2. CHARACTERISTICS OF ARCTIC BIODIVERSITY
The Arctic is made up of the world’s smallest ocean surrounded by a relatively narrow fringe of island and continental tundra (Box 4). Extreme seasonality and permafrost, together with an abundance of freshwater habitats ranging from shallow tundra ponds fed by small streams to large deep lakes and rivers, determine the hydrology, biodiversity and general features of the Arctic’s terrestrial ecosystems. Seasonal and permanent sea ice are the defining features of the Arctic’s marine ecosystems.

The Arctic tundra, freshwaters and seas support more than 21,000 species of plants, fungi and animals – even when endoparasites and microorganisms are excluded, of which thousands of species may remain undescribed (Tab. 1). Although they are less rich in species than other biomes on Earth (see for example, vascular plant richness in Fig. 1), Arctic terrestrial and marine ecosystems provide room for a range of highly adapted and particularly cold-resistant species, as well as species that fill multiple ecological niches.

The Arctic fox is highly adapted to cold and snow by short extremities, winter whiteness and insulation through fur. Photo: Carsten Egevang/ARC-PIC.com

1 A parasite that lives within another organism.
The Antarctic continent has been isolated from the rest of the world’s land masses for about 23 million years (Trewby 2002), and together with an almost total ice cover for 15 million years this has left the Antarctic with a very sparse terrestrial fauna and flora. While the Antarctic continent is huge and almost totally ice covered, the Arctic is made up of the world’s smallest ocean surrounded by a relatively narrow zone of island and continental tundra at the edge of the two large northern continents. This means that the Arctic has a rich terrestrial fauna and flora derived from the Eurasian and North American continents and including many species that were widespread at lower latitudes during the Pleistocene. Indeed, about 14,000 terrestrial Arctic species are known to science – even when endoparasites and microorganisms are excluded. The periodic advances and retreats of Arctic continental ice sheets during the Pleistocene caused many local extinctions, but also created intermittent dispersal barriers and population bottlenecks, accelerating divergent evolution of some taxa (see Christiansen & Reist, Chapter 6 and Josefson & Mokievsky, Chapter 8).

One of the results of this is that the Arctic – in contrast to the Antarctic – is inhabited by a variety of terrestrial mammalian predators. The absence of this faunal element from the Antarctic allowed millions of flightless penguins to breed on the continental land mass – a behavior which would be precluded in the Arctic by the presence of Arctic foxes, wolves and polar bears. Not even massive harvest by humans during the last century altered the apparently genetically fixed confidence of much of the Antarctic fauna, so that one can approach the animals almost to within touching range. The presence of land predators in the Arctic meant that the ‘northern penguin’, the flightless great auk *Pinguinus impennis* only lived at the margins of the Arctic, on islands where polar bears, wolves, Arctic foxes and humans were absent – until European mariners reached their breeding grounds a few centuries ago and drove them to extinction.

While the Arctic is very much richer in terrestrial biodiversity than the Antarctic, this is not so for marine life. With c. 7,600 marine species, the Arctic has similar species richness to the Antarctic, even though the species composition of the marine phytoplankton and sea-ice algal communities is different between the two polar regions. The open southern ocean that has encircled the Antarctic for millions of years has allowed many Antarctic marine taxa to disperse around the entire continent. Given the greater extent of the ice-free southern ocean, compared with Arctic waters, it is not surprising that the total numbers of marine organisms living in Antarctic waters exceed those of similar Arctic species. For example, the most numerous seal species in the world is the Antarctic crabeater seal *Lobodon carcinophaga* with an estimated population in the region of 50 to 80 million individuals (Shirihai 2008); while at least 24 Antarctic and sub-Antarctic seabird species number more than 1 million individuals, ‘only’ about 13 Arctic and sub-Arctic seabirds reach this level (cf. Cramp 1983-1989, Williams 1995, Brooke 2004, Shirihai 2008, Ganter & Gaston, Chapter 4). In contrast to Antarctica, Arctic marine waters are separated into Pacific and Atlantic zones, each with its own evolutionary history, so that many Arctic genera are represented by different species in the two ocean basins. In addition, marine food webs differ between the two polar regions (Smetacek & Nicol 2005). Taken together, ecosystem structure, sea extent and the presence of humans and mammalian predators in the Arctic have resulted in great differences in structure, composition and functioning between both marine and terrestrial ecosystems in the Arctic and Antarctic regions.

