Arctic biodiversity has been exposed to strong selection pressures in the harsh and highly fluctuating Arctic environment over periods of up to three million years with repeated glaciations interrupted by relatively short interglacial periods. Photo: dalish/shutterstock.com
**Chapter 2**

**Species Diversity in the Arctic**

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**Contents**

Summary ............................................................... 68
2.1. Introduction .................................................... 68
2.2. Characteristics of Arctic biodiversity ......................... 70
  2.2.1. Biotic and abiotic factors that structure diversity ...... 70
  2.2.2. Spatial distribution of Arctic biodiversity ................. 71
2.3. Origins of Arctic biodiversity .................................. 72
  2.3.1. Terrestrial and freshwater ............................... 73
  2.3.2. Marine .................................................... 73
2.4. Future prospects for Arctic biodiversity ....................... 74
Acknowledgements .................................................. 75
References ......................................................... 75

When there is an earthquake, we say that the mammoth are running. We have even a word for this, holgot.

Vyacheslav Shadrin, Yukaghir Council of Elders, Kolyma River Basin, Russia; Mustonen 2009.
Species richness is generally lower in the Arctic than at lower latitudes, and richness also tends to decline from the low to high Arctic. However, patterns of species richness vary spatially and include significant patchiness. Further, there are differences among taxonomic groups, with certain groups being most diverse in the Arctic.

Many hypotheses have been advanced to explain the overall decline of biodiversity with increasing latitude, although there is still no consensus about a mechanistic explanation. Observed patterns are likely the result of complex interactions between various biotic and abiotic factors. Abiotic factors include lower available energy and area at high latitudes, and the relatively young age of Arctic ecosystems. Among biotic factors, latitudinal differences in rates of diversification have been suggested, but empirical evidence for this as a general principle is lacking. Recent evidence suggests that ‘tropical niche conservatism’ plays a role in structuring latitudinal diversity.

Physical characteristics of the Arctic important for structuring biodiversity include extreme seasonality, short growing seasons with low temperatures, presence of permafrost causing ponding of surface water, and annual to multi-annual sea-ice cover. The Arctic comprises heterogeneous habitats created by gradients of geomorphology, latitude, proximity to coasts and oceanic currents, among others. Superimposed on this is spatial variation in geological history, resulting in differences in elapsed time for speciation.

Over 21,000 species of animals, plants and fungi have been recorded in the Arctic. A large portion of these are endemic to the Arctic or shared with the boreal zone, but climate-driven range dynamics have left little room for lasting specialization to local conditions and speciation on local spatial scales. Consequently, there are few species with very small distributions. In terrestrial regions, high-latitude forests were replaced by tundra about 3 million years ago. Early Quaternary Arctic flora included species that evolved from forest vegetation plus those that immigrated from temperate alpine habitats, but the most intensive speciation took place in situ in the Beringian region, associated with alternating opportunities for dispersal (over the Bering land bridge, when sea levels were low) and isolation (during high sea levels). In the marine realm, the evolutionary origin of many species can be traced to the Pacific Ocean at the time of the opening of the Bering Strait, about 3.5 million years ago.

More than 20 cycles of Pleistocene glaciation forced species to migrate, adapt or go extinct. Many terrestrial species occupied southern refugia during glaciations and recolonized northern areas during interglacials. Ice-free refugia persisted within the Arctic proper; species occupying these refugia diverged in isolation, promoting Arctic diversification. The most significant Arctic refugium was Beringia and adjacent parts of Siberia. Pleistocene glaciations also resulted in a series of extinction and immigration events in the Arctic Ocean. During interglacials, marine species immigrated mainly though the Arctic gateways from the Pacific and Atlantic Oceans, a process that continues today.

Throughout the Pleistocene, Arctic species responded to climatic cycles by shifting their distributions, becoming extirpated or extinct, persisting in glacial refugia, and evolving in situ. Although the last 10,000 years have been characterized by climatic stability, the Earth has now entered a period of rapid anthropogenic climate change that is amplified in the Arctic. Generalism and high vagility typical of many Arctic species impart resilience in the face of climate change. However, additional anthropogenic stressors including human habitation, overharvest, industrial and agricultural activities, contaminants, altered food webs and the introduction of invasive species pose new challenges. The consequences of current warming for Arctic biodiversity are therefore not readily predicted from past periods of climate change.

