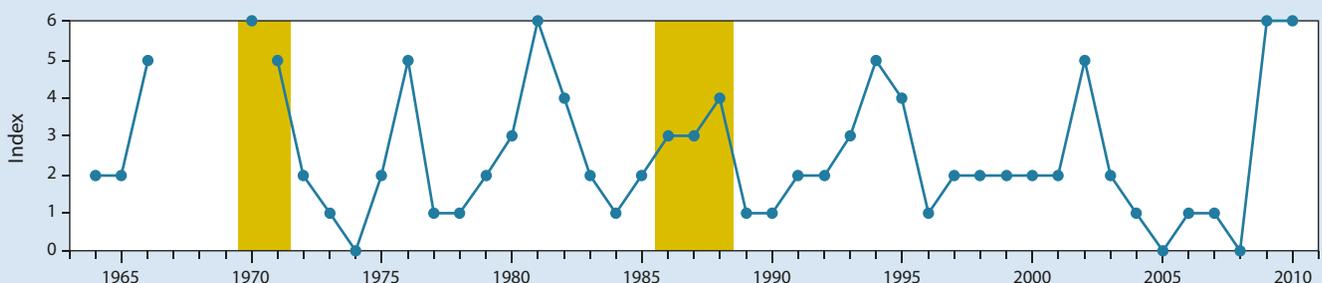
Other researchers, referring to EEH, propose that plant-herbivore interactions cause the lemming cycles (Turchin *et al.* 2000, Oksanen *et al.* 2008). Resolving the controversy regarding whether bottom-up vs. top-down processes cause Arctic small rodent cycles is at present hampered by limited time series data from few monitoring sites (Oksanen *et al.* 2008, Gauthier *et al.* 2009, Krebs 2011). Nevertheless it is important for understanding the functioning of tundra ecosystems.

A major difference between high Arctic lemming cycles and low Arctic vole cycles is their seasonal dynamic. Whereas lemmings typically reach peak densities before snow melt, because they breed under the snow, the exclusively summer-breeding voles usually reach their peaks in the fall (Ims & Fuglei 2005). High densities in spring, when predators reproduce, make lemmings a particularly important resource for specialized Arctic predators. Recent results suggest that lemming peaks are limited by snow conditions and winter climate (Kausrud *et al.* 2008, Gilg *et al.* 2009, Ims *et al.* 2011), setting a southern border for lemming-dominated small rodent communities and their associated predator guild (Section 12.2.1.1, Fig. 12.3). An alternative explanation could be that southern species of voles competitively exclude lemmings at their southern border.

Competition, facilitation and indirect interactions
Besides the trophic interactions reviewed above, other types of inter-specific interactions also structure tundra food webs. Their effects can be mutually negative (competition) or positive (facilitation) and be mediated by direct or indirect ('apparent') interactions. Cases of influential direct competitive interactions in tundra ecosystems have been found between predators (e.g. between the Arctic and the red fox; Tannerfeldt *et al.* 2002), herbivores (i.e. between lemming species; Morris *et al.* 2000) and plants (e.g. shading effects of tall shrubs; Totland *et al.* 2004). However, for plants in particular it has been noted that positive interactions ('facilitation') may be prominent and even dominate towards the climatically most extreme high Arctic subzones (Svoboda & Henry 1987, Callaway & Walker 1997). Facilitation may also take place among tundra herbivores as indicated by the positive association between reindeer and lemmings in snow-bed habitats (Ims *et al.* 2007). In the latter case, the underlying mechanism was thought to be a positive engineering effect of lemming moss grazing on growth of palatable herbaceous plants (Fig. 12.7; see also Oksanen *et al.* 2008). Conversely, abundant semi-domestic reindeer may have both habitat engineering and trophic effects that impact biodiversity negatively (see Section 12.3.3.4).

An influential indirect facilitation effect in tundra food webs is the well-documented link between the lemming cycle and the breeding success of ground nesting birds (Bety *et al.* 2001, 2002). In lemming peak years, predators concentrate on lemming prey, and, as a consequence, predator pressure on geese and shorebirds relaxes, and they breed successfully. In contrast, in subsequent years, when the lemming population crashes,

predators such as Arctic foxes, which have become numerous during the lemming peak, switch to prey on the eggs and chicks of ground nesting birds. As a result, the reproductive success of geese and shorebirds drops dramatically (e.g. Summers 1986). It has been suggested that the shorebird species most sensitive to predation by Arctic foxes are limited in their distribution to areas with regular lemming peaks (Gilg & Yoccoz 2010), because they are only able to maintain viable populations due to years when the predation pressure imposed by Arctic foxes is released by high lemming abundance. This assumption is supported by the fact that the highest diversity of *Calidris* species is found to coincide with the distribution area of lemmings, although alternative interpretations of such distribution patterns are possible.

12.2.2.2. Ecosystem functions

Above- and below-ground linkages
There is growing evidence that plant functional traits (PFT) (Lavorel & Garnier 2002) might have parallel implications both for herbivores and for decomposers (Cornelissen *et al.* 2004, Diaz *et al.* 2004, Cornwell *et al.* 2008, De Deyn *et al.* 2008, Fortunel *et al.* 2009). Thus, shifts in plant community composition will likely have important cascading effects above and below ground (Wookey *et al.* 2009). Conversely, soil microbes (the 'unseen majority', as described by van der Heijden *et al.* (2008)) may have important effects on Arctic plant diversity and productivity (Wallenstein *et al.* 2007). Furthermore, in spite of the major research emphasis on above-ground plant biomass, it is clear that below-ground plant biomass generally substantially exceeds above-ground in tundra (Jackson *et al.* 1996, Chapin & Ruess 2001, Mokany *et al.* 2006, Hollister & Flaherty 2010) with root:shoot ratios of ~ 4.8-6.6.

Undoubtedly, any analysis of the structure and function of Arctic ecosystems must therefore give appropriate emphasis to below-ground biota, even where the 'functional role' of the organisms themselves is not clearly known. Microbial communities do not necessarily respond to abiotic environmental factors in the same way as 'macro-organisms'; the latter show well-established declines in diversity with increasing latitude and altitude, but this is not apparent for soil microorganisms (Neufeld & Mohn 2005, Fierer & Jackson 2006, Bjorbaekmo *et al.* 2010, Chu *et al.* 2010, Fierer *et al.* 2011, but see Geml *et al.* 2009). However, such generalizations mask potentially important specific links between plants and microbes in the form, for example, of mycorrhizal associations (see Bjorbaekmo *et al.* 2010, Timling & Taylor 2012), endophyte/endorhizal fungi (Newsham *et al.* 2009, Peters *et al.* 2011) or symbiotic nitrogen-fixers; even here, though, the diversity of Arctic mycobionts appears high (Gardes & Dahlberg 1996, Peters *et al.* 2011) and not substantially constrained by large-scale (i.e. open ocean) dispersal barriers (Geml *et al.* 2012). Host-specificity of mycorrhizal fungi in the Arctic appears to be low (Walker *et al.* 2011c, Timling & Taylor 2012; see also Dahlberg & Bültmann, Chapter 10). The dominant ectomycorrhizal (ECM) fungi also show wide

ecological, and host, amplitude (Ryberg *et al.* 2009, 2011). Such 'cosmopolitan' strategies are likely clues to the success of these taxa in the Arctic.

Quantifying and understanding the links between soil biodiversity and ecosystem processes and functions remain a grand challenge globally, as well as for Arctic ecosystems. For the remainder of this section, we present examples of above- and below-ground linkages and processes in Arctic ecosystems, with specific emphasis on both C and nutrient cycling, and on energy fluxes, with their broader implications for biogeochemical and biophysical processes that link to the climate system. Examples include changes in net fluxes of GHGs, such as carbon dioxide (CO_2) and methane (CH_4), and alterations in surface roughness and albedo.

Effects of shifts in plant communities on net fluxes of GHGs

Global change drivers may operate directly on individual ecosystem components (e.g. producers, consumers and decomposers, and their component species), but also indirectly via responses in the other components. The timescales of responses may vary between ecosystem components (Shaver *et al.* 2000), and the question emerges whether traditional concepts of 'climax' ecosystems, or above- and below-ground processes and state variables being in equilibria, still apply. Indeed in the Arctic, where below-ground C and nutrient stocks are massive (Schuur *et al.* 2008, Tarnocai *et al.* 2009, Hugelius 2012) and have been accumulating over millennia, the potential exists for very substantial shifts in GHG budgets, with global implications in terms of the C cycle, CO_2 and CH_4 concentrations in the atmosphere, and thus the climate system. Shifts in plant communities (including treeline species, as well as the increasingly robustly documented 'shrub expansion' (see Section 12.3.3.1) and changes associated with disturbance (e.g. thermokarst or tundra fire) will lead to mismatches in above- and below-ground C stocks and fluxes. Thus the 'dynamic disequilibria' paradigm (Luo & Weng 2011) may now be a more useful framework for understanding ecosystem dynamics and coupling to the Earth System. Expressed very succinctly, however, "climate-induced ecological shifts in the plant community will affect the transfer of carbon-dioxide between biological and atmospheric pools" (Natali *et al.* 2012); in specific cases, the same assertion applies to net CH_4 fluxes.

Examples involving named species are few, especially from the Arctic, but changes in plant traits, with associated mycorrhizal shifts, have the potential to alter the magnitude, as well as the direction, of net CO_2 fluxes. Hartley *et al.* (2012) demonstrated that colonization of ericaceous heath (dominated by crowberry) by mountain birch *Betula pubescens* in the mountain birch forest-tundra heath ecotone in sub-Arctic Fennoscandia would likely result in a net loss of C to the atmosphere, even though the mountain birch forest is more productive than the heath (Fig. 12.10). It was thought that high plant (tree) activity in mid-season stimulates the decomposition of older soil organic matter (SOM) through so-called
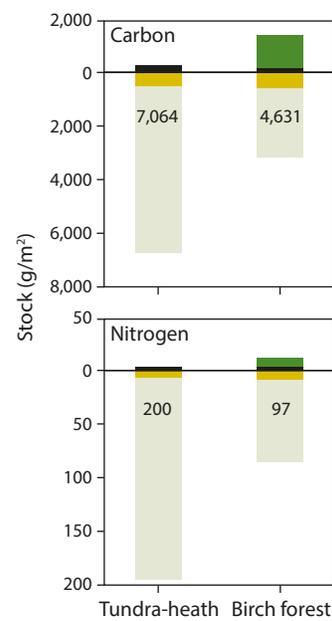
Figure 12.10. C and N storage in two ecosystems. The stocks are divided into above-ground tree biomass (green fill), above-ground shrub biomass (black fill), roots (yellow fill) and soils down to the underlying parent material (white fill). Above-ground stocks are shown above the x-axis; below-ground stocks are shown below the x-axis (from Hartley *et al.* 2012).

rhizosphere 'priming' (Kuzyakov 2002), and that this may relate to a shift from the ericoid mycorrhizal status of the heath, toward ECM dominance beneath birch; the latter resulting in more efficient decomposition of SOM. The net result of these changes in C stock might be a release of CO_2 to the atmosphere, possibly resulting in a positive contribution to global warming. The study supports the assertion of Read *et al.* (2004) that symbioses control nutrient cycles, productivity, species composition and functioning of heathland and boreal ecosystems. In a related study, Ryberg *et al.* (2009) concluded that the low host-specificity of ECMs in alpine cliff locations (c. 300-490 m in elevation above the previous study, but in the same region) is "likely to be able to facilitate the succession of the alpine tundra to subalpine forest by serving as mycorrhizal partners for establishing pioneer trees." This illustrates the potential interdependence of plants and their symbionts when individual species or communities are shifting, and the potential consequences for ecosystem C balance (see Hogberg & Read 2006). However, much more research is needed in order to understand and model the processes robustly, as well as to identify the microbial 'actors' involved, and whether ECMs are associated with specific rhizobacteria (see e.g. Courty *et al.* 2010, Hrynkiewicz *et al.* 2010), including 'mycorrhization helper bacteria' (Aspray *et al.* 2006).

The on-going Arctic greening, with its apparently strong component of increasing deciduous shrub abundance and height (Section 12.3.3.1), also raises the prospect of complex cascading effects on physical environment, biotic processes and interactions, and links with the broader earth system (Fig. 12.11). Our understanding of these cascades and their feedback implications for energy budget and climate relies heavily on a few local- to regional-scale field campaigns (Thompson *et al.* 2004, Beringer *et al.* 2005, Sturm *et al.* 2005a, 2005b) and modelling studies (McFadden *et al.* 2001, Loranty *et al.* 2011, Bonfils *et al.* 2012, Pearson *et al.* 2013).
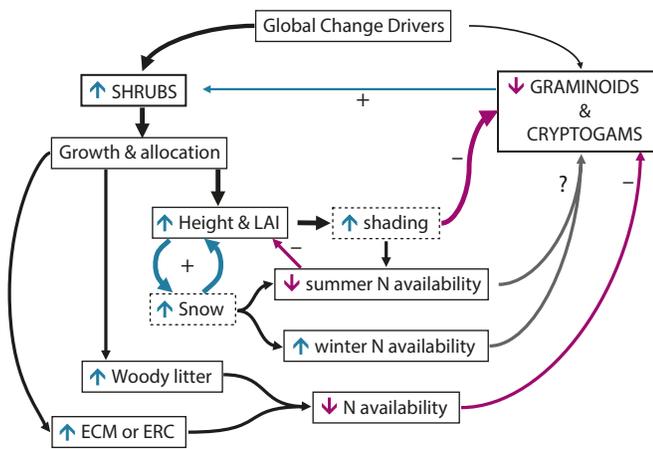
Figure 12.11. Ecosystem cascades and feedbacks resulting in an increase in deciduous shrubs and a decline in both graminoids and cryptogams (mosses and lichens) in response to increasing warmth and duration of the growing season in Arctic tundra. Note that stronger responses to climate drivers among deciduous shrub species result in a positive feedback between increasing height and leaf area index (LAI) and increased trapping of snow. Changes in the depth, duration and both physical properties and chemical composition of the snowpack can have either positive or negative impacts on N availability through altering soil thermal and moisture regime. Increased height and LAI of shrubs will likely have a negative impact on graminoids and cryptogams through shading effects. Furthermore, increased prevalence of species with ectomycorrhizas (ECM) or ericoid mycorrhizas (ERC) will likely decrease nutrient availability to other species, with further negative consequences. Increases in the proportion of low-N, but high lignin woody litter (leaf and stem litter of woody species associated with increasing shrub dominance) will also tend to reduce N availability (from Wookey *et al.* 2009). For clarity, the figure does not address herbivory directly; this is discussed in the text.

Although increasing shrub height and canopy density is likely to trap more snow and reduce sublimation losses, this process depends on regional snow availability and distribution patterns in the landscape, as well as on vegetation structure (McFadden *et al.* 2001, Liston *et al.* 2002). The implications for surface energy budget and the partitioning of net radiation into ground, latent and sensible heat fluxes (particularly during late winter and spring) also depend on whether snow entirely covers the vegetation, or whether branches protrude substantially above the snow. Using an Earth System Model, Bonfils *et al.* (2012) determined that taller and aerodynamically rougher shrubs lower the albedo (reflectance) earlier in the spring than short shrubs, and they also transpire more (H$_2$O vapor) following bud-burst; both factors contribute to regional warming. Indeed, the shrub expansion can accentuate the 'polar amplification' of climate change (Serreze *et al.* 2000, Chapin *et al.* 2005, Bhatt *et al.* 2010).