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**Box 4. Two very different polar areas**

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Species richness is unevenly distributed over the Arctic and varies both with latitude and longitude and Pleistocene glacial history. It is also to some extent taxon specific. In most organism groups, species richness declines from the low to high Arctic. Areas that were unglaciated during the last ice age possess higher richness of vascular plants, bryophytes, diadromous and freshwater fishes and terrestrial mammals (Reid et al., Chapter 3, Christiansen & Reist, Chapter 6, Daniëls et al., Chapter 9). The area around the Bering Strait and eastern Siberia is particularly rich in species (e.g. plants, terrestrial invertebrates, shorebirds and mammals), probably due to the existence of unglaciated refugia during the Quarternary (Fig. 2) in combination with isolation east and west of the strait and on islands during interglacial periods with elevated sea levels (Payer et al., Chapter 2, Reid et al., Chapter 3, Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7, Daniëls et al., Chapter 9, Ims and Ehrich, Chapter 12). Marine fish have very high richness in the Bering Sea, but much lower richness on the Arctic side of the Bering Strait sill (Christiansen & Reist, Chapter 6). While Iceland and Greenland have

<table>
<thead>
<tr>
<th>Group</th>
<th>Species occurring in the Arctic</th>
<th>Ratio of worldwide total</th>
<th>Mainly Arctic species</th>
<th>IUCN Endangered, Vulnerable, or Near Threatened</th>
<th>Extinct in modern times</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrestrial mammals</td>
<td>67</td>
<td>1%</td>
<td>18</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Marine mammals</td>
<td>35</td>
<td>27%</td>
<td>11</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Terrestrial and freshwater birds</td>
<td>154&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2%</td>
<td>81&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Marine birds</td>
<td>45&lt;sup&gt;a&lt;/sup&gt;</td>
<td>15%</td>
<td>24&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Amphibians/reptiles</td>
<td>6</td>
<td>&lt;1%</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Freshwater and diadromous fishes</td>
<td>127</td>
<td>1%</td>
<td>19</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Marine fishes</td>
<td>c. 250&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1%</td>
<td>63</td>
<td>4&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Terrestrial and freshwater invertebrates</td>
<td>&gt; 4,750</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marine invertebrates</td>
<td>c. 5,000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vascular plants</td>
<td>2,218</td>
<td>&lt;1%</td>
<td>106&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bryophytes</td>
<td>c. 900</td>
<td>6%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terrestrial and freshwater algae</td>
<td>&gt; 1,700</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marine algae</td>
<td>&gt; 2,300</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-lichenized fungi</td>
<td>c. 2,030</td>
<td>4%</td>
<td>&lt;2%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lichens</td>
<td>c. 1,750</td>
<td>10%</td>
<td>c. 350</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lichenocolous fungi</td>
<td>373</td>
<td>&gt;20%</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Includes only birds that breed in the Arctic. <sup>b</sup> Excludes the sub-Arctic Bering, Barents and Norwegian Seas. <sup>c</sup> Most marine fish species have not been assessed by IUCN. <sup>d</sup> Includes Arctic endemics only.
particularly low diversity of freshwater fish and terrestrial mammals, Greenland is rich in lichens (Dahlberg & Bültmann, Chapter 10). Marine benthic invertebrates show highest species richness in the Barents/Kara Sea area, although some of those latter patterns partly may result from more intensive sampling in these areas (Josefson & Mokievsky, Chapter 8).