2.1. Introduction

Arctic ecosystems are relatively young in a geological sense, having developed mainly in the last 3 million years (Murray 1995), although some Arctic species’ lineages diverged and adapted to cold, polar conditions much earlier (see Section 2.3). In general, species richness is lower in the Arctic than in more southerly regions (Fig. 2.1). This is consistent with the general observation that biodiversity declines from the Equator to the poles (Rosenzweig 1995, Gaston & Blackburn 2000, Willig et al. 2003). The strength and slope of latitudinal biodiversity gradients differ between regions and are more pronounced in terrestrial and marine systems than in freshwater environments, and, in general, most pronounced in organisms with greater body mass and those occupying higher trophic levels (Hillebrand 2004). With the recent development of global distributional and phylogenetic datasets, however, it has become apparent that the pattern is much more complex than previously assumed (Jetz et al. 2012).

A number of hypotheses have been advanced to explain the latitudinal trend of biodiversity, although no consensus exists for a mechanistic explanation (Currie et al. 2004). Hypotheses may be grouped into those based on ecological mechanisms of species co-occurrence, evolutionary mechanisms governing rates of diversification, and earth history (Mittlebach et al. 2007). Until recently, ecological hypotheses have dominated the discussion, but with the development of large DNA-based phylogenies there is now more focus on understanding the underlying historical processes. The hypotheses proposed to date are not necessarily mutually exclusive, and observed patterns are likely the result of complex interactions between various biotic and abiotic factors.

The decline of available energy (Allen et al. 2002) and decreasing biome area (Rosenzweig 1995) with increas-
ing latitude should both contribute to declining species richness in the North. Rohde (1992) posited that the ultimate cause could be a positive relationship between temperature and evolutionary speed. Relative to the tropics, the Arctic has limited insolation (lower solar energy input and thus colder temperatures) and a shorter elapsed time for diversification. In Rohde’s (1992) view, all latitudes could support more species than currently exist, and, given adequate evolutionary time, the Arctic could support biodiversity rivaling that of lower latitudes. Because of great variation in speciation rates, however, the number of species in taxonomic groups is uncoupled from the age of groups (Rabosky et al. 2012). Further, several Arctic groups (notably waterfowl and gulls) underwent significant recent increases in speciation rates (Jetz et al. 2012). Thus, there is no general latitudinal change in speciation rates (as assumed, e.g. by Wiens et al. [2010]), and Jetz et al. (2012) instead point out hemispheric or even more local differences.

The recently proposed ‘tropical niche conservatism’ hypothesis may reconcile some of these diverging tendencies. This hypothesis assumes that most organismal groups originated during times when the global climate was warm (paratropical), and these groups tend to retain their adaptations to such conditions (Webb et al. 2002). Thus, as the global climate became cooler during the Oligocene, and again in the late Miocene, the ancient groups contracted their geographical distributions towards the Equator to maintain their original niches. The long time for speciation in tropical environments, compared with cold environments, would explain the large accumulation of species, and phylogenetically overdispersed communities, in the humid tropics (Wiens 2004). The most significant increases in speciation rates are associated with ecological shifts to new habitats that arose outside the humid tropics, notably in montane regions and archipelagos (Fjeldså et al. 2012, Jetz et al. 2012; see also Budd & Pandolfi 2010). However, only some groups have (yet) responded by adapting to these new environments, resulting in small and phylogenetically clustered communities in the Arctic.

The diversification process within the Arctic may have been strongly affected by the climatic shifts caused by variations in Earth’s orbit known as Milankovitch oscillations. This includes a tilt in the Earth’s axis that varies on a 41,000-year cycle (precession), an eccentricity in Earth’s orbit that varies on a 100,000-year cycle, and 23,000 and 19,000-year cycles in the seasonal occur-
rence of the minimum Earth-Sun distance (perihelion; Berger 1988). Milankovitch oscillations cause variations in the amount of solar energy reaching Earth, and these variations interact with characteristics of the Earth’s atmosphere such as greenhouse gas concentration and surface albedo, resulting in rapid, nonlinear climatic change (Imbrie et al. 1993). The present interglacial period, which has extended over the last 10,000 years, is a period of exceptional climatic stability; stable conditions have typically lasted only a few thousand years, and > 90% of the Quaternary Period (2.6 million years ago to present) has been characterized by more climatically dynamic glacial periods (Kukla 2000).

Webb & Bartlein (1992) noted that Milankovitch oscillations are associated with changes in size and location of species’ geographical distributions. Dynesius & Jansson (2000) called these recurrent changes “orbitally forced species’ range dynamics” (ORD), and noted that they constrain evolutionary processes acting on shorter time scales. The effects of Earth’s precession and orbital eccentricity on surface temperatures are greatest at high latitudes (Wright et al. 1993), resulting in increasing ORD along the latitudinal gradient from tropics to poles. Predicted evolutionary consequences of enhanced ORD are apparent in general characteristics of Arctic biota, including enhanced vagility and larger species’ geographic range sizes (Rapaport’s rule), and therefore increased mixing of locally-adapted populations, increased proportion of polyploids within plant taxa, and reduced rates of speciation (Dynesius & Jansson 2000, Jansson & Dynesius 2002). There is spatial variation in these processes within latitude, however, which must be considered when evaluating current diversity patterns. For example, the Pleistocene temperature amplitude was lower in E Siberia and the Bering Strait region than in areas around the North Atlantic, leading to less glacialization (Allen et al. 2010) and enhanced opportunities for speciation in the Siberian-Beringian region (see below).