Although still challenging to quantify and model, albedo effects are relatively well-understood compared with the implications of increased 'shrubiness' in terms of regional snow depth and duration and soil thermal

regimes throughout the year (Blok *et al.* 2010, Lawrence & Swenson 2011, Bonfils *et al.* 2012). These are, however, critical factors influencing ecosystem C balance through their influence on soil biological activity (Sturm *et al.* 2005b, Cahoon *et al.* 2012a). Sturm *et al.* (2005b) highlighted that shrub expansion on the low Arctic North Slope of Alaska, with associated increases in depth of winter snow, would increase substantially the days when soils beneath the snow remain warm enough (down to -6 °C, or even lower) to support continued biological activity; this has the potential to increase plant-available nitrogen (N) during the thaw period (Fig. 12.11), further supporting shrub growth. Further, Weintraub & Schimel (2005) hypothesized that the interplay between N and C cycling and shrub expansion has the potential to increase C sequestration because wood has the highest C:N ratio of any plant tissue and decomposes slowly. Cornelissen *et al.* (2007) concur that "the ongoing warming-induced expansion of shrubs with recalcitrant leaf litter across cold biomes would constitute a negative feedback to global warming", although they caution that this negative feedback has to be evaluated against any direct warming-related increases in decomposition rate (and therefore, potentially, nutrient availability), a phenomenon that is well-documented (Rustad *et al.* 2001). Whether 'shrubification' alters the fire-susceptibility of plant communities also warrants serious attention (Higuera *et al.* 2008, 2011), especially as wild-fires have profound ecological consequences not just for vegetation and wildlife, but also for surface energy budget, permafrost and C cycling, as dramatically illustrated by the Anaktuvuk River tundra fire of 2007 in low Arctic Alaska (Jones *et al.* 2009, Mack *et al.* 2011, Rocha & Shaver 2011b).

'Shrub-related' changes in soil physical conditions, as well as mycorrhizal status, have major implications for soil microbial communities and their functioning, and these will be superimposed upon the direct responses of soil microbes to climate change drivers. Wallenstein *et al.* (2007) compared the bacterial and fungal community structure of tussock, intertussock and shrub organic and mineral soils at Toolik Lake, low Arctic Alaska. They found that shrub soils were consistently dominated by Proteobacteria, while tussock and intertussock soils were dominated by Acidobacteria. It was concluded that shrub soils contained an active, bioavailable C fraction, while tussock and inter-tussock soils were dominated by more recalcitrant substrates for microbes. This result might appear at odds with Weintraub & Schimel's (2005) and Cornelissen *et al.*'s (2007) suggestion that shrub litter is recalcitrant, but subtler rhizosphere and mycorrhizal processes, such as rhizosphere 'priming' (see above and Hartley *et al.* 2012) may also be at play (as noted by Clemmensen *et al.* 2006). Thus, several shrub species, with their associated ECMs, may function similarly to mountain birch in 'priming' organic matter decomposition (see Hartley *et al.* 2012, as discussed above) and accelerate C release from soils. The net effect on ecosystem CO$_2$ fluxes will depend on both rates of primary production and decomposition (De Deyn *et al.*

2008, Cahoon *et al.* 2012a), and the results of a long-term nutrient addition experiment in low Arctic Alaskan tussock tundra (Mack *et al.* 2004) caution against the assumption that increased plant productivity necessarily means greater ecosystem-level C sequestration.

The actual species involved in the shrub expansion will likely also play a significant role. The key genera are *Betula* (birch), *Salix* (willow) and *Alnus* (alder), and there are regional contrasts in the way the shrub expansion is expressed (Myers-Smith *et al.* 2011a). Although these are all deciduous shrubs, their stature varies both within and among genera, as, potentially, does their interaction with snow (Sturm *et al.* 2005a). A key functional contrast may also exist between *Alnus* and the other shrub genera; the former is able to fix N in symbiosis with the actinomycetous genus *Frankia* (Huss-Danell 1997), and is likely also strongly dependent on ECM symbionts to meet the increased phosphorus (P) demands of nodule formation (Gentili & Huss-Danell 2003). This tripartite symbiosis undoubtedly has major implications for ecosystem nutrient recycling and C fluxes, but has not been explicitly addressed in the context of the pan-Arctic shrub expansion.

Effects of plant community shifts on biophysical processes

Several studies indicate that the Arctic 'shrubification' will likely have negative consequences for cryptogams (mosses, lichens, liverworts and hornworts; Cornelissen *et al.* 2001, van Wijk *et al.* 2004, Stewart *et al.* 2011, Elmendorf *et al.* 2012, Lang *et al.* 2012; see also Daniëls *et al.*, Chapter 9 and Dahlberg & Bültmann, Chapter 10). The broader consequences of a shift in plant community composition for ecosystem physical properties (e.g. soil temperature and moisture status, and active layer depth) and function (i.e. nutrient cycling, N fixation and trace gas fluxes) remain unclear (Cornelissen *et al.* 2007, Stewart *et al.* 2011, Street *et al.* 2012). However, we do know that key bryophyte genera (e.g. *Sphagnum*) are 'peat-forming' and play a key role in C balance (Cornelissen *et al.* 2007). For example "*Sphagnum*-dominated peatlands head the list of ecosystems with the largest known reservoirs of organic carbon" (Hajek *et al.* 2011). Van Breemen (1995) refers to *Sphagnum* as an 'ecosystem engineer' through its ability to outcompete vascular plants for light, through its influence on peat moisture content and thermal status, and because of its resistance to decay. The explanation for the latter remains the subject of active research, but the synthesis of both recalcitrant polyphenols and cell-wall pectin-like polysaccharides ('sphagnan'), as well as the strong acidification of the environment, are implicated (Hajek *et al.* 2011). Clearly, the decay resistance of *Sphagnum* litter has profound implications for C sequestration, soil thermal and moisture regimes, and interactions with vascular plants (Keuper *et al.* 2011). The role of bryophytes, more generally, as modifiers of soil thermal regime (and biological processes) and surface energy budget has been modeled by Beringer *et al.* (2001) and demonstrated experimentally by Gornall *et al.* (2007). Furthermore, both bryophytes and lichens are associated with cyanobacterial

N-fixing communities (Gavazov *et al.* 2010), but their broader role as the main pathway for new N supplies to tundra ecosystems is often overlooked. Turetsky *et al.* (2012) emphasize the functional role of mosses more generally in northern ecosystems, noting the need for studies that increase our understanding of slow ecosystem processes that "play out over centuries – permafrost formation and thaw, peat accumulation, development of microtopography." Generally, cryptogam functional ecology merits much more research attention in the Arctic (see Daniëls *et al.*, Chapter 9).

Effects of permafrost thaw

Permafrost thaw (through both active-layer deepening and thermokarst) has the potential for far-reaching consequences for ecosystem structure and function, as well as for down-stream processes in surface waters (see Wrona & Reist, Chapter 13). Tarnocai *et al.* (2009) estimate that permafrost soils contain ~ 50% of the estimated total global below-ground organic C pool. This C is not sequestered in a stable or safe site: deepening of the active layer will alter ecosystem net C flux (both for CO_2 and for CH_4), both by bringing 'old' soil organic matter into contact with actively metabolising microbial communities, and also through direct effects of changes in the thermal and moisture regimes in the active layer itself (Christensen *et al.* 2003, Schuur *et al.* 2008, 2009). In a recent modeling study, Koven *et al.* (2011) report that inclusion of permafrost in coupled models changes both the magnitude and direction of net C flux – from sink to source – at high latitudes (> 60° N). They emphasize that a major constraint for modeling is quantifying and understanding fine-scale controls on hydrological processes (at plot, hillslope and headwater catchment scale) that strongly modulate CO_2 and CH_4 emissions from soils (Fig. 12.12).

Permafrost thaw will influence emissions of CO_2 and CH_4 from soils and sediments directly through changes in temperature, oxygen status and the amount of organic material available for decomposition or fermentation, and also indirectly. Changes in microbial communities (Mackelprang *et al.* 2011) and vegetation in areas affected by permafrost thaw (due often to changes in hydrological status and the mixing of mineral and organic soils) will also influence net GHG fluxes. In a 'natural gradient' study in the sub-Arctic alpine tundra of the northern foothills of the Alaska Range, three sites were used to represent stages in the process of permafrost thawing and thermokarst over several decades (Schuur *et al.* 2007, 2009). The study recorded substantial shifts in plant community composition, from graminoid-dominated tundra in the least disturbed (and cold) site to shrub-dominated tundra at the most subsided (and warm) site (a feature also noted in Yamal, Russia; Walker *et al.* 2009). In spite of demonstrating the highest productivity, the shrub-dominated site showed a net loss of CO_2 to the atmosphere. Further studies are required on the consequences of permafrost thaw for net GHG emissions to the atmosphere, but it is logical to assume that a net release is likely, at least until net primary productivity 'catches up'.
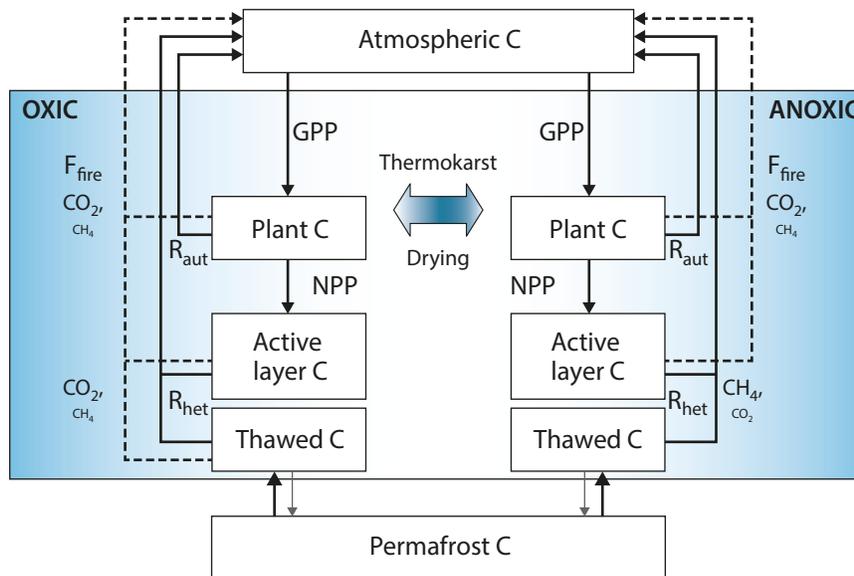
Figure 12.12. Conceptual diagram of the effect of permafrost thawing on climate. Permafrost C, once thawed, can enter ecosystems that have either predominantly oxic (oxygen present) or predominantly anoxic (oxygen limited) soil conditions. There is a gradient of water saturation on the landscape that ranges from fully oxic to fully anoxic, and ecosystems can become drier as permafrost thaws (shrinking lake area, drying wetland/peatlands), or wetter (thermokarst lakes). Soil oxygen status is a key determinant of the rate and form of C loss to the atmosphere. Decomposition in oxic soils releases primarily CO_2, whereas anoxic decomposition produces both CH_4 and CO_2, but at a lower total emission rate. Fire releases mostly CO_2, but also some CH_4, and can burn upland and wetland ecosystems, although burning of organic soils at depth is restricted in wetter environments unless there is a severe drought. These emissions of C through decomposition are offset by gross and net primary productivity (photosynthesis and net plant growth). Under some local conditions, it is possible that C will enter the permafrost pool (grey arrows), although this total amount is small relative to C that is expected to thaw from permafrost as a result of climate change. Abbreviations: C = carbon, CH_4 = methane, CO_2 = carbon dioxide, F = fire, carbon flux from fire, GPP = gross primary productivity, NPP = net primary productivity, R_{aut} = autotrophic respiration, R_{het} = heterotrophic respiration (from Schuur *et al.* 2008).

Shifts in hydrological conditions, and associated shifts in plant communities, can also have substantial consequences for CH_4 emissions, as CH_4 formation and emissions are modulated by individual plant species. In high Arctic NE Greenland (Zackenberg) Ström *et al.* (2003) found the sedges Arctic cotton-grass *Eriophorum scheuchzeri* and outspread tundra grass *Dupontia psilosantha* differed in release rates of acetate, which was hypothesized to be a precursor of CH_4 formation. The overall message is that key processes in the global C cycle (and the climate system) are not independent of the specific species involved.

12.2.2.3. Linking trophic interactions and ecosystem function

Recent studies have demonstrated an explicit link between trophic interactions and ecosystem function relating to GHG; specifically, they highlight the potential interactions that may arise between climate change drivers and the responses of biota across more than one trophic level (including pathogens). For example, climate and herbivores represent potential dual controls of vegetation communities and major ecotones in Arctic and alpine ecosystems (Section 12.2.2.1). For C cycling, however, major research emphasis on quantifying and understanding the abiotic controls on primary production and decomposition has resulted in a systematic

neglect of the ecological role of biotic factors, including trophic interactions, consumers and pathogens.

For invertebrate and vertebrate (mammalian and avian) herbivores, there is growing evidence of links between trophic interactions and ecosystem-level processes such as net CO_2 exchange. In a factorial warming × herbivore (muskox and caribou) exclusion experiment in low Arctic W Greenland, Cahoon *et al.* (2012b) showed that removal of the herbivores resulted in dramatic increases in shrub cover, ecosystem photosynthesis and a c. threefold increase in net C uptake. Warming accentuated these responses, but only when herbivores were absent. Concurrently, there was no clear indication of a change in soil respiration, so the conclusion is that herbivory constrains shrub productivity and limits C sequestration in this region. Similarly, Sjögersten *et al.* (2011) found that excluding grazing barnacle geese *Branta leucopsis* turned plots from sources to sinks of CO_2 at a high Arctic wet moss meadow in Svalbard, with associated changes in above-ground biomass and the proportion of vascular plants to bryophytes, but no effects on CH_4 fluxes, the total litter C pool or the soil C concentration. A related study (Sjogersten *et al.* 2012), with both grazing manipulation and experimental warming, revealed that high grazing intensity combined with warming reduced C storage and promoted decomposition both above and below ground.

Finally, milder winters can have unexpected effects on trophic interactions, with implications for ecosystem functions such as C cycling. The well-documented link between geometrid moth (*Operophtera brumata* and *Epirrita autumnata*) outbreaks and mild winters (Tenow & Bylund 2000, Jepsen *et al.* 2008, 2009, 2011), and the dramatic defoliation of mountain birch and corresponding shifts in the understory vegetation at the forest-tundra ecotone in northern Fennoscandia (Jepsen *et al.* 2013), has recently been shown to have major consequences for ecosystem C balance (Heliasz *et al.* 2011). Another scenario of winter warming in the Arctic might involve increases in depth (and possibly duration) of winter snow-pack. Olofsson *et al.* (2011), using snow fences to increase snow cover in sub-Arctic Swedish Lapland, found that plant biomass actually decreased owing to an outbreak of a host-specific parasitic fungus, *Arwidssonia empetri*, which killed the majority of the shoots of the dominant plant species, crowberry. Thus plant diseases can alter, and even reverse, the effects of a changing climate on tundra C balance. Outbreaks of both defoliating and parasitic fungi may become more frequent and widespread in the future, also in the Arctic.