Although the relationship between diversity and productivity remains unclear (e.g. Currie et al. 2004), zones of high productivity often support higher diversity of species. Deltas and estuaries of large Arctic rivers are among such areas of high local productivity due to riverine nutrient inputs, mixing zones and upwellings from deep marine waters. These areas contain high fish biodiversity, consisting of mixtures of wholly freshwater species inside the deltas, diadromous species moving between fresh and marine waters, and nearshore marine species tolerant of waters of widely varying salinities (Christiansen & Reist, Chapter 6).
2.1. Terrestrial ecosystems

The terrestrial Arctic makes up about 5% of the Earth terrestrial surface. Most of it is within relatively short distance from icy coasts that make up one fifth of the total coastline of the world. Compared with most other biomes on Earth, the terrestrial Arctic is generally low in species diversity, which is explained by a number of properties, such as its relatively young age, low solar energy input, extreme climatic variability and decreasing biome area with increasing latitude (Payer et al., Chapter 2). The high Arctic has particularly low vascular plant diversity compared with lower latitudes in the Arctic (Daniëls et al., Chapter 9). But at a small scale, species diversity can be very high. In sample-plots of 25 square meters, for example, almost 100 species of vascular plants, bryophytes and lichens can grow together (Vonlanthen et al. 2008) with an unknown number of other fungi, algae and microbes, which is as high as in the richest grasslands of temperate and subtropical regions (Daniëls et al., Chapter 9, Dahlberg & Bültmann, Chapter 10). Together with the absence of woody
plants and sedges (*Carex* spp.), this makes this marginal northern rim of the Arctic a unique ecosystem of the world (e.g. Matveyeva 1998, Vonlanthen *et al.* 2008, Ims & Ehrich, Chapter 12).

Terrestrial Arctic ecosystems are characterized by a short productive summer season, but also by large regional differences including markedly steep environmental gradients. For example on the Taimyr Peninsula in Siberia only 500 km separate the relatively lush sub-Arctic and the high Arctic ‘desert’ (CAVM Team 2003, Callaghan 2005). The defining features of the terrestrial Arctic are cool summers (see Box 1) and short growing seasons resulting in low primary productivity and reduced biomass in comparison with southerly latitudes. Adaptations include slow growth and long life cycles in plants and fungi, small fungal sporocarps and small average body sizes in invertebrates (Callaghan 2005, Dahlberg & Bültmann, Chapter 10). Another prominent feature of much of the Arctic is extreme seasonality with ground-level differences of up to about 80 °C between winter minimum and summer maximum temperatures and with strong spatial north-south and coast-inland gradients. Arctic organisms are well adapted to this seasonality either by their ability to migrate during winter, or through characteristics making them suited to the cold and snow (Callaghan *et al.* 2004a). These include short extremities, winter whiteness, insulation through fur, feathers and fat, freeze tolerance, endogenous antifreeze compounds, hibernation and the ability to survive desiccation and oxygen deficiency, together with behavior exploiting the insulative properties of snow. Similarly, sessile organisms such as plants have developed a variety of individual strategies to economize or reduce loss in biomass and to persist through adverse conditions, such as asexual reproduction, small and compact growth, furry or wax-like coatings, positive photosynthesis balance at low temperature and survival at extremely low temperatures and levels of water content during winter dormancy.

Arctic terrestrial biodiversity has had to adapt to the high variability of the Arctic climate both in the form of inter-annual variability (including extreme events) and more regular (short or long-term) climatic fluctuations (see Walsh *et al.* 2011). This variability can drive, and may regionally synchronize, fluctuations in wildlife populations (e.g. Vibe 1967, Krupnik 1993, Hansen *et al.* 2013). Inter-annual variability in weather includes extraordinarily severe winters, highly varying amounts of snow, spells of winter rain and thaw (ice crust formation on land; see Rennert *et al.* 2009), variable timing in spring snow melt and sea ice break up, and poor summer weather including periods of strong winds and snowfall. There is increasing evidence that such events occur in cyclical patterns governed by geophysical phenomena such as the Arctic, North Atlantic and Pacific Decadal Oscillations (see Hurrell *et al.* 2003). Moreover, the internally driven (endogenous) multi-annual, high-amplitude cycles in animal and plant biomass driven by trophic interaction in tundra food webs, contribute to the temporal variability of biodiversity (Ims & Fuglei 2005, Ims & Ehrich, Chapter 12). There is rarely a ‘normal’ year in the Arctic.