Although ORD increases risk of extinction associated with habitat change, this is mitigated by enhanced generalism, vagility and genetic mixing at high latitudes (Dynesius & Jansson 2000). This has important implications for risk of extinction associated with climate change and other stressors, as will be discussed in subsequent chapters of this Assessment.

### 2.2. Characteristics of Arctic biodiversity

#### 2.2.1. Biotic and abiotic factors that structure diversity

Physical characteristics important for structuring Arctic biodiversity include extreme seasonality with dramatic intra-annual variation in insolation, generally cool summers, presence of permafrost resulting in unusual landforms, and annual to multi-year sea-ice cover. The resulting landscape is generally devoid of trees (a defining feature of the Arctic; see Section 2 in Meltofte et al., Introduction) because tree growth, reproduction and survival are limited by short, cold growing seasons, lack of suitable substrates and nutrient deficiencies (Grace et al. 2002, Walker et al. 2012). Large areas of the Arctic’s land surface are characterized by flat terrain underlain by permafrost, resulting in wetlands characterized by waterlogged soils and ponding of surface water (Gutowski et al. 2007). The Arctic Ocean has a deep central basin surrounded by the most extensive shelves of all the world’s oceans, and is characterized by extensive (though declining) ice cover for much of the year (Michel, Chapter 14).

Species diversity is ultimately a product of both niche-based factors, e.g. adaptation to different environmental conditions, and dispersal-based factors, e.g. immigration from species pools. Of niche-based factors, adaptation to different environmental conditions or habitats is significant for generating diversity worldwide (Whittaker 1960). In general, complex, heterogeneous environments support higher diversity than homogeneous ones. Although the Arctic lacks the rich diversity provided by multistoried canopies in forested regions, it is far from homogeneous. The Arctic comprises vast numbers of different habitats created by gradients related to geomorphology (e.g. depth in the marine environment and elevation in the terrestrial realm), latitude, history of glaciation, proximity to coastlines, and oceanic currents, among other factors. In the marine environment, ice cover provides habitats unique to the Arctic with characteristic flora and fauna on both the bottom (secondary bottom habitats) and top (melt-water pools) of the ice surface. In the terrestrial Arctic, spatial heterogeneity in ice-associated processes such as freeze-thaw cycles and thermokarst create a dynamic mosaic of freshwater pools and shallow wetlands, which provide habitats for diverse taxa. This habitat heterogeneity is superimposed on spatial variation in geological history, resulting in differences in elapsed time for speciation.

In addition to these niche-based factors, barriers for dispersal affect status and trends in regional biodiversity, and, over the long term, opportunities for speciation. For example, terrestrial areas in the high Arctic comprise archipelagos separated from each other and from areas farther south by pack ice, which affects dispersal rates for several species (e.g. Daniëls et al., Chapter 7). One well-known barrier in the marine environment is the huge ice plug occupying M’Clure Strait, Melville Sound and M’Clintock Channel in the Canadian High Arctic. This ice plug has persisted as a stable feature for > 1,000 years (although it is probably not stable on longer time scales), and effectively separates stocks of some marine mammals (Dyke et al. 1996). Polynyas (persistent open water areas within sea ice), which typically form in the shear zone between landfast and pack ice, provide important foraging areas during the breeding season and serve as winter refugia for a variety of seabirds and marine mammals (Stirling 1997), thereby contributing to Arctic biodiversity. Similarly, ice cover on land (glaciers and ice sheets) fragments terrestrial and freshwater habitats. Such fragmentation may enhance
biodiversity (Fedorov et al. 2003), although the opposite effect of reduced range size leading to increased risk of extirpation or extinction must be considered (Rosenzweig 1995). This relationship is reversed for some ice-adapted Arctic species, with warming leading to habitat fragmentation, isolation and reduced ranges. Responses of Arctic biota to barriers related to climatic changes are therefore complex and not completely analogous to those of temperate taxa (Cook, Chapter 17).