12.3. TRENDS

In Section 12.2 we reviewed our current understanding of how climate and other abiotic pressures and disturbances interact with the structure and functions of tundra ecosystems as to shape biodiversity based on spatial analogues, experiments and models. In this section, we review observations of temporal trends in tundra ecosystems and the extent to which they can be attributed to specific drivers of change. Both the current status of terrestrial Arctic biodiversity and how it has been recently changing ought to be interpreted in light of its historical context and long-term trends (Section 12.3.1). Thus, even though our main purpose is to assess recent trends in ecosystem structure and function relative to contemporary anthropogenic drivers (Sections 12.3.2 and 12.3.3), it is generally important to keep in mind that non-equilibrium processes may also be involved, such as long-term recoveries from historical events. Finally, while we focus on trends in biodiversity at levels of communities or species guild, we also consider individual (keystone) species for which trends are expected to have knock-on effects on many other species, and the overall structure and functions tundra ecosystems.

12.3.1. Historical context

12.3.1.1. Environmental history and paleogeography

Present biodiversity patterns of Arctic terrestrial ecosystems became established during the Quaternary period, which spans the past c. 2.4-2.6 million years (see Section 2.3 in Payer *et al.*, Chapter 2). The Quaternary has been characterized by numerous fluctuations between globally cooler and warmer conditions with a periodicity of

c. 40,000 years. During the cold intervals, ice sheets accumulated on the northern continents, especially over northwestern Eurasia and northern North America. For the last 0.8-1.0 million years BP these fluctuations have been of larger amplitude than previously and have had a predominant periodicity of c. 100,000 years (Imbrie *et al.* 1984). This period is often referred to as the Quaternary Ice Age, with the cold intervals referred to as glacial stages, and the warmest intervals, with global climatic conditions broadly similar to those of the recent historic past, referred to as interglacial stages. These large climatic fluctuations are linked to major changes in the geography of the Arctic. Because of the accumulation of large volumes of ice in the continental ice sheets, global sea level was lowered by 100-120 m during glacial maxima (Fairbanks 1989), resulting in an extensive area of land in the region of the Bering Sea between Alaska and eastern Siberia, referred to as Beringia (Hopkins 1967, Hopkins *et al.* 1982). This region has been of considerable importance in relation to the history of Arctic biodiversity (Hultén 1937). During the glacial stages, the North Sea basin of NW Europe was also exposed, as well as large areas of additional land north of eastern Siberia. Although the coldest intervals during glacial stages occupy only perhaps 10% of the last 0.8-1.0 million years, glacial stages *sensu lato* account for > 85% of this time, while interglacials occupy < 15%. Thus, for most of the past million or so years, the geography of the Arctic has been very different from that with which we are familiar, with substantial ice sheets over northern North America and the western half of Eurasia, sea level markedly lowered and no connection between the North Pacific and the Arctic Ocean.

As a result, for much of the past one million years the extent of terrestrial ecosystems has been much reduced in the high Arctic and biota have been confined to nunataks during glacial stages. A similar displacement by ice occurred over much of northern continental North America and NW Eurasia, leaving central and eastern Siberia together with Beringia as the only extensive areas at Arctic latitudes supporting terrestrial ecosystems during glacial stages. On the other hand, the much colder climatic conditions of glacial stages have allowed many species that are today restricted to higher latitudes to extend their distributions to much lower latitudes. These same climatic conditions also led to the extension of permafrost to much lower latitudes, especially in Europe (Dawson 1992, van Huissteden *et al.* 2003). It would, therefore, be inappropriate to view the effects of Quaternary history on Arctic biodiversity only from an Arctic perspective. Thus the geographical scope of this discussion includes those areas of the boreal and north temperate zone that supported characteristically Arctic biota during glacial stages.

12.3.1.2. Paleodiversity of Arctic terrestrial ecosystems

The expansion of cold Arctic habitats provided opportunities for the evolution in the Arctic of taxa adapted to these conditions (Lister & Sher 2001, Abbott & Bro-
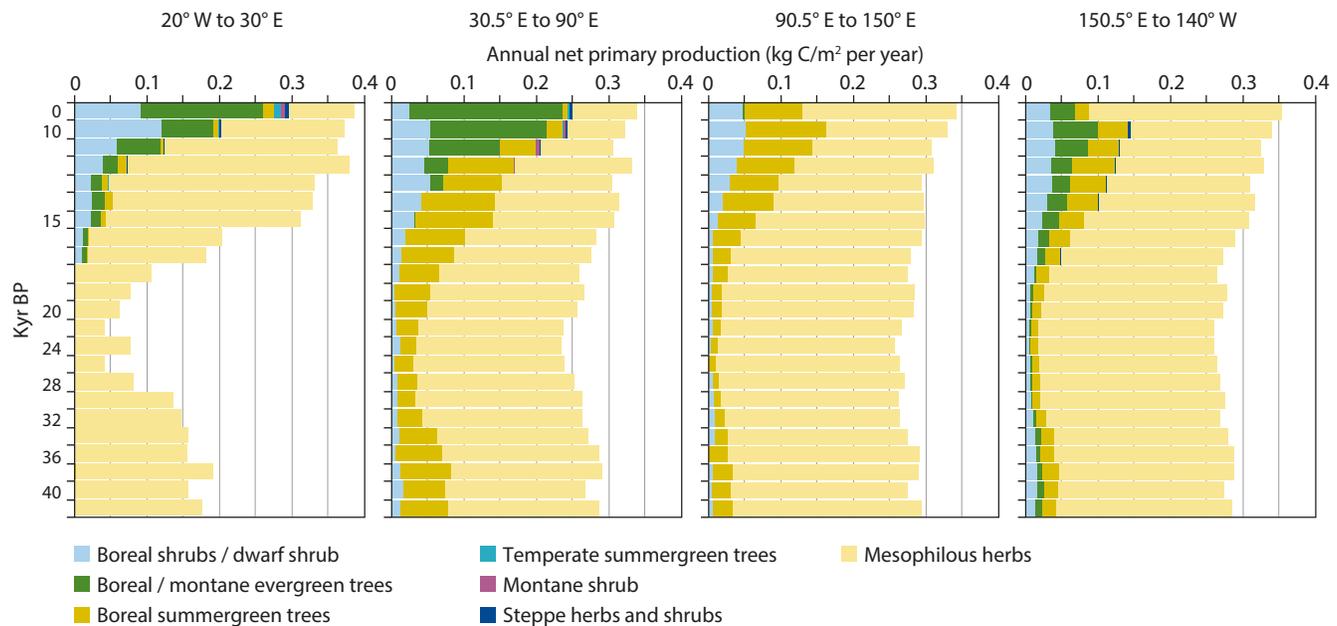
Figure 12.13. Simulated annual net primary productivity of 11 aggregate plant functional types during the later part of the last glacial stage and the early Holocene (42,000-10,000 years BP) for northern Eurasia and Beringia. Each panel represents a longitudinal section north of 60.5° N. For details of the methods used to make these simulations, see Allen *et al.* (2010).

chmann 2003, Harington 2008). Plant species evolved from shrubs and herbs that occupied open areas of the northern forest and from alpine species that migrated northward along mountain ranges (Murray 1995). Newly evolved mammalian species contributed to a long-term increase in biodiversity in the region (Lister 2004). Recently, this trend has reversed. Iconic species like woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis* and other 'megafauna' are now extinct (Lister & Sher 1995, Stuart *et al.* 2004, Stuart 2005), having failed to survive rapid environmental changes during the transition to the Holocene (Lister & Stuart 2008). While the underlying causes of these extinctions, and especially the extent to which humans played a part, remain a matter of debate (Barnosky *et al.* 2004, Stuart 2005, Guthrie 2006, Nogués-Bravo *et al.* 2008), the loss of these species represents a (geologically) highly recent decrease in Arctic biodiversity. Furthermore, the extinction of these and other large herbivores may have had long-term impacts upon many other components of Arctic ecosystems (Zimov 2005, Johnson 2009).

These cold-adapted large vertebrates had maximum distributional extents during glacial stages (Stuart *et al.* 2004). Extant Arctic and sub-Arctic species, such as reindeer/caribou, muskox and Arctic fox, were also present in the faunas characterized by the now extinct species. So too were species that today are associated with steppe or prairie ecosystems, notably saiga antelope *Saiga tatarica* and horse *Equus ferus*. Paleovegetation evidence indicates that these extensive ecosystems of glacial stages were composed of mixtures of plant species principally found today either in tundra or steppe ecosystems, often with a predominance of grasses Poaceae and sedges Cyperaceae accompanied by a wide

variety of mesic forbs (Edwards *et al.* 2000, Anderson *et al.* 2004). The macrofossil evidence that so far has been studied indicates that these ecosystems likely comprised a mosaic of tundra-like and more steppic communities, related to topographic and climatic gradients, and that these communities also were relatively diverse compared with many contemporary tundra communities (Edwards & Armbruster 1989, Goetcheus & Birks 2001, Kienast *et al.* 2005, Zazula *et al.* 2006a, 2006b).

The presence of a large biomass of herbivores in the glacial stage ecosystem raises the so-called productivity paradox: how could there have been enough primary production to have supported such a diverse fauna? A recent study using a dynamic vegetation model (Smith *et al.* 2001, Miller *et al.* 2008) to simulate the past vegetation cover of northern Eurasia and Beringia, north of 35° N and for the period 42,000-10,000 years BP, shows a higher productivity of mesic herbs in treeless northern regions during much of the last glacial stage than in modern tundra, but a reduced productivity of shrubs and dwarf shrubs (Fig. 12.13; Allen *et al.* 2010). These findings are in broad agreement with the observation that ecosystems dominated by palatable forbs and grasses are able to support more grazers than are those dominated by woody plants, such as modern shrub-tundra (Guthrie 1982). These glacial ecosystems represent a distinct biome that does not exist today, except for potential small-scale analogues in the continental interiors of Alaska, Yukon and Siberia (Edwards & Armbruster 1989, Zazula *et al.* 2006a), but that was often extensive during the Quaternary period, reaching its greatest extent during glacial stages and most probably being restricted to eastern Siberia during interglacial stages prior to the Holocene (Sher 1997). This biome is most often referred

to as 'steppe-tundra', reflecting the mixed composition of its biota: steppe and tundra biomes would have become contiguous over large areas with the virtual disappearance of boreal forest under the dry, cold glacial conditions (Edwards & Armbruster 1989, Guthrie 2001, Walker *et al.* 2001b, Elias & Crocker 2008).

Whereas the steppe-tundra biome may often have been extensive in the past, it seems likely that some components of the modern tundra biome are more extensive today than they have been during most of the past 0.8-1.0 million years. Discontinuously-vegetated tundra and polar desert are inferred to have occupied some drier regions of the high Arctic during glacial stages, and also to have occurred on nunataks, but their extent nonetheless was less than today. Tussock-tundra (dominated by cotton grasses *Eriophorum* spp.) and shrub-tundra communities that are today characteristic of more mesic, continuously-vegetated areas were not important components of the glacial-stage biomes. Pollen data show these communities expanding to replace steppe-tundra with the onset of interglacial conditions in Beringia (Oswald *et al.* 2003, Anderson *et al.* 2004).

Many species considered today to be typical dry tundra species were components of the very different steppe-tundra biome for most of their evolutionary history. Whereas, for much of the Quaternary, plant species requiring more mesic conditions (e.g. dwarf birch, shrub birch *Betula glandulosa* and cotton grass) would have been restricted to locally favorable habitats, species that are adapted to dry, steppic habitats (e.g. saiga antelope) and Arctic steppe plants are geographically much more limited today than during glacial stages (Murray *et al.* 1983, Edwards & Armbruster 1989). The niches of other species, however, are such that they were widely distributed in both glacial and interglacial ecosystems (e.g. reindeer/caribou). Thus, over the past 0.8-1.0 million years, many species' geographical distributions and populations are likely to have been reduced and/or fragmented during interglacial stages, whilst for other taxa the reverse is probable.

The early Holocene (c. 11,400-8,000 years BP) may have been an interval of extreme range reduction for Arctic terrestrial taxa with tundra affinities (e.g. Kraaijeveld & Nieboer 2000). In many regions, although not all, boreal forests extended to higher latitudes than today (MacDonald *et al.* 2000, Payette *et al.* 2002), responding to and also amplifying the warmer climatic conditions (Gallimore *et al.* 2005). Globally the area of tundra has been estimated to have been reduced by ~ 20% compared to the present (Callaghan *et al.* 2005). This is likely to have represented significant bottlenecks for some taxa, reducing Arctic biodiversity at least regionally, and perhaps even globally, especially at the intra-specific level. For example, a marked reduction in genetic diversity in muskoxen is dated to between c. 21,000 and 5,000 years BP (MacPhee *et al.* 2005). This reduction in genetic diversity is associated with regional extinction of the species across much of Eurasia during this interval. A well-documented global extinction of an essentially Arc-tic species during the middle Holocene is that of woolly mammoth, the last known population of which went extinct on Wrangel Island ~ 4,000 years BP (Vartanyan *et al.* 1993). On the other hand, the more favorable mid-Holocene climatic conditions are also likely to be implicated in greater productivity at very high latitudes, as reflected in the colonization of high Arctic islands by reindeer/caribou (Gravlund *et al.* 1998) and the extension of the range of muskoxen to N and NE Greenland (Bennike & Andreasen 2005, Campos *et al.* 2010), both of which apparently date from the middle Holocene.

Thus, in the context of recent geological history, the present biodiversity of the Arctic and its ecosystems is relatively low. Cold-adapted biota, including many species that today are restricted to the Arctic, were more widely distributed during much of the Pleistocene. The repeated changes between glacial and interglacial periods may have promoted an increase in Arctic biodiversity through allopatric[3] speciation, promoted by range fragmentation and dispersal-related founder effects. The nature of the climatic transition to the Holocene, and of the warmer climatic conditions in high northern latitudes during the early and middle Holocene, however, appears to have been uniquely deleterious in its impacts upon Arctic biota, leading to regional and even global extinctions of some Arctic taxa. Seen against this background, current global climatic warming poses a severe threat to the maintenance of the present, already impoverished, biodiversity of the cold-adapted Arctic biota.

12.3.2. Contemporary trends in drivers of change

12.3.2.1. Climate change

Climate in the Arctic is currently warming rapidly. In the five years following the Arctic Climate Impact Assessment (ACIA 2005) the annual temperature anomalies averaged over a pan-Arctic domain (60-90° N) exceeded values measured since 1880 and were the warmest five years in the entire record (Walsh *et al.* 2011). Considering a wider time frame, four of the five warmest decades of a reconstruction of the climate for the last 2000 years occurred between 1950 and 2000 (Kaufman *et al.* 2009). There is, however, considerable spatial and temporal variability in the present Arctic warming (Walsh *et al.* 2011). Warming is greatest in autumn and winter over the Arctic Ocean and adjacent areas, consistent with the recent loss of Arctic sea ice (Serreze *et al.* 2009). Summer warming is particularly strong in eastern Eurasia, the Canadian high Arctic and Greenland (IPCC 2007, NASA-GISS 2010). Some of the key manifestations of a warmer climate in terrestrial areas include: (1) later freeze-up and onset of snow cover in autumn, (2) earlier snow melt in spring (Derksen &

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3 Allopatric speciation is speciation that occurs when biological populations of the same species become isolated from each other to an extent that prevents genetic interchange.