### 2.2. Freshwater ecosystems

The Arctic landscape is characterized by a wide range of types and sizes of freshwater systems including...
flowing systems (rivers and streams) and many types of standing water systems (lakes, ponds) (ACIA 2005, Wrona et al. 2006, Vincent et al. 2008). High seasonality and in many cases ephemerality characterize all systems (Pielou 1994). A unique combination of climatic, geological and biophysical features, related cold-regions processes and the interactions among them produce a diverse range of environmental conditions that shape Arctic freshwater ecosystems and distinguish them from those found at lower latitudes.

Although freshwater ecosystems are abundant in the Arctic, they do not generally support the levels of biodiversity found in more southerly regions. The regional numbers of freshwater species typically decrease sharply poleward, although the differences among regions in the Arctic can be considerable. Fish species diversity is generally low at both regional and local scales in high latitudes, although considerable diversity of the fishes exists below the species level (Reist et al. 2006). Although Arctic freshwater systems gener-
ally display less biological diversity than temperate or tropical systems, they contain a diversity of organisms that display specialized adaptation strategies to cope with the extreme environmental conditions they face. Examples of adaptations include life-history strategies incorporating diapause and resting stages, unique physiological mechanisms to store energy (i.e. lipids) and nutrients, an ability to grow and reproduce quickly under short growing seasons, and extended life spans relative to more temperate species (Wrona et al. 2005).

2.3. Marine ecosystems

Arctic marine ecosystems differ from other marine ecosystems on the planet. Dominated by large areas of seasonally-formed sea ice over extensive shelves and a large central area of perennial (multi-year) pack ice – at least until recent times – the Arctic Ocean is characterized by seasonal extremes in solar irradiance, ice cover and associated atmospheric exchanges, temperature and, on the shelves, riverine inflow. The seasonality in environmental conditions and the physiography of the Arctic Ocean, together with its connection to the Atlantic and Pacific Oceans through the ‘Arctic gateways’, are key elements structuring its diversity of species and ecosystems.

The Arctic Ocean is stratified because the large freshwater inflow from rivers and seasonal sea-ice melt makes the upper layer of the ocean less salty than other oceans (Fig. 3). The surface stratification is important in that it can limit nutrient supply from nutrient-rich deep waters to the upper water column, where primary production takes place when there is sufficient light in spring/summer. During winter, the absence of light limits photosynthetically driven primary production, which will resume upon the return of the sun, and is, therefore, dependent on latitude. When sufficient light

![Figure 3. Schematics of different water masses in the Arctic Ocean, emphasizing vertical stratification (from AMAP 1998).]
Figure 4. Circumpolar map of known polynyas. Note that some polynyas no longer exist in the form known from their recent history (from Barber & Masson 2007). Photo: yui/shutterstock.com
is available in or under the ice, or at ice edges and in open water areas (e.g. in polynyas and ice-free waters in the Barents Sea), short and highly productive phytoplankton or ice algal blooms develop, delivering of energy and materials to zooplankton and other trophic levels that also display a high seasonality in feeding, reproduction and migration patterns.

In the marine Arctic, the central Arctic basins are typically (in the presence of multi-year ice) regions of low productivity. However, some of the most productive marine ecosystems on Earth are found in the outer Arctic seas (e.g. Barents, Chukchi and Bering Seas) and in polynyas, i.e. recurrent areas of open water amid sea ice (Fig. 4). Many species of invertebrates, fish, seabirds and marine mammals occur in large aggregations at such particularly productive sites. Interestingly, Arctic sea ice can host productive microbial communities, and the deep waters of the Arctic Ocean also have unique hot vent communities adapted to very high temperatures, highlighting the range of extremes found in Arctic marine ecosystems.