Another feature of importance for Arctic biodiversity is regional heterogeneity in productivity. This is particularly true for the marine environment, where high productivity occurs in open waters close to the ice edge (Michel, Chapter 14). Diversity is often related to productivity in a unimodal (hump-shaped) fashion (Currie 1991, Currie et al. 2004), with diversity being highest in systems with mid-range productivity. However, this relationship is poorly documented in the Arctic, and may vary by taxonomic group or community type (Witman et al. 2008). Regardless of the exact relationship, differences in ice cover, mixing between warm- and cold-water currents, or currents with different nutrient content create a mosaic of oligotrophic and more enriched areas, which is reflected in differences in population density and species diversity. Good examples of enriched areas are the Bering and Barents Seas, which harbour species-rich invertebrate, fish and avian faunas (Ganter & Gaston, Chapter 4, Christiansen & Reist, Chapter 6, Josefson & Mokievsky, Chapter 8). In contrast, the deep seafloor of the central Arctic Ocean is oligotrophic and species poor.

In general, the terrestrial and marine Arctic are highly heterogeneous with many edge effects and potential dispersal barriers, creating the expectation of high species diversity associated with differential adaptation to distinct habitats. Despite this heterogeneity, however, the Arctic is less diverse than lower-latitude areas for several taxa, including mammals (Fig. 2.1a), most birds (Fig. 2.1b), plants (Fig. 1.1 in Meltofte et al., Chapter 1) and especially herpetofauna (amphibians and reptiles), which are represented by just six species at the southern rim of the circumpolar Arctic (Kuzmin & Tessler, Chapter 5). As mentioned above, extreme seasonality, short growing seasons, overall harshness of climate, and widespread persistent or seasonal ice cover are all likely factors driving these relationships. Diversity in several other groups of organisms may equal or exceed that of corresponding groups at lower latitudes, however. Examples include marine benthic invertebrates (Renaud et al. 2009, Piepenburg et al. 2011), marine crustaceans and phytoplankton (Archambault et al. 2010), and Calidris sandpipers (Fig. 1.2 in Meltofte et al., Chapter 1; Ganter & Gaston, Chapter 4). Very high species richness is also displayed in some terrestrial and freshwater invertebrate groups such as Collembola (springtails), which have the additional distinction of including many species that are endemic to the Arctic (Hodkinson, Chapter 7).

### 2.2.2. Spatial distribution of Arctic biodiversity

The Arctic supports > 21,000 species of mammals, birds, fish, invertebrates, plants and fungi, plus an estimated several thousand species of endoparasites and

<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*</td>
<td>2%</td>
<td>81*</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Marine birds</td>
<td>45*</td>
<td>15%</td>
<td>24*</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>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marine fishes</td>
<td>c. 250b</td>
<td>1%</td>
<td>63</td>
<td>4</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*</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>Lichenicolous fungi</td>
<td>373</td>
<td>&gt; 20%</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- a) Includes only birds that breed in the Arctic.
- b) Excludes the sub-Arctic Bering, Barents and Norwegian Seas.
- c) Most marine fish species have not been assessed by IUCN.
- d) Includes Arctic endemics only.
microorganisms, many of which have yet to be described (Tab. 2.1). Species richness varies spatially and is not uniform across taxa. Consistent with the global latitudinal gradient in diversity described previously, species richness generally declines from the low to the high Arctic. There are also distinct regional hotspots of high biodiversity found throughout the Arctic, suggesting that despite general geographic trends, local factors are important contributors to regional diversity. For example, extraordinarily high species diversity occurs in microalgae of Hudson Bay (Archambault et al. 2010), and in terrestrial and freshwater invertebrates in the Disco Bay area of W Greenland (Hodkinson, Chapter 7). Beringia, which is defined as the area from the Lena River in northeastern Siberia to the Mackenzie River in northwestern Canada, and from the Arctic Ocean to southern Alaska and the middle Kurile Islands (Fig. 2.2), was first identified as a biodiversity hotspot for vascular plants by Hultén (1937). Subsequent work demonstrated its significance for diversity in other groups like birds and mammals. Henningsson & Alerstam (2005) suggested that the high diversity observed in shorebirds of Beringia results from geological history, high productivity and accessibility to multiple flyways. Similarly, species richness of mammals is greatest in Quaternary glacial refugia, particularly those such as Beringia that maintained connections to boreal regions (Reid et al., Chapter 3). During and after the last glacial maximum (26,500-20,000 years ago), many herbivorous mammals persisted much longer in Beringia than western Eurasia, possibly because their favored forage (mesophilous herbs) persisted in this refugium (Allen et al. 2010). The role of Siberia and Beringia as the cradles of Arctic terrestrial biodiversity is reflected in a recent reassessment of the biogeographic regions of the World, based on linkages between distributions and phylogenetic relationships of > 20,000 terrestrial vertebrate species (Holt et al. 2013). This analysis identified a large Arctico-Siberian region, where the barren circumpolar Arctic environments associate with the wooded permafrost regions of