Box 12.3. Rain-on-snow (ROS) events on Svalbard

The high Arctic Svalbard archipelago harbours one of the northernmost terrestrial ecosystems of the world (74°-81° N, 10°-35° E). However, a branch of the North Atlantic Current that runs to the west of the archipelago causes mean winter temperatures to be up to 20 °C warmer than found at similar northern latitudes elsewhere.

A main climatic driver in the Svalbard ecosystem is ROS events in winter, which occur regularly due to the oceanic climate and cause icing and inaccessible pastures. Icing events have a strong impact on the population dynamics of Svalbard reindeer *Rangifer tarandus platyrhynchus* and sibling vole *Microtus levis* (Box 12.3 Fig. 1; Hansen *et al.* 2011, Stien *et al.* 2012), as well as the two other resident vertebrates, the Svalbard rock ptarmigan *Lagopus muta hyperborea* and the Arctic fox. Thus the ROS events synchronize the dynamics of the entire herbivore guild (reindeer, vole and ptarmigan) and the only predator (Arctic fox), the latter with a one year lag (Hansen *et al.* 2013). The population dynamics of the Arctic fox seem to be driven mainly by fluctuations in the density of Svalbard reindeer carcasses in late winter (Fuglei *et al.* 2003, Eide *et al.* 2012), and this causes a delayed response in the Arctic fox population dynamics to the ROS driven fluctua-tions observed in the reindeer population (Hansen *et al.* 2013). Variations in the Arctic fox population size have knock-on effects on the breeding success of geese (Tombre *et al.* 1998, Fuglei *et al.* 2003). Furthermore, icing is also found to impact the soil invertebrate community (Coulson *et al.* 2000).
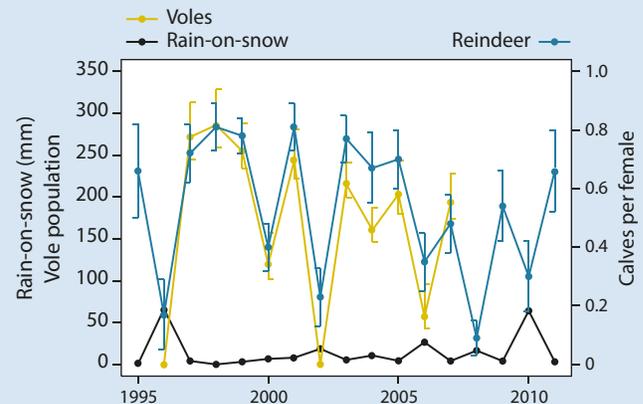
Box 12.3 Figure 1. Rain-on-snow events (mm) synchronize annual estimates of sibling vole population sizes and calves per female of Svalbard reindeer (from Stien *et al.* 2012).

Brown 2012), (3) warming and thawing of permafrost, (4) increase in the frequency and severity of extreme weather events, and (5) increase in the frequency of tundra fires (IPCC 2007, Bartsch *et al.* 2010, Bhatt *et al.* 2010, Hu *et al.* 2010, Xu *et al.* 2013).

In addition to decadal temperature trends, there is widespread concern over changing patterns of precipitation (Walsh *et al.* 2011). Snow is a dominant feature of Arctic terrestrial landscapes. Snow has low thermal conductivity, which allows it to insulate the surface from large heat losses in winter, and at the same time its high albedo contributes to keeping the Arctic cold. In addition to the duration of snow cover and snow depth, the quality of the snow is an important determinant of ecosystem functioning. Over the pan-Arctic terrestrial region (excluding Greenland) snow cover duration decreased by 3.4 days per decade between 1972 and 2009 (Callaghan *et al.* 2011a). At the same time, however, snow depth has increased in some areas, notably in Eurasia. Mild spells in winter inducing freeze-thaw cycles and sometimes heavy precipitation in the form of rain-on-snow (ROS) (Rennert *et al.* 2009, Bartsch *et al.* 2010, Hansen *et al.* 2011, 2013) create either very ice-crusted snow packs or sometimes even layers of pure ice on the ground (Box 12.3). While ROS is a sufficiently regular phenomenon in the oceanic parts of the Arctic not to be defined as an extreme event, it is considered extreme for the continental parts of the Eurasian Arctic (AMAP 2011).

While climate has always fluctuated dramatically in the northern high latitudes, the warming phase underway is important in several respects. First, it is taking place at a time when the Arctic is host to large numbers of human residents (Larsen *et al.* 2010). Second, pressures for strategic access to the region, for resource exploitation and geopolitical purposes, are at an all-time high, with major implications for future energy supplies and governance regimes (AMAP 2007, AGP 2010, Smith 2010). Finally, the current warming trend began from a higher baseline mean temperature than was the case for the most recent previous warming trend at the end of the Pleistocene approximately 11,000 years BP.

12.3.2.2. Land-use, natural resource management and industrial development

There is no crop agriculture in the Arctic, and the major form of land-use is reindeer herding by indigenous people, mostly in Eurasia. The tundra areas in Eurasia occupied at least seasonally by semi-domestic reindeer herds are immense, even if many regions are shared with wild herds. Trends in the herding industry including changes in the size of herds have recently been reviewed elsewhere (Forbes & Kumpula 2009, Forbes 2010, Hausner *et al.* 2011, Huntington, Chapter 18) and will be mentioned only very briefly here. Reindeer management is important because the animals lie at the center of a complex web of ecosystem goods and services.

Herds constitute a critical renewable resource upon which people and wildlife depend, including predators vital to regional biodiversity (e.g. lynx *Lynx* spp., wolf, wolverine, bears and eagles). Strong predator control is often an integral part of the reindeer management regime that ultimately may result in regional extermination of top predators such as wolf (Tveraa *et al.* 2007). Due to their large numbers, reindeer exert a number of important controls on ecosystem structure and function, through their effects on vegetation and the associated guild of scavengers (see Section 12.2.2.1 and Box 12.6). Herd sizes in the Nordic countries and the Nenets portions of northern Russia have increased considerably during the last decades and are at or near historic highs (Forbes & Kumpula 2009, Forbes *et al.* 2009). In other areas of Russia, herd sizes have on the contrary declined (Vors & Boyce 2009, Huntington, Chapter 18). The best ways to manage herds and pastures is subject to political discussion (Hausner *et al.* 2011). Some authors write about overabundance of reindeer, and concerns about the sustainability of pasture use are arising (e.g. Moen & Danell 2003).

Wild ungulates such as caribou/wild reindeer, muskoxen or Eurasian elk/moose are important hunting resources for people living in tundra areas, and as such they are managed in many parts of the Arctic (see Reid *et al.*, Chapter 3 and Huntington, Chapter 18). Although wild populations usually do not reach as high densities as the semi-domestic reindeer herds, management decisions may have consequences for the ecosystem. Muskoxen have been reintroduced in several areas in Alaska and the Russian Arctic, notably on the Taimyr Peninsula, as well as in W Greenland. On Wrangel Island both muskoxen and reindeer have been introduced during the 20th century (1975 and 1950 respectively, Gruzdev & Sipko 2007a, 2007b).

The present distribution of large-scale industrial developments is very localized (AMAP 2007, Kumpula *et al.* 2011, 2012). Onshore oil and gas extraction is concentrated on the North Slope of Alaska, Canada's Mackenzie River valley and delta regions, and in Russia within the Timan-Pechora and W Siberian basins (Nuttall & Wessendorf 2006). However, industrial development is spreading rapidly across many sectors of the circumpolar North (Walker *et al.* 1987, NRC 2003, Rasmussen & Koroleva 2003, AMAP 2007, Mikkelsen & Langhelle 2008, Kumpula *et al.* 2011). This trend is expected to continue in conjunction with a warmer climate, as existing resources become potentially easier to access and new sources become more economically viable (IPCC 2007, Smith 2010). In terrestrial ecosystems, the chief concerns surrounding industrial development are that (1) most types of human impact invariably reduce species richness in tundra vegetation and may induce vegetation transitions, and (2) the results of these impacts can persist for many decades, if not centuries (Vilchek *et al.* 1996, Forbes *et al.* 2001). However, to some extent anthropogenic mechanical disturbances resemble those resulting from natural phenomena, such as land-slides or cryoturbation, which are inherent parts of the functioning of the tundra that stimulate ecosystems dynamics (Walker 1996; see Section 12.2.1.2).

12.3.3. Contemporary trends in ecosystem structure and function

12.3.3.1. Climate change and trends in vegetation

Remote sensing studies show that the NDVI (see Box 12.1) has increased across much of the Arctic between 1982 and 2008 (Fig. 12.14; Bhatt *et al.* 2010), indicating increased productivity (Raynolds *et al.* 2006). The latest and most robust NDVI dataset shows that between 1982 and 2012 about a third of the Pan-Arctic has substantially greened, < 4% browned and > 57% did not change significantly (Xu *et al.* 2013). The greatest changes occurred in N Alaska and on the Beaufort Sea coast, whereas some regions along the Bering Sea and Chukchi Sea coasts show a decrease in NDVI. The increase in NDVI was correlated with sea ice declines and warmer summer temperatures (Raynolds *et al.* 2008, Bhatt *et al.* 2010), as well as with a prolongation of the growing season (Xu *et al.* 2013). Vegetation seasonality in the Arctic region has had a 7° latitudinal shift equatorward during the last 30 years (Xu *et al.* 2013). The observed changes in NDVI are attributed to increased growth of shrubs, as evidenced in Alaska, and to increased plant density in the high Arctic (Bhatt *et al.* 2010). Using a newly developed regression model between NDVI and above-ground tundra plant biomass (Epstein *et al.* 2012), Raynolds *et al.* (2012) show that biomass has increased most in southern bioclimate subzones (E to C). Results also showed that heterogeneity was high across regions and vegetation types. Changes in NDVI, and thus in plant biomass and phenology, are however not caused by climate alone but are a result of multiple ecological and social factors that affect primary tundra productivity (Walker *et al.* 2009). For example, studies on the Yamal Peninsula in Russia showed no strong spatial correlation between summer warmth and NDVI. In fact, much of Yamal has greener vegetation than expected based on the circumpolar correlation of temperature and NDVI, and much intra-regional variation in NDVI was associated to landscape structure and land-slides (Walker *et al.* 2009).

Increased plant productivity with climate warming has been documented at high latitudes, notably for a high Arctic heath and wet sedge tundra on high Arctic Ellesmere Island, Canada (Hudson & Henry 2009) between 1981 and 2008. On high Arctic Bylot Island, Canada, plant biomass in wetlands at the peak of summer production has increased by 123% over the last 23 years (Box 12.4; Gauthier *et al.* 2013). Changes in productivity are often associated with changes in plant community composition. Hence, on Herschel Island, the cover of grasses and dwarf shrubs increased at the expense of lichens in some upland habitats (Kennedy *et al.* 2001). In the tundra heath of Ellesmere Island, the productivity of evergreen shrubs and mosses increased, whereas deciduous shrubs,

Spring 50% sea ice (magnitude of change, percent)

-80 -70 -60 -50 -40 -25 -10 -1   1 10 25 40 50 60 70 80

Summer Warmth Index (percent change)

-200 -100 -75 -50 -25 -10 -5 -1   1   5 10 25 50 75 100 200

Summer Open Water (magnitude of change, percent)

-40 -35 -30 -25 -20 -15 -10 -5   5 10 15 20 25 30 35 40

Max NDVI (percent change)

-25 -20 -15 -10 -8 -6 -4 -2   2   4   6   8 10 15 20 25

a. Sea ice within 100 km from coasts

b. Summer Warmth Index, full tundra

c. MaxNDVI, full tundra

Percent change (1982-2011)

d. Time-Integrated NDVI, full tundra

Percent change (1982-2011)

Box 12.4 Increased primary production under climatic warming on Bylot Island

Bylot Island is located in the Canadian Arctic Archipelago, at 73° N, 80° W (subzone C). From 1976 to 2010, the area has experienced a strong warming trend in the fall (+4.3 °C over a 35-year period) and in spring and summer (+2.8 °C) but not in winter (December to February; Gauthier *et al.* 2011).

Two 100 km² study areas centered on glacial valleys have been the focus of continuous monitoring and intensive observational and experimental studies since 1989. Monitoring at Bylot aims to obtain quantitative data on all important ecosystem components. The strongest temporal trend detected on Bylot is a more than doubling (123% increase) of annual above-ground graminoid production (mostly tundra grass *Dupontia fisheri* and Arctic cotton-grass *Eriophorum scheuchzeri*) in wetlands over a 23-year period (Box 12.4 Fig. 1). This is largely due to an increase in summer temperature, because the sum of thawing degree-days explains a significant proportion of the annual variation in plant growth (Gauthier *et al.* 2013). The proportion of the primary production consumed by herbivores also shows a decreasing trend over time. A trophic balance model showed that < 10% of the total annual primary production is consumed by herbivores, whereas 20-100% of the herbivore production is consumed by predators (Legagneux *et al.* 2012). This suggests that predation plays a key role in the functioning of this ecosystem, and that increased plant production has little effect on higher trophic levels in this top-down regulated food web. Allochthonous subsidies may be important to maintain

high predator populations. For instance, high goose populations may help to sustain fox populations, especially in low lemming years (Giroux *et al.* 2012). In winter, predators like snowy owls and Arctic foxes use the sea ice for extensive periods of time (though this may be variable among years for foxes; Tarroux *et al.* 2010, Therrien *et al.* 2011), and thus they may depend upon the marine environment for their survival.
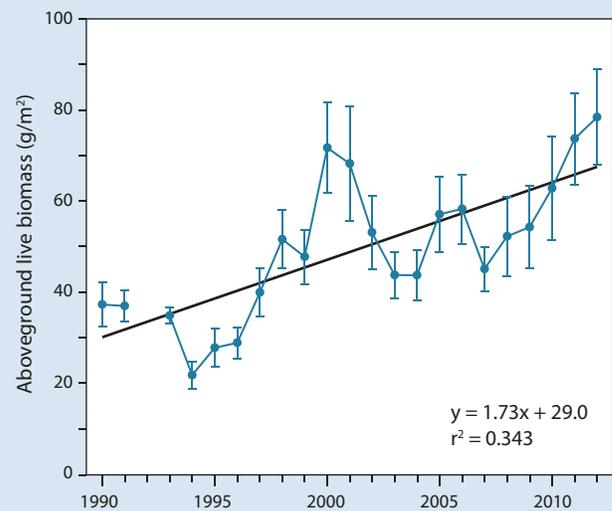
Box 12.4 Figure 1. Annual above ground production of wetland graminoid plants on Bylot Island, 1990-2012. Mean ± SE (n = 12 samples per year; trend equation based on individual samples). From Gauthier *et al.* (2013).

Figure 12.14. Trends in sea ice, open water, land temperature and NDVI for the circumpolar Arctic.