2.4. Arctic species and foodwebs

On a global scale, Arctic terrestrial ecosystems are relatively young, having developed mainly during the last three million years (Payer et al., Chapter 2, Ims & Ehrich, Chapter 12). The early Quaternary Arctic flora included species that evolved from high-latitude forest vegetation by adapting to colder conditions, plus others that immigrated from alpine habitats in temperate regions of Asia and North America. During the Quaternary Period, Arctic ecosystems have been profoundly molded by climatic history, including more than 20 cycles of glacial advance and retreat, along with associated changes in sea-ice cover. In many areas, these broad-scale changes displaced, then readmitted, biological communities. Consequently, many Arctic species are well adapted to climate variability and extremes, but poorly adapted for secondary ecological stressors such as increased competition, parasites and diseases (Callaghan et al. 2004a).

Many Arctic animal, fungal and plant species are widely distributed within the circumpolar region, with a significant proportion having circumpolar distributions. Endemic species, for which ranges are restricted to a limited geographic region such as the Arctic or parts of the Arctic, are found in many groups of Arctic animals, plants and fungi. However, because of the shifting conditions, local-scale adaptation and speciation is rare outside Beringia, leading to low numbers of local endemics. Among invertebrates, endemic species range from single cell testate amoebae to the higher arthropods such as spiders, mites, springtails and beetles (Hodkinson, Chapter 7). Among marine invertebrates, the moss animals (bryozoans), being sessile and generally characterized by restricted dispersal ability, show a relatively high degree of endemism (Josefson & Mokievsky, Chapter 8). Some helminth parasites also have restricted geographic distributions coinciding with their avian, mammalian and piscine hosts (Hoberg & Kutz, Chapter 15). Among vascular plants, endemic species include more than one hundred narrow-range species especially in Beringia and even some planktonic cold-adapted algae (Daniëls et al., Chapter 9). Among fungi, there are many endemic or restricted range lichens, especially from Svalbard, Greenland, Novaya Zemlya, eastern Chukotka and Ellesmere Island. Most of these are rock-dwelling microlichens confined to the high Arctic (Dahlberg & Bültmann, Chapter 10). Among terrestrial insects, several beetle species are endemic to the Beringia region of NE Siberia. Several species of char Salvelinus spp., several whitefishes Core-
Figure 5. Circumpolar *Calidris* sandpiper species richness. The dark grey line denotes the border between the Arctic and the sub-Arctic. Adapted from Zöckler (1998).
gonus spp. and a few other freshwater and marine fishes are endemic or near endemic to the Arctic (Christiansen & Reist, Chapter 6). In birds, the loons/divers Gaviidae and the auks Alcidae are mainly found in the Arctic and sub-Arctic, while the eiders Somateria spp. and Polysticta, gulls (Laridae) and Calidris sandpipers reach their highest diversity there (Fig. 5; Ganter & Gaston, Chapter 4). Also among mammals, a number of highly adapted species are found almost exclusively in the Arctic (Reid et al., Chapter 3).

Among flying birds, few of the Arctic species can be classified as restricted range species, i.e. species with a total historical breeding range of less than 50,000 km² (BirdLife International 2012). However, among other groups, several species exhibit more limited distributions. Some Arctic endemics are confined to one or a few locations, such as longfin char Salvethymus svetovidovi and small-mouthed char Salvelinus elgyticus, which are found only in Lake El’gygytgyn, a three million-year-old meteorite crater lake in central Chukotka (Christiansen & Reist, Chapter 6). Mammals with restricted ranges include some species of shrews and lemmings, such as the Pribilof Island shrew Sorex pribilofensis and the Wrangel Island brown lemming Lemmus portenkoi, which inhabit islands that were once part of a broader land mass but became isolated by rising sea levels after the last ice age.