Top: The left panel shows the magnitude of changes in sea ice break-up (as represented by 50% sea ice concentration) and percent change for Summer Warmth Index for land area. The right panel panel shows the magnitude of changes in summer (May-Aug) open water and percent change in tundra MaxNDVI (annual maximum NDVI, usually reached in early August). Magnitude of change is the slope of the simple linear regression trend line multiplied by the number of years of record (30 years: 1982–2011). The sea ice concentration and open water data were derived from SMMR and SSM/I passive microwave records. Ice concentration time series were assembled using data averaged over a three-week period centered on the week when mean concentrations were 50%; the more negative the value on the scale, the earlier 50% ice concentration, or break-up, occurs. Open water indicates the integrated summer open water amount. NDVI and land surface temperatures (SWI) information were derived from AVHRR data and the NDVI is from the Global Inventory, Modeling and Mapping Studies (GIMMS) dataset.

Bottom: Percentage change for northern hemisphere, North America, Eurasia and major Arctic seas and adjacent land for (a) Open water, (b) Summer Warmth Index calculated as the sum of monthly mean temperatures on land exceeding 0 °C, (c) MaxNDVI, and (d) Time-Integrated NDVI (based on Bhatt *et al.* 2010, updated to 2011). Stars denote statistically significant changes.

forbs, graminoids and lichens did not change (Hudson & Henry 2009). A strong increase in above- and below-ground biomass was also documented over the past 25 years in wet sedge tundra on Ellesmere Island (Hill & Henry 2011). This increase in productivity is most likely due to indirect effects of increased temperature on mineralization and nutrient availability.

One of the best documented trends of change in the tundra ecosystem is increased growth of tall shrubs in the low Arctic tundra subzones (see Myers-Smith *et al.* 2011a for a review). Sturm *et al.* (2001) and Tape *et al.* (2006) compared aerial photographs from 1945-1955 with equivalent photos taken in 1990-2002 in N Alaska and documented a significant expansion of shrubs. Myers-Smith *et al.* (2011b) reported an increase in canopy cover and height of dominant willows on low Arctic Herschel Island, Canada, and Forbes *et al.* (2010) documented that a warming trend over the last six decades in the NW Russian Arctic was accompanied by a significant increase in growth of tall willow. Climate warming may also indirectly promote shrub growth. For example, Lantz & Kokelj (2008) show that retrogressive thaw slump activity resulting from permafrost thaw has increased in recent decades in western Canada. Such disturbances lead to increased nutrient availability and active layer thick-

ness which in turn create opportunities for increased growth of shrubs, notably alder, and overall change in plant community composition (Lantz *et al.* 2009). Apart from vegetation succession that follows from the abrupt disturbance effect of thawing permafrost, the changed hydrology (either drying out or paludification) associated with lost permafrost or changed depth of active layers is expected to cause large-scale vegetation changes. Fire is another source of disturbance, which may promote shrub growth in the low Arctic (Lantz *et al.* 2010). The expansion of tall shrubs in the tundra has been reported as well by indigenous tundra residents such as Nenets in Yamal (Forbes & Stammler 2009, Forbes *et al.* 2010). Kitikmeot Inuit observed that the vegetation in Nunavut, N Canada, became more lush and plentiful in the 1990s, and that in particular shrubs expanded and grew larger (Thorpe *et al.* 2002).

The observed changes in vegetation composition are to some extent in agreement with changes predicted from experimental studies. A meta-analysis of 61 warming experiments carried out over up to 20 years showed that warming led to an overall increase in the growth of deciduous shrubs, while mosses and lichen decreased (Elmendorf *et al.* 2012). There was, however, large variation in the response of different plant groups to warming depending on natural variation in site warmth and moisture. The International Polar Year Project *Back to the Future* (Callaghan *et al.* 2011b) revisited numerous Arctic research sites that were established 15-60 years ago and documented changes in plant community composition. Daniëls *et al.* (2011), for instance, observed a decrease of a number of widely distributed Arctic and middle Arctic species and an increase of several low Arctic and boreal species, by comparing the present day vegetation around Tasiilaq in low Arctic E Greenland with descriptions from 1912. They suggested that climatic change may be triggering a trend towards 'sub-Arctification' of the area.

At the southern border of the Arctic, the treeline is predicted to move northwards with climate warming.

Thus processes in the forest-tundra ecotone are pivotal to the future extent of the Arctic tundra. In a recent review, Harsch *et al.* (2009) analyze a large number of reports and conclude that treelines are either advancing or remaining stable. This result is consistent with what might be expected if treelines were responding to increasing global temperature, but were also constrained by other factors. Indeed, treeline dynamics are affected by a complex interaction of abiotic and biotic factors such as changes in hydrology and grazing, which have to be understood to make realistic predictions of forest encroachment in tundra (Aune *et al.* 2011). A global-scale analysis of spatial patterns of boreal tree density that included the forest-tundra ecotone suggested that forest-tundra transitions were likely to be controlled by non-linear (tipping-point) processes (Scheffer *et al.* 2012). In the northern boreal forest zone, there is evidence for a climate change-related impact that is the opposite of the 'greening of the Arctic tundra', that is 'forest browning' (Sturm 2010, Beck & Goetz 2011). Such a browning is believed to result from a combination of droughts, fires and insect outbreaks (Sturm 2010). Such processes are also likely to become involved in the dynamics of the forest-tundra ecotone. Indeed, in the mountain birch forest-tundra in northern Fennoscandia two species of geometrid moths (*Operophtera brumata* and *Epirita autumnata*) have expanded their outbreak range into more northern and alpine areas, causing large-scale devastation of birch forest during the last decade (Hagen *et al.* 2007, Jepsen *et al.* 2008). The expansion of a third defoliating moth species (*Agriopis aurantiaria*) is now promoted by warmer springs (Jepsen *et al.* 2011). The outbreaks of these species have had dramatic cumulative impacts on the forest tundra ecosystem by cascading to the understory vegetation (causing a shift in dominance from ericoid dwarf shrubs to graminoids) and to the herbivores (causing a shift from browsers to grazers; Jepsen *et al.* 2013). At present, irruptive defoliating insects affect primarily sub-Arctic birch forests, but their larvae occur also in dwarf birch in the shrub tundra beyond the tree line (Fig. 12.15; Torp *et al.* 2010, Karlsen *et al.* 2013), indicating that in the future tundra vegetation

Figure 12.15. The devastating impact of an outbreak of the invasive geometrid moth *Operopthera brumata* on dwarf birch *Betula nana* in the shrub tundra above the mountain birch *Betula pubescens* treeline on Varanger Peninsula, NE Fennoscandia (from Karlsen *et al.* 2013).

may also be affected. It is, however, unclear whether these larvae currently are resident tundra populations or whether they spread to these areas from the nearby forest tundra.

The controlling impacts that tundra herbivores exert on several important plant functional groups and vegetation communities are now robustly demonstrated (see Section 12.2.2.1). Therefore, both the current trends in cover of shrubs and positioning of the treeline must be evaluated in light of potentially matching temporal trends in populations of keystone herbivores either due to change in climate (i.e. folivorous insects, caribou and lemmings) or anthropogenic land-use in tundra regions and farther south (semi-domestic reindeer; Section 12.3.3.4 and geese; Section 12.3.3.3).

As reviewed in Section 12.2.2.2, the climate-induced expansion of shrubs into open tundra landscapes is expected to have important feedback effects on global climate by altering fluxes of GHG and heat. However, while there have been many modeling studies and 'mensurative experiments' across spatially contrasting vegetation types, there are few time-series studies that have actually documented trends in such feedback processes. A study of C fluxes over eight years in eastern Siberia showed that primary production increased more with warmer summers than with the length of the growing season, but that it was mostly compensated by higher respiration (Parmentier *et al.* 2011). Net C uptake was highest in the shortest and coldest growing season. A study in high Arctic Svalbard showed that a considerable part of the annual CO_2 effluxes (14 to 30%) occurred in winter, and that soil respiration was strongly affected by near-surface soil temperature (Elberling 2007). Experimental increase of snow depth, leading to higher soil temperatures, has also been shown to increase soil respiration in winter (Morgner *et al.* 2010). Results from a circumpolar modeling study (Hayes *et al.* 2011) suggest that whereas the tundra was a sink for C during the 1960s and 1970s, it has become a net source of C since the 1990s.

12.3.3.2. Climate change and phenology

Earlier snow melt results in advanced spring and earlier onset of the growing season. June snow cover has decreased by 17.8% per decade since satellite records began in 1979, i.e. more than the concomitant reduction in Arctic summer sea ice (Fig 12.16.; Derksen & Brown 2012). Ecosystem-based monitoring at Zackenberg Research station in high Arctic Greenland revealed how this impacted much of the ecosystem including spring phenology of plants and arthropods (Box 12.5). Tulp *et al.* (2008) modeled the timing of peak insect abundance in high Arctic Taimyr, Russia, as a function of weather, date and cumulative temperature, and 'hindcasted' the timing of this peak using existing weather data. Their simulations showed that the period of high insect abundance may have advanced by seven days between 1973 and 2003.
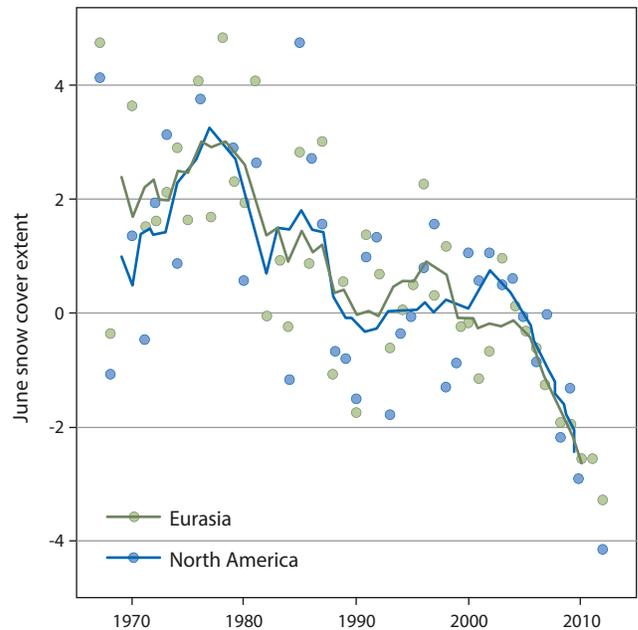
Figure 12.16. Trends in terrestrial June snow cover 1967-2012 based on averages for the North American and Eurasian continents, virtually all of it in the Arctic. Values are standardized anomalies with respect to the 1988-2007 mean. Solid lines are five-year running means (adapted from Derksen & Brown 2012).

Trophic mismatch is the temporal mismatch between herbivores and food plants or predators and prey which may result from the phenological responses of species to climate change (e.g. Visser *et al.* 1998, Miller-Rushing *et al.* 2010). Large phenological shifts make it likely that trophic mismatch, notably between migrating and local species, could become a serious problem. In the future, chicks of long-distance migrants such as shorebirds and passerines risk hatching after the peak of insect abundance, on which they depend to survive and grow, if the timing of migration is based on clues which do not change correspondingly (Tulp & Schekkerman 2008). At present, however, there are no data to assess whether this is already a problem for Arctic breeding birds, although years with early springs have been found to be associated with reduced gosling growth (Dickey *et al.* 2008). Post & Forchhammer (2008) reported that the advancement of plant phenology in W Greenland over a period of 13 years created a trophic mismatch with caribou, whose reproductive cycle follows the seasonal changes in daylight. As calving date is thus rather fixed, the peak demand for resources by reproductive females now falls later than the peak of nutritional value in their food plants, shortly after their emergence. This trophic mismatch was closely related to early caribou calf mortality. Interestingly, studies on semi-domestic reindeer in sub-Arctic northern Norway showed an opposite trend and documented a positive effect of earlier onset of spring on calf weight in fall, which is related to survival probability over the first winter (Pettorelli *et al.* 2005, Tveraa *et al.* 2013).

Box 12. 5. Change in spring phenology at Zackenberg

Zackenberg Research Station is located in central NE Greenland in bioclimate subzone C. The concept of ecosystem monitoring applied at Zackenberg follows the recommendations of the Arctic Climate Impact Assessment (ACIA 2005), and at present the integrated monitoring program Zackenberg Basic is the only program that addresses these recommendations within a single ecosystem (Forchhammer *et al.* 2008). Since its implementation in 1995, Zackenberg Basic annually includes more than 1,500 parameters from the biological and geophysical environments (Meltofte *et al.* 2008a).

Through the monitoring period, climatic conditions have changed markedly: some have exhibited trends, while others have, just as importantly, exhibited large inter-annual variability (Hansen *et al.* 2008). The most dramatic increase in temperature has been registered during the summer months (June through August) with rates as high as 1.4-2.2 °C per decade (Schmidt *et al.* 2012b). Snow and ice are the primary drivers of ecosystem changes at Zackenberg (Box 12.5 Table 1; Forchhammer *et al.* 2008). Inter-annual changes in timing of snow and ice melt not only affect most species directly, but these drivers have significant indirect, cascading

effects through species interaction within and across trophic levels. Some of the most significant changes are related to spring phenology. The timing of clearance of snow and ice cover together with spring temperature is pivotal for the onset of production plant communities and the emergence of arthropods (Høye *et al.* 2007a, 2007b). There are, however, indications of some plant species approaching their limit of phenological change (Iler *et al.* 2013). The affected arthropods include those that act as pollinators (Olesen *et al.* 2008) and food base for several avian species (Klaassen *et al.* 2001). A narrow phenological range together with host and predator specialization could make these species particularly vulnerable to trophic mismatch (Høye & Forchhammer 2008). In addition, a shortening of the flowering season in a warmer Arctic has been observed, with negative consequences for flower-visiting arthropods (Høye *et al.* 2013) as temperatures increase. Hence, in addition to its direct effect on the reproductive phenology of shorebirds (available nest sites; Pellissier *et al.* 2013), variability in the timing of snow clearance has an indirect impact on shorebirds through shorebird-arthropod interactions (Meltofte *et al.* 2007). Change in snow cover is also the likely primary driver of the observed lemming collapse at Zackenberg (Schmidt *et al.* 2012a).

Box 12.5 Table 1. Key ecological changes observed in the ecosystem monitoring program at Zackenberg since 1995.

Observed changes		Likely physical driver	References
Active layer	Increased active layer depths	Timing of snow melt, temperature	Christiansen *et al.* 2008, Sigsgaard *et al.* 2010)
Vegetation	Advanced flowering phenology across multiple species	Timing of snow melt, temperature	Høye *et al.* 2007b, Ellebjerg *et al.* 2008
	Marked changes in plant composition and biodiversity in some vegetation types	Snow (water availability), temperature	Schmidt *et al.* 2012b, Elberling *et al.* 2008
Growing season	Earlier growing season initiation	Timing of snow melt, temperature	Grøndahl *et al.* 2008, Sigsgaard *et al.* 2010
	Longer growing season	Timing of snow melt, temperature	Grøndahl *et al.* 2008, Sigsgaard *et al.* 2010
	Initial increase in heath carbon uptake, but recently apparently levelling off	Timing of snow melt, temperature	Grøndahl *et al.* 2008, Sigsgaard *et al.* 2010, Lund *et al.* 2012
	Increased primary productivity in fen areas	Temperature, CO_2 fertilization	Tagesson *et al.* 2012
Invertebrate community	Advanced emergence phenology of multiple taxa	Timing of snow melt, temperature	Høye & Forchhammer 2008
	Shorter flowering season and declining flower visitors	Timing of snow melt, temperature	Høye *et al.* 2013
	Climate-driven phenotypic variation in spiders	Timing of snow melt	Høye *et al.* 2009
Vertebrate community	Collapse of lemming cycles with negative cascading effects on the entire predator guild	Snow	Schmidt *et al.* 2008, Gilg *et al.* 2009, Schmidt *et al.* 2012a
	Varying nest initiation in shorebirds	Timing of snow melt	Meltofte *et al.* 2007, Meltofte *et al.* 2008b
	Initial increase in musk oxen numbers, but with recent decline	Timing of snow melt, temperature (plant productivity)	Hansen *et al.* 2009
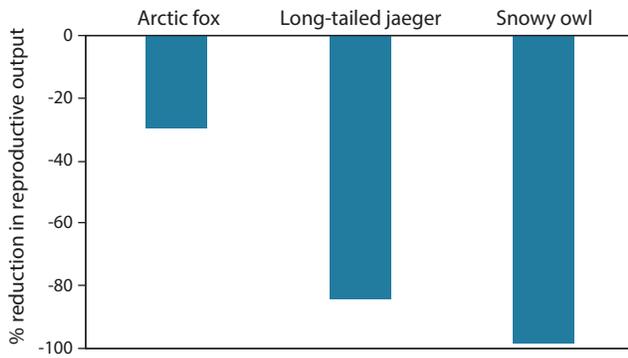
Figure 12.17. The impact of a collapse of the lemming cycle on the reproductive performance of three Arctic predator species with different degrees of specialization to lemming prey. The percent reduction in reproductive output is based on a comparison of yearly mean number of predator young produced during two periods with presence (1998-2000) and absence (2000-2011) of regular peak years of the population of collared lemmings at Trail Island, NE Greenland. Data were derived from Table 12.1 in Schmidt *et al.* (2012a).

12.3.3.3. Cascading impacts of trends in keystone animal species

Changed small rodent population dynamics
Small rodent population cycles are a keystone process of the tundra ecosystem with strong impacts both for the vegetation and the predator community (Ims & Fuglei 2005). In recent decades, a fading out or collapse of lemming population cycles has been reported from several Arctic regions (Gilg *et al.* 2009, Ims *et al.* 2011, Nolet *et al.* 2013) and has been attributed to increased frequency of melting-freezing events leading to ground ice-crust formation (Ims *et al.* 2008, Kausrud *et al.* 2008, Stien *et al.* 2012) as well as a to a longer snow-free season (Gilg *et al.* 2009, Nolet *et al.* 2013).

Changes in dynamics and community composition of small rodents affect predator guild composition (Ims & Fuglei 2005). The guild of small and medium-sized terrestrial Arctic predators is composed of species with different degrees of diet specialization (Fig. 12.3). Data from high Arctic NE Greenland show that snowy owl fledgling production declined by 98% after the collapse of the collared lemming cycle (Fig. 12.17), and no lemming nests with signs of predation from stoat have been found since then (Schmidt *et al.* 2012a). Breeding of long-tailed jaeger and Arctic fox was affected as well, but these species were the least negatively affected, probably because they are more able to switch to other resources than are the other predators in the guild (cf. Elmhagen *et al.* 2000, Gauthier & Berteaux 2011). Snowy owls (Jacobsen 2005) and Arctic foxes (cf. Box 12.6) have been declining in sub- and low Arctic northern Fennoscandia during the last century, and this decline in recent decades coincided with a dampening of the small rodent cycle (Ims & Fuglei 2005). In a modeling study, Henden *et al.* (2008) showed that whereas cycle length (periodicity) had relatively little impact on the growth rate of the

fox population, the mean of small rodent abundance had a substantial effect, supporting the causal link between climate-induced changes in small rodent dynamics and the decline of the Arctic fox.

Finally, as expected from the indirect facilitation provided by lemmings on breeding success of ground nesting birds (i.e. mediated by relaxed predation pressures during lemming highs; see Section 12.2.2.1), recent time series analyses have indicated that growth rates of brant geese *Branta bernicla* in high Arctic Taimyr (Nolet *et al.* 2013) have become negatively impacted by dampened lemming cycles. Unfortunately, data on predator dynamics was missing in this study, so the connection could not be confirmed. In general, long-term, simultaneous monitoring data on linked herbivore species, predator guilds and direct climatic drivers in the Arctic are very scarce and seriously limit our knowledge of food-web-level changes.

Increasing species
Human-induced passive or active transfer of species (exotics/invasives) appears to have increased in the Arctic (see Lassuy & Lewis, Chapter 16), but there is still no evidence for this to have had cascading effects on other component of tundra ecosystems. Natural range expansion of species following climate warming is starting to be observed, especially among insects (e.g. Leung & Reid 2013), some of which may have strong ecosystem impacts (Section 12.3.3.1; Jepsen *et al.* 2013), whereas others may not. Finally, there are some species with a long-term presence within the tundra biome that have increased substantially in abundance to the extent that knock-on effects now are evident.

The red fox is a wide-spread generalist predator, which has expanded its range northwards during the last century (Reid *et al.*, Chapter 3), an increase that has been attributed to climate warming-induced increased secondary productivity (Hersteinsson & Macdonald 1992). More generally, increased abundance of medium-sized generalist predators (meso-predators) often results from human intervention in ecosystems, and the impacts on biodiversity can be severe both through increased competition with other predators and through their impact on prey populations (see Prugh *et al.* 2009 and Ritchie & Johnson 2009 for reviews). Interspecific competition from the red fox in conjunction with dampened and/or irregular lemming cycles is likely to be one of the main causes of the depressed populations of the Arctic foxes in some sub- and low Arctic areas (Tannerfeldt *et al.* 2002, Angerbjorn *et al.* 2013). Killengreen *et al.* (2007) showed that Arctic foxes on low Arctic Varanger Peninsula had ceased to use their traditional breeding dens in the most productive habitats where red foxes currently are very abundant. In this region, the abundant red fox population appears to be subsidized by an increased herd size of semi-domestic reindeer that provides carrion resources during the winter (Killengreen *et al.* 2011; Box 12.6). In other areas of the Arctic, such as in north Yukon, there is however no indication of an increase of

Figure 12.18. Numbers of nesting geese from 1963 to 1997 (solid squares) and the proportion of total area of salt-marsh as exposed sediment from 1986 to 1997 (blue triangles) at La Pérouse Bay, Manitoba, low Arctic Canada (from Jefferies *et al.* 2006). The background picture shows a salt marsh degraded after intense grazing by geese. Photo: Ken Abraham.
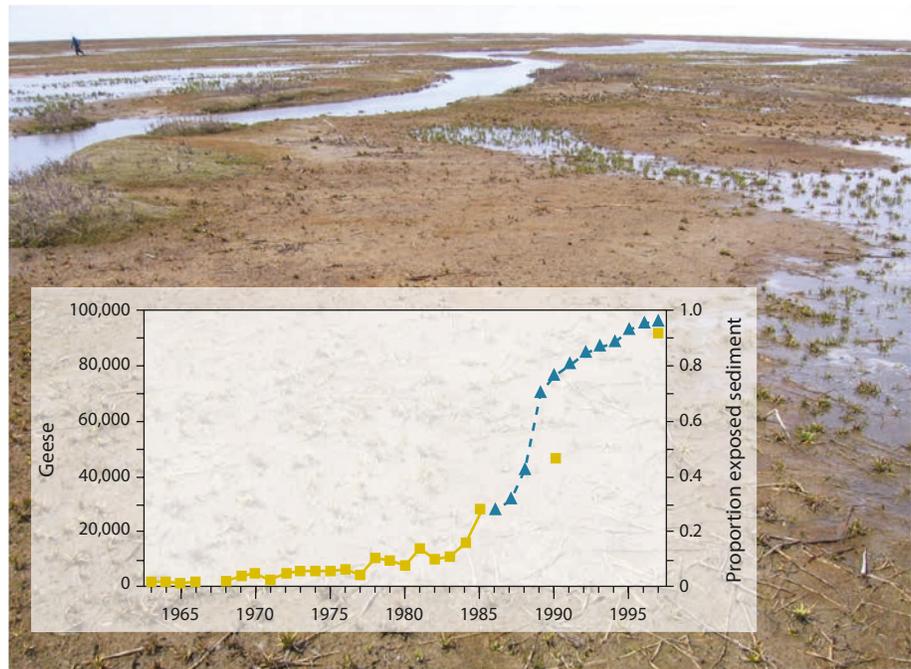
red foxes although climate warming has been substantial there (Gallant *et al.* 2012).

Northwards expanding and generally more abundant and stable populations of red foxes and other generalist boreal predators are likely to have detrimental consequences for many potential prey species, notably ground-nesting birds. Using artificial nests, McKinnon *et al.* (2010) showed that nest predation declined more than two-fold along a gradient from the sub-Arctic to the high Arctic in Canada. This gradient may be explained by a corresponding gradient in the abundance of generalist predators such as red foxes or corvids (crow *Corvus corone* and raven *C. corax*). In particular, corvids are known to prey on eggs and young of ground-nesting birds such as ptarmigans (Watson & Moss 2004, Stoen *et al.* 2010), waterfowl (Stien *et al.* 2010) and shorebirds (Parr 1993, Wallander *et al.* 2006). Both species abundance and richness within generalist predator guilds have recently been demonstrated to be closely linked to ecosystem productivity gradients in low Arctic tundra (Killengreen *et al.* 2012). The impact of an increasing population of generalist predators has also been suggested as an explanation for the decline of the willow ptarmigan in Norway during the last decade (Ehrich *et al.* 2012). The increase of the red fox population in northern Scandinavia has sparked drastic actions to control their numbers in the context of conservation of both the Arctic fox (Angerbjorn *et al.* 2013) and the lesser white-fronted goose *Anser erythropus* (DN 2011). However, apart from studies on red fox in Fennoscandia (Elmhagen & Rushton 2007, Selås & Vik 2007) there is no solid information about temporal trends in important generalist predators such as eagles and corvids (Ganter & Gaston, Chapter 4); although in particular the corvids may be favored by increasing human land use. Thus, among 16 local hunters and fishermen interviewed in Khatanga and Novaya (sub-Arctic eastern Taimyr) in fall 2012, 14

said that there were more ravens now than earlier and nine had observed an increase in the presence of crows. Ravens were now observed close to Lake Labaz and Lake Taimyr, two large tundra lakes, whereas this was not the case earlier (D. Ehrich unpubl.).

Populations of some species of geese breeding in the Arctic have increased strongly in abundance during the last decades (Ganter & Gaston, Chapter 4). This increase, which may primarily be due to causes outside the Arctic such as increased food supplied by changes in agriculture and decreased hunting during migration and in wintering areas, has a significant local impact on several components of the tundra ecosystem. Thus, the tremendous increase of lesser snow geese in the Hudson Bay area has caused persistent degradation of salt marshes (Fig. 12.18; Jefferies & Drent 2006). The resulting loss of vegetation triggers profound changes in sediment properties, including the development of hypersalinity and aridification. Re-establishment of vegetation on the hypersaline sediments is very slow (Abraham *et al.* 2005). This habitat degradation has been shown to have negative fitness consequences for the geese (Williams *et al.* 1993), and degraded patches are gradually abandoned, as the geese move to other areas (Jefferies & Drent 2006). Plant community alterations and vegetation damage resulting from increasing goose populations have also been reported with varying degrees of severity from other areas in the Canadian Arctic such as the low Arctic Karrak Lake, Nunavut (Alisauskas *et al.* 2006) and high Arctic Svalbard (van der Wal *et al.* 2007). On high Arctic Bylot Island, Canada, a decrease in plant primary production has been documented in the goose colony (Valery *et al.* 2010). In Jameson Land, high Arctic NE Greenland, an increase in primary plant production related to climate change allowed for a threefold increase in the number of molting geese from 1982-84 to 2008 (Madsen *et al.* 2011). Goose grazing impacted

species composition, but did not lead to serious habitat degradation, possibly because molting geese feed only on the above-ground parts of plants. Apart from local disturbance effects (van der Wal *et al.* 2007, Pedersen *et al.* 2013), there is at present no evidence for severe goose-driven habitat degradation in the Eurasian Arctic, although goose populations have been increasing considerably in several areas (Jefferies & Drent 2006).

Vegetation degradation caused by overabundant geese in Canada has also been shown to have consequences for other components of the tundra ecosystem. Thus, Milakovic & Jefferies (2003) showed that the abundance of both spiders and beetles decreased in salt marshes degraded by overgrazing. The population of savannah sparrows *Passerculus sandwichensis* in the area declined by 77% over a period of 25 years (Rockwell *et al.* 2003). At the same time, the goose increase did not lead to any overall decrease in most other groups of breeding birds over a period of 16 years at Cape Churchill, low Arctic Canada, although at the habitat patch scale most species were less abundant in the degraded habitats (Sammler *et al.* 2008). Herring gulls *Larus argentatus*, however, exhibited an increase in numbers probably due to increased prey availability, possibly leading to enhanced predator pressure on

eggs and chicks of large ground nesting birds such as willow ptarmigan (Sammler *et al.* 2008). At Karrak Lake, there was a strong negative correlation between habitat alteration by geese and local abundance of lemmings and voles (Samelius & Alisauskas 2009). This negative impact of geese on small rodents was attributed to a reduction in both food availability and protective cover.

12.3.3.4. Trends related to land-use changes

Increased grazing by reindeer in the tundra has been predicted to lead to transitions between vegetation states (Fig. 12.19; van der Wal 2006), although the propensity for such transitions is likely to differ between regions as reviewed in Section 12.2.2.1. Rees *et al.* (2003) documented a transition from dwarf shrub to graminoid dominated tundra over a 12 year period in an area where reindeer numbers increased locally in the low Arctic Nenetsky district of NW Russia. Nenets reindeer herders, who were involved in this study, confirmed that such a transition was the usual consequence of intense grazing. In Yamal, Russia, vegetation shifts from lichen, dwarf shrub and *Sphagnum* mosses to more grasses, sedges and ruderal bryophytes have been observed locally in areas where reindeer concentrate, such as around camp sites

Figure 12.19. While avoiding the sorts of negative impacts of herbivore overabundance that have been documented in some regions, an appropriately high density of semi-domestic reindeer appears to be able to keep shrub tundra in almost an open savannah-like grassland state by preventing recruitment of willow saplings between patches of tall shrubs. Here from a low Arctic riparian landscape on Varanger Peninsula, NE Norway. Photo: L.A. Støvern.

Box 12.6. Issues of ungulate management in Varanger Peninsula

Varanger Peninsula in NE Norway harbors the westernmost fringe of the Eurasian Arctic tundra at 70-71° N, 30° E and belongs to subzone E. The Arctic tree-line (mountain birch) runs across the peninsula. Since 2004, research has focused on semi-domestic reindeer management as a potential driver of vegetation states and other components of the food web.