In response to extreme seasonality, many Arctic species are migratory. This involves a high proportion of bird species and several marine mammals that migrate out of the Arctic entirely, whereas others such as reindeer/caribou migrate long distances within the Arctic or to adjacent sub-Arctic areas. Migratory birds, in particular, visit the Arctic to breed or feed intensively during the summer burst of productivity, both on land and in the sea. Many of them spend more than half the year outside the Arctic, where they may be found in practically every other part of the world, except inland Antarctica (Ganter & Gaston, Chapter 4).

A special kind of migration is shown by diadromous fish, which either spend each summer in the sea to fatten up, or live there for most of their lives before going up rivers to reproduce in fresh water (Christiansen & Reist, Chapter 6).

Arctic ecosystems have generally been considered to possess shorter food chains with fewer trophic levels heterozygous genomes, which may buffer against interbreeding and genetic drift through periods of dramatic climate change. Moreover the ecological amplitude of polyploids is broad and thus they have a greater ability to cope with a changing climate and adapt to more diverse ecological niches than a diploid could (Brochmann et al. 2004, Daniëls et al., Chapter 9). Among birds, plumage polymorphism is widespread (e.g. skuas/jaegers Stercorariidae, northern fulmar Fulmar glacialis, snow geese Chen spp., Iceland gull Larus glaucoides, nesting murres Uria spp.), perhaps as a result of population differentiation and introgression during the Pleistocene glacial and interglacial periods (see also Box 17.10 in Cook, Chapter 17).

Therophytes (annual plant species) are rare in the Arctic because of short growing seasons, marked interannual variability and nutrient-poor soils. Conversely, polyploidy is common across the Arctic vascular plant flora, in particular in the northern and longer-glaciated North Atlantic areas of the Arctic (e.g. Brochmann et al. 2004, Solstadt 2009). The evolutionary success of polyploids in the Arctic may be based on their fixed

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2 More than two sets of chromosomes occurring in an organism.

3 Fish migrating between fresh and marine waters.
than other biomes (Callaghan 2005). However, this concept is increasingly challenged (see e.g. Hodkinson, Chapter 7 and Michel, Chapter 14), and Arctic marine ecosystems are found to be as diverse as more southern marine ecosystems (Smetacek & Nicol 2005, Josefson & Mokievsky, Chapter 8). However, the numerical dominance of relatively few key species in Arctic food webs, together with highly variable climatic conditions, makes them prone to strong food web interactions (for instance leading to community-wide cycles) and environmentally driven fluctuations with cascading effects through entire ecosystems (Post et al. 2009, Gilg et al. 2012, Hansen et al. 2013). Consequently, Arctic ecosystems are unstable in terms of species composition and abundance, but nevertheless have shown substantial resilience to natural variability in the Holocene, largely because of the wide distributions and mobility of their constituent organisms. This mobility, which enables much of the fauna and flora to move and seek new habitat elsewhere in response to unfavorable circumstances, is often an essential part of their adaptation to locally and regionally variable conditions. Mobility can be active, in which animals seek out new habitat, or passive, involving non-directed dispersal of animals, fungi and plants by wind, surface melt-water and streams, and local ocean currents or by phoretic dispersal on the bodies of vertebrates or larger flying insects. When planning for Arctic conservation, it is essential to consider the vast spatial scales over which many organisms operate as well as the existing barriers to mobility that influence the current distribution of some species (e.g. marine barriers to movements of some terrestrial mammals such as the Arctic ground squirrel *Spermophilus parryii*).

Each spring, millions of birds migrate to the Arctic from almost all parts of the world to take advantage of the bounty of plant and invertebrate production in the short Arctic summer. Red knots, dunlins, grey plovers and bar-tailed godwits staging in the European Wadden Sea before taking off to the Siberian tundra in late May. Photo: Jan van de Kam.