The abundance of semi-domestic reindeer has more than tripled over the last four decades. Reindeer herders have experienced that warmer falls (cf. Karlsen *et al.* 2009) interfere with reindeer migration, so that an increasing number of deer reside on Varanger Peninsula during winter. This provides carrion subsidies to a species-rich guild of scavengers that spills over from the adjacent forest-tundra zone (Box 12.6 Fig. 1; Killengreen *et al.* 2012), where the population of moose is also growing (Ims *et al.* 2013). In particular, the competitively dominant red fox is maintained in high numbers in the tundra even in the low-phase of the rodent cycle (Killengreen *et al.* 2011). This increase and less lemming prey appear to be the main causes of the decline of the Arctic fox in this area (Killengreen *et al.* 2007, Angerbjorn *et al.* 2013, Hamel *et al.* 2013). Adaptive management attempting to actively control the red fox has been run since 2005 with promising results so far (Angerbjorn *et al.* 2013, Hamel *et al.* 2013).
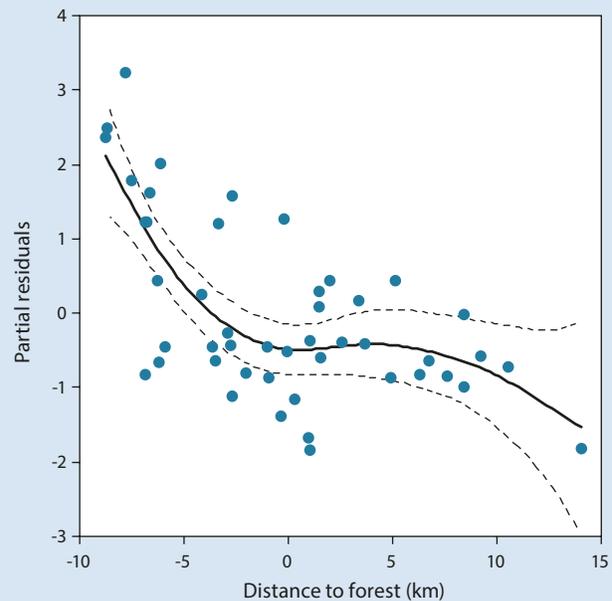
Box 12.6 Figure 1. Species richness of vertebrate scavengers recorded by camera traps at reindeer carrion as a function of distance from sub-Arctic birch forest on Varanger Peninsula in winter 2006. The graph shows the predicted species richness (whole line) with standard error envelopes (dotted lines) and partial residuals (dots) from a general additive model. The distance from the forest is 0.1-23.5 km. Adapted from Killengreen *et al.* (2012).

(Forbes *et al.* 2009). These lush habitats constitute nutrient-rich and easily digestible forage attractive for further grazing by reindeer. The somewhat contrasting results for Russia and northern Fennoscandia (Bråthen *et al.* 2007 cf. Section 12.2.2.1) may be due to different scales of investigation, as notably the increased productivity documented by Forbes *et al.* (2009) was very local, or possibly to different bedrock qualities (higher fertility in Russia where large sediment plains dominate). A profound reduction in lichen cover resulting from increased abundance of semi-domestic reindeer has been reported from sub-Arctic northern Fennoscandia (Suominen & Olofsson 2000, Moen & Danell 2003, Forbes & Kumpula 2009) and from Yamal in Russia (Podkorytov 1995). Recently, Tømmervik *et al.* (2012) showed that this change was reversible, as lichens recovered rather rapidly on plots from which reindeer were excluded over seven years.

Owing to a combination of governmental policies and social factors (Hausner *et al.* 2011, 2012) some semi-domestic reindeer herds in sub-Arctic northern Fennoscandia have risen in size to become likely the most densely stocked herds worldwide (Ims *et al.* 2007). Apart from the effect on lichens on the winter pastures, reindeer impacts on tall willow shrubs in summer pastures are the most robustly demonstrated impact of reindeer herding on tundra ecosystems. Intense reindeer brows-

ing leads to reduced vertical growth (den Herder *et al.* 2004, 2008, Kitti *et al.* 2009) as well as areal fragmentation or shredding of willow thickets (Ravolainen *et al.* 2013), thus supporting the suggestion arising from studies based on small-scale experiments (Post & Pedersen 2008, Olofsson *et al.* 2009, Ravolainen *et al.* 2011) that large ungulates may counteract the climate driven expansion of shrubs. The herbaceous vegetation may be locally dominated by the unpalatable grass *Deschampsia cespitosa* (tussock grass; Ravolainen *et al.* 2013, Soininen *et al.* 2013). Presently, the impact of semi-domestic reindeer on tall willow shrubs and associated vegetation in riparian habitats in low Arctic Fennoscandia is regionally so severe that wildlife species are negatively affected. Such negative impacts have been documented for willow ptarmigan (Henden *et al.* 2011a, Ehrich *et al.* 2012) and more generally for the community of land birds (Ims & Henden 2012). On riparian sediment plains on the Varanger Peninsula, species richness of land birds was reduced by 50% in areas where tall willows had been entirely eliminated by heavy reindeer browsing. However, tundra voles appear to be unaffected by these changes in vegetation state (Henden *et al.* 2011b).

High reindeer abundances together with a practice of leaving some reindeer on summer pastures in winter have led to increased availability of reindeer carcasses for

Images of scavenger species involved as they were obtained from the camera trap placed on tundra and baited with reindeer carrion. From the top left: Arctic fox, hooded crow *Corvus cornix*, wolverine, white-tailed eagle *Haliaeetus albicilla*, red fox, golden eagle *Aquila chrysaetos* and common raven *Corvus corax*.

predators/scavengers in winter. This additional resource has been shown to contribute to maintaining a high abundance of boreal generalist predators (Box 12.6).

12.3.3.5. Impact of industrial development

Industrial development in the Arctic implies construction of roads and other infrastructure, oil-drilling, seismic exploration, tracks from vehicles, increased human presence and in some cases severe pollution, factors which all either lead to local destruction of the ecosystem or to different degrees of disturbance causing habitat and vegetation transformation. The area affected by habitat transformation around industrial development sites varies considerably and often increases over time. The area visibly affected was estimated to be 67 km² around the Toravei oil field in 2005 (Nenetsky Autonomous Okrug, Russia; Kumpula *et al.* 2011) and 836 km² around the Bovanenkovo gas field in 2011 (Yamalo-Nenets Autonomous Okrug, Russia; Kumpula *et al.* 2012), while 70 km² were covered by infrastructure in the North Slope oil fields in Alaska (NRC 2003; see Tab. 19.1 in Huntington, Chapter 19). Off-road vehicle tracks, in particular those left by the heavy Russian all-terrain tracked vehicles, remain visible for decades on satellite images. Traffic of vehicles used for seismic exploration during winter has been shown to cause long-term (20 years) changes

to plant communities and permafrost stability in the coastal plain of Alaska (Jorgenson *et al.* 2010). Indirect impacts on tundra landscapes, such as thermokarst, may develop with a lag of many years (Walker *et al.* 1987). The number of vascular and non-vascular plant species adapted to grow on disturbed ground surfaces tends to decrease with latitude, in part because the set of colonists is derived mainly from local floras, so temperate ruderal taxa are largely absent (Chernov & Matveyeva 1997). In sub-Arctic and low Arctic ecosystems, the colonizers easily spreading and persisting on anthropogenically disturbed terrain are low shrubs, graminoids (grasses and sedges), composite forbs and ruderal bryophytes (Vilchek *et al.* 1996, Sumina 1998, Forbes *et al.* 2001).

Plant communities recolonizing disturbed ground differ from natural communities by a lower cover of most plant groups and lower total species diversity, but an increased cover of graminoids (Forbes *et al.* 2009, Jorgenson *et al.* 2010, Kumpula *et al.* 2011). Willows, in particular, are active colonizers of disturbed sites in moist habitats in sub-Arctic and low Arctic regions (Cooper & van Haveren 1994, Densmore 1994). Lichens are the most easily removed component of tundra communities, and on disturbed sites they regenerate even more slowly than vascular plants and bryophytes. Only a few of the most widespread lichen species of *Stereocaulon*, *Peltigera* or *Cladonia* are found on disturbed habitats. Despite a general trend toward graminoid-dominated tundra, vegetation changes on disturbed surfaces vary considerably depending on substrate, humidity and the nature of the disturbance (Forbes *et al.* 2001). Another effect of infrastructure is caused by dust from gravel roads. In both Russia and Alaska, calcareous dust has been shown to increase soil pH in initially acidic tundra, to reduce species richness and biomass, and to increase graminoid and cloud berry *Rubus chamaemorus* cover at the expense of *Sphagnum* mosses, lichen and dwarf shrubs (Forbes 1995, Auerbach *et al.* 1997, Myers-Smith *et al.* 2006).

Pollution has a strong local impact on the vegetation surrounding mining sites in Russia such as the nickel smelters in sub-Arctic Norilsk and Nikel or the coal mine complex in low Arctic Vorkuta. Virtanen *et al.* (2002b) observed an increase in graminoid coverage in sites impacted by industrial activity in Vorkuta. Willow cover increased at the expense of dwarf birch with increasing pollution levels, and lichen were absent from sites with major pollution. The area around Norilsk is characterized by the most intense sulphur deposition in the sub-Arctic (Forsius *et al.* 2010) as well as high heavy-metal contamination. Soils in the vicinity of the smelter are acidic, and the microbial community is affected both regarding species composition and reduced functional activity (Bogorodskaya *et al.* 2012). Whereas the vegetation is destroyed or severely disturbed in the immediate surroundings of the industrial area (Tutubalina & Rees 2001, Zubareva *et al.* 2003, Bogorodskaya *et al.* 2012), direct pronounced effects of Norilsk industrial activities are absent from the tundra region on the Taimyr Peninsula (Zhulidov *et al.* 2011).

Whereas impacts of industrial development on tundra vegetation have been thoroughly documented, not much is known about impacts on animals. Kevan *et al.* (1995) showed that abundance of soil arthropods was reduced on old tractor tracks on high Arctic Ellesmere Island, Canada, but diversity was not. Whether such very local changes in abundance have an impact on ecosystem processes is at present unclear. In the vicinity of Prudhoe Bay, low Arctic Alaska, the density of calving caribou declined exponentially with road density and the main calving grounds were moved to inland areas with lower forage biomass (Cameron *et al.* 2005). On the low Arctic Varanger peninsula, the likelihood of presence of the endangered Arctic fox declined with decreasing distance from roads (Hamel *et al.* 2013). One reason suggested for this was increased presence of the competitively dominant red fox. Indeed, generalist predators such as the red fox and corvids are favored by human presence (Restani *et al.* 2001, Liebezeit *et al.* 2009, Stoen *et al.* 2010). Feral dogs around settlements (Kumpula *et al.* 2011) can also act as generalist predators with serious negative impacts notably on local populations of ground nesting birds.

12.4. KEY FINDINGS

12.4.1. How the structure and functioning of tundra ecosystems are determined

12.4.1.1. Abiotic controls on ecosystem structure

The Arctic tundra is a bioclimatically defined biome that geographically is restricted to a band around the margins of the Arctic Ocean. Hence, large parts of the tundra are subject to neighborhood effects both from marine and boreal forest ecosystems. Within its domain, the Arctic tundra biome has a zonal structure as described by bioclimate subzones A-E of the Circumpolar Arctic Vegetation Map (CAVM Team 2003), which provides a framework for describing the structure of tundra ecosystems. A key structuring force is the bottom-up effect of decreased vegetation productivity and complexity with increasing environmental severity. Accordingly, there are trends of decreasing food-web complexity in terms of diversity within and among trophic guilds of consumers with increasing latitudes. However, the four trophic levels of producer-plants, consumer-herbivores, consumer-carnivores and decomposers are present, even at high Arctic sites with very low terrestrial primary productivity, likely due to available resource subsidies from the adjacent marine food webs. Low food-web complexity in the most northern subzones (i.e. subzones A and B) may also partially be attributed to island biogeographic features (area size and isolation), as large parts of these subzones are located on islands in the Arctic Ocean and Nordic seas. Similarly, a substantial proportion of the high biodiversity of low Arctic subzones (D and E) stems partly from the close neighborhood and 'spillover effects' from sub-Arctic forested ecosystems. Microbial and plant communities, being less constrained by dispersal ability

and area size requirements than animals, appear to be less influenced by such geographical constraints.

Besides latitudinal zonation there are other large-scale and long-term structuring forces such as present and past climates (including glaciation history), substrates and topography that have shaped unique communities. One notable case is steppe-tundra, which constituted very extensive, productive and species-rich ecosystems during past climates (Pleistocene), but which is currently found only as small remnant communities in the oldest regions of the terrestrial Arctic and with distinct continental climates.

At sub-regional scales, the terrestrial Arctic harbors diverse mosaics of communities that are structured by gradients in climate, substrate and hydrology often associated with topography and disturbance factors. Unique within- (alpha-) and among-community (beta-) diversity is shaped by the cryosphere (above-ground snow and below-ground permafrost). Examples are topographic (hill-slope) communities shaped by snow-depth and soil-moisture related processes along gradients from ridge to snow-bed communities, and the micro-scale patterning of tundra vegetation and below-ground biota due to the action of permafrost. Thus, hot spots of high regional (gamma) diversity are currently found in topographically and geologically complex regions.

12.4.1.2. Biotic processes shaping biodiversity and tundra ecosystem functioning

The architecture of tundra food webs is modulated by direct and indirect inter-specific interactions within and between trophic levels. Although there is still no scientific consensus about the relative importance of bottom-up and top-down trophic controls in Arctic food webs, some generalizations can be made:

- Herbivores can regionally exert strong top-down controls on the state of tundra vegetation. Notable cases are (1) elimination of lichens from tundra heaths and tall shrubs from low Arctic riparian plains by abundant reindeer, (2) the ameliorating impact of lemming grazing on primary productivity in mesic tundra and snow beds, (3) outbreaks of insect defoliators impacting tundra-forest ecotone dynamics, and (4) over-abundant goose populations causing degradation of wetland plant communities.
- The consumption by predators controls at least regionally (1) the abundance of small mammal herbivores and (2) the reproductive success of ground nesting birds. The strength of this control can be enhanced by marine or anthropogenic subsidies.
- Trophic cascades and other indirect effects in food webs affecting biodiversity include (1) negative impacts of abundant reindeer on riparian bird communities and (2) positive impacts of cyclic lemming peaks on breeding success in ground nesting birds.
- Multi-annual, cascading interaction cycles mediated by fluctuating small rodent populations are crucial for the maintenance of terrestrial Arctic biodiversity in

many tundra ecosystems, including species endemic to the Arctic. In particular, lemmings appear to be keystone species in tundra ecosystems.

Terrestrial Arctic biota play essential roles in the regional-global climate system. They are involved in both biogeochemical processes that control the fluxes of GHG and biophysical processes that control heat fluxes between the earth surface and the atmosphere. A wealth of recent research indicates that the actual composition of terrestrial biodiversity may determine whether the Arctic will become a source or a sink for GHGs in a warming climate and whether the Arctic amplification will become stronger or weaker. Indeed, knowledge of the composition and the functions of Arctic biodiversity appears to be crucial for our ability to predict future climate. Key findings are related to which plant functional traits (PFTs) dominate in tundra vegetation and how these functional traits link to biophysical and biogeochemical processes and biotic interactions:

- PFTs have 'engineering' influences on biophysical processes. Notable cases are (1) increase of tall shrubs and trees, resulting in reduced albedo and accentuating the Arctic amplification of climate change, and (2) decline of mosses accentuating permafrost thaw and causing a cascade of geophysical and biogeochemical processes that leads to GHG release from the massive below-ground stocks of C in frozen Arctic soils.
- PFTs are linked to below-ground biological processes that influence the transfer of C between biological and atmospheric pools. For instance, vegetation shifts from ericoid dwarf-shrub heaths to forest-tundra may induce a net loss of C to the atmosphere via mycorrhizal activity that increases the rate of decomposition of soil organic matter. Indeed, the complexity of soil-plant interactions cautions against the assumption that increased plant productivity necessarily means greater ecosystem-level C sequestration.
- Ecosystem functioning depends also on the traits of the consumers that are involved. Notable cases are (1) the ability of mammalian herbivores to control tall shrubs and thereby albedo and net GHG fluxes, (2) the capacity of geese, lemmings and ungulates to shift tundra plant communities from moss to graminoid dominance, with implications for GHG fluxes, (3) the gross vegetation state shifts in tundra-forest ecotones caused by outbreaks of insect defoliators turning the ecosystem from sink to source of C, and (4) plant fungal pathogens altering the C balance of tundra heaths.

12.4.2. Trends attributed to drivers of change

12.4.2.1. Climate change

The Arctic tundra biome has been subject to dramatic changes driven by large fluctuations in past climates. In particular, the climatic transition to the warmer climate during the Holocene appears to have been uniquely deleterious in its impacts upon cold-adapted terrestrial Arctic biota, leading to extinctions of some taxa. Seen against this background, future climatic warming, expected to be more rapid than ever, poses severe threats to the maintenance of the present, already impoverished Arctic biodiversity. Conversely, in light of their persistence over episodes of climate change in the past, extant Arctic biota could be expected to show some resilience to at least the incipient stages of contemporary warming.

Climate warming is expected to relax critical climate-related constraints on plant growth. Current trends in vegetation are mostly consistent with this expectation:
- Vegetation seasonality in the Arctic region has had a 7° latitudinal shift equatorwards during the last 30 years. Remote sensing has shown that the Arctic tundra has become greener over vast stretches of the circumpolar Arctic. As verified by both observations and experiments on the ground, this is due to increasing vascular plant biomass.
- Increase of deciduous shrubs in the low Arctic sub-zones is particularly well demonstrated, sometimes associated with changes in disturbance factors such as permafrost thaw and tundra fires and ecosystem functions such as net C fluxes and albedo.
- The increase of vascular plants occurs at the expense of cold-adapted mosses and lichens. Permafrost-thaw and changed hydrology also impact these cryptogams directly.
- Cascading impacts of changed tundra vegetation dynamics have begun to become demonstrated in terms of (1) phenological mismatches and novel matches between herbivores and their food plants, and (2) changed net ecosystem C fluxes associated with shifts in dominant plant functional traits and related below-ground biota.

Trophic interactions within the tundra food web appear to be notoriously climate-sensitive. In particular those involving keystone species are expected to mediate cascading climate impacts on a host of other species and functions in the ecosystem:
- Climate-induced collapses or dampening of lemming population cycles have caused reduced reproductive success in lemming predators and ground nesting Arctic birds in Greenland and Eurasia. Arctic predators such as the Arctic fox and the snowy owl have been placed on national red lists in regions where lemming populations have exhibited irregular and/or dampened cycles for many decades.
- Climate-induced outbreaks of insect defoliators and fungal plant pathogens have just begun to emerge at the southern border of the Arctic, causing transitions between vegetation states across the tundra-forest ecotone and as a consequence the net release of C to the atmosphere.

None of the trends in Arctic tundra ecosystems are spatially uniform. A large spatial heterogeneity is due to the fact that climate change itself is spatially heterogene-

ous and that there is also considerable spatial variation in other important controlling processes.

12.4.2.2. Land-use, resource management and industrial development

Change in human population, land-use and resource management practices have resulted in the increased abundance of certain species that may have pervasive impacts on ecosystem structure and functioning. Recent research in the terrestrial Arctic has highlighted three notable cases:

- Reindeer herding, which is the most spatially extensive form of land-use in the Arctic, has been subject to changing policies and/or socio-economic regimes that regionally have given rise to abnormally dense reindeer stocks. This in turn has caused (1) reduced areal extent of low erect shrubs with cascading negative impacts on the shrub-associated fauna and (2) changes in the associated predator guilds due to active control (persecution) of large predators and/or increase of meso-predators that are subsidized by reindeer carrion.
- The increase of boreal meso-predators in the low Arctic, best demonstrated for the red fox, most likely results from increased anthropogenic resource subsidies. Negative impacts of northwards red fox expansion on endemic Arctic species has been demonstrated (Arctic fox), or suspected (willow ptarmigan and lesser-white fronted goose), to the extent that red fox control is currently implemented as a conservation measure in sub- and low Arctic Fennoscandia.
- The increase of populations of Arctic breeding geese results mainly from changed land-use or hunting practices on wintering and staging grounds farther south. Overabundant geese have local ecosystem impacts ranging in severity from apparently irreversible habitat degradation of wetlands to moderate changes in plant community composition.

The distribution of industrial developments in the terrestrial Arctic and their associated anthropogenic pressures is currently patchy but expanding. Impacts on local ecosystems include:

- Increase of plants that are resilient to, or facilitated by, mechanically disturbed ground surfaces; mostly grasses and deciduous shrubs, but including the notable perennial herb, fire-weed *Chamerion angustifolium*.
- Declines in pollution-sensitive growth forms such as lichens around mining sites.
- Local declines of disturbance sensitive (shy) animals such as caribou as a response to the presence of human infrastructure, but increases in human commensal species like the red fox and corvids.

12.5. CONCLUSIONS AND RECOMMENDATIONS

12.5.1. Status and trends: Implications for the future

The Arctic tundra biome is a bio-climatically defined zone, the integrity of which is ultimately conditional on cold climates. Based on an extensive peer-reviewed literature, the present assessment testifies to the fact that all aspects of tundra ecosystems and their embedded biodiversity are shaped by past and current climates, although in conjunction with other environmental factors. This also means that future climate warming – in combination with other drivers of change – will fundamentally alter Arctic biodiversity. Indeed, our review of contemporary trends demonstrates that the tundra ecosystems have already changed as a result of recent climate warming as well as by intensified human land-use, including industrial development in certain areas.

Concerning the impacts of drivers of change in general and those related to climate warming in particular, the present assessment arrives at the following conclusions:

- Impacts of change are often indirect, both in the abiotic and biotic domains of tundra ecosystems.
- In the abiotic domain, climate warming exerts some of its most profound impacts through second-order disturbances in the cryosphere, such as ground surface icing (ROS) and permafrost thaw, or through drought-related increase of tundra fires.
- In the biotic domain, pervasive driver-impacts are mediated both by bottom-up and top-down cascades in trophic webs. Both types of cascades have recently been found ultimately to harm species endemic to the Arctic such as lemming-dependent predators and grazing-sensitive cryptogams.

Concerning the functioning of tundra ecosystems, new insights have emerged about the essential but complex roles of terrestrial Arctic biota in the evolution of regional-global climates:

- Ecosystem structure in terms of the composition of species guilds, communities and trophic webs may determine whether the terrestrial Arctic will become a future sink or source for GHGs, and whether it will strengthen or weaken the Arctic amplification of climate warming.
- The set of species traits that dominate in an ecological community is important for overall ecosystem functionality, implying that the processes involved in the global C cycle are not independent of the species (and functional traits) involved.
- An important overall message is that 'the Devil is in the details' regarding how terrestrial Arctic biodiversity interacts with climate change, which is indeed an argument for emphasizing Arctic biodiversity in climate research.

The tundra biome's geographic configuration alone, as an irregular and in places very narrow strip of low-lands squeezed in between boreal forest and the Arctic marine environment, implies that the whole biome is vulnerable to climate change-related 'edge effects'; i.e. species-invasions from sub-Arctic ecosystems (e.g. northward expansion of forests) and marine encroachment (erosion of coastlines and rising sea levels). Considering paleo-ecology, the whole biome can already be considered a refugium. Moreover, certain tundra subzones and regions may be particularly sensitive and vulnerable:

- The high arctic subzone A should be considered to be endangered. It is currently restricted to a very small area, about 2% of the non-glaciated terrestrial Arctic, mostly islands surrounded by perennial sea ice. An increase in July mean temperature of only 1-2 °C will permit the introduction of prostrate shrubs, sedges and other temperature-limited species. Disappearing sea ice may also change the levels of marine nutrient and production subsidies to the otherwise extremely nutrient/production limited high Arctic terrestrial food webs.
- The low Arctic subzones (D and E) are particularly vulnerable to increased pressures from range-expanding species with current strongholds in the sub-Arctic. Reported cases include boreal shrubs and trees, outbreaks of insect defoliators and meso-predators. 'Human commensal' meso-predators may also be synergistically enhanced by intensified land-use and expanding infrastructure/industries.
- Steppe-tundras that currently are confined to a few regions with continental climate and calcareous substrate are expected to be strongly affected by increased humidification of the climate and acidification of the substrate.

12.5.2. Conservation and management actions

The Arctic tundra biome is still characterized by relatively pristine ecosystems over large areas compared with other biomes on Earth. However, the impact of ongoing and future climate change is expected to be huge and represents the single most severe threat to terrestrial Arctic ecosystems. Moreover, there is significant spatial overlap with other stressors indicating that we must pay special attention to potential synergies. Area protection (reserves and national parks) will be an important means for preserving Arctic biodiversity in the era of climate change, especially since it will act to diminish synergistic impacts of local anthropogenic stressors and climatic warming. With regards to climate warming, there are certain biogeographical features that will make some areas particularly valuable for protection:

- Topographically diverse areas with mountain ranges that include landscape-scale climatic gradients may have 'buffer-capacity' to maintain cold refuges in a warmer climate.
- Remote high Arctic islands that are far north of southern bioclimate subzones and boreal ecosystems,

and where Arctic marine waters will serve at least as a partial barrier ('filter') to invasions from the south.

However, regardless of how remote and well-protected, no Arctic reserves or national parks will be immune to the impact of climate change. To conserve Arctic biodiversity it may be necessary to implement active management actions especially within protected areas:

- Encroachment of tall shrubs and trees into tundra can be counteracted, with the added benefit that plant community diversity can be maintained under future warming, by management of large herbivores as shown by recent research in Fennoscandia and Greenland. Such management needs to consider both the positive and negative effects of increasing grazing pressures, other ecological effects of high herbivore densities (e.g. subsidies to meso-predators) and the economies of local people (see Huntington, Chapter 18).
- Certain boreal species expanding their range northwards and anthropogenically introduced invasive species may be controlled locally in the manner currently attempted with meso-predators in northern Fennoscandia.
- Increasing populations of human commensal species should be counteracted, for instance by effective waste management associated with human settlements or encouragement of hunting.

Indeed, in a much warmer climate, a network of 'Arctic parks' which are actively managed to maintain ecosystem processes that are representative of the main geographic regions and subzones of the tundra biome may be the only way to conserve terrestrial Arctic biodiversity in the future.

12.5.3. Research and monitoring

As evident from the present assessment, there is a wealth of research and monitoring conducted over recent decades that has provided crucial new insights regarding the structure and functioning of Arctic terrestrial ecosystems, as well as estimates of recent trends. However, this science has also revealed big challenges that remain to be met before we can answer critical questions about contemporary and future states of tundra ecosystems and their biodiversity.

12.5.3.1. Needs for area- and ecosystem-representative measurements

Over most of the Arctic, it will continue to be easier (and cheaper) to detect changes from space than on the ground. Thus, remote sensing and technological advances to improve it will undoubtedly be important for monitoring the terrestrial Arctic, and Arctic ecologists ought to be in the forefront of the application of such technologies. However, although we may be able to detect changes in gross ecosystem properties from space, we need to be on the ground to explain and manage those changes. Moreover, most of the biodiversity and

many of the factors that drive its dynamics will remain unseen from space regardless of future improvements in remote sensing technologies.

Ground-based measurements currently have very poor geographical coverage considering the vast spatial extent of the tundra biome and the large spatial heterogeneity in its habitats and biota. This heterogeneity must be accounted for, if we are to obtain robust estimates of status and trends, for instance by means of meta-analysis (e.g. Elmendorf *et al.* 2012). To do this, research and monitoring efforts need to become much more area-representative than is now the case. This means that many more long-term sites ought to be established, with the demand that sampling design, measurement methods and criteria for classifications are harmonized among sites.

Those processes that exceed the spatial scale of small plots or include ecosystem components dominated by microbial communities and invertebrates are currently underrepresented in terrestrial Arctic research and monitoring. Both of them are, however, critically important for understanding the important biogeochemical and biophysical processes coupling the tundra ecosystem to the climate system. These problems of lack of area- and ecosystem-representativeness are acute challenges that need to be addressed in the upcoming CBMP (see Box 1.4 in Meltofte *et al.*, Chapter 1).

12.5.3.2. Needs for ecosystem-based approaches

A key message emerging from this assessment is that essential attributes of Arctic biodiversity, some of which have global repercussions, are ultimately dependent on how interactions within ecological communities and trophic webs are impacted by external drivers. This provides a compelling argument for research, monitoring and management of Arctic terrestrial biodiversity to adopt ecosystem-based approaches. At present, however, there are very few sites in the Arctic where long-term projects are explicitly ecosystem-based. This state of affairs must be improved, and CBMP ought to play a key role by helping to orchestrate an area-representative, circumpolar network of ecosystem-based monitoring sites.

The planning of a future network of ecosystem-based programs should strive to harmonize monitoring design and measurement protocols and to accommodate a common set of 'essential biodiversity variables' (Pereira *et al.* 2013). However, the fact that the ecosystems are structurally and functionally heterogeneous across subzones and regions of the tundra biome, as well as partly subjected to different external drivers of change, implies also a need for site-specific efforts to focus on site-specific processes and components of the ecosystem. Ecosystem-based monitoring should be guided by the best empirical knowledge and most plausible hypotheses regarding key drivers, processes and trends in the focal ecosystem (Lindenmayer & Likens 2009). In order to be relevant to stakeholders, managers and policy mak-

ers, those drivers and components of the ecosystem that actually can be amenable to actions in ecosystem-based management ought to be given particular attention in monitoring programs (Westgate *et al.* 2013).

The magnitude of climate warming in the Arctic during the present century may become as extreme as 10 °C. However, the projected temperatures and precipitation patterns vary so much between different models and geographic regions (Overland *et al.* 2011, Xu *et al.* 2013) that one may question the value of the many attempts now taken to derive explicit model-based predictions about how Arctic species and ecosystems will respond. Moreover, the combination of unprecedented rates of climate change, abnormal levels of other stressors, evolution of novel climates (Williams *et al.* 2007) and ecosystem structures (Macias-Fauria *et al.* 2012) accentuate the possibility that present knowledge about past changes, contemporary ecosystems states and trends may have little bearing on what will become the future states of terrestrial high latitude ecosystems (Post 2013b). In such a dire situation it becomes crucial to establish flexible observation systems to enable real-time detection, documentation and understanding of cause-effect relations (Ims *et al.* 2013). The framework of adaptive monitoring as proposed by Lindenmayer *et al.* (2010) may be particularly suitable in the context of ecosystems as likely to be prone to uncertainties and surprises as those currently located in the terrestrial Arctic.

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LIST OF ACRONYMS

C: carbon

CH_4: methane

CO_2: carbon dioxide

GHG: greenhouse gasses

NDVI: Normalized Difference Vegetation Index (see Box 12.1)

GLORIA: Global Observation Research Initiative in Alpine Environments

SOM: soil organic matter

ECM: ectomycorrhiza

ROS: rain-on-snow

PFT: plant functional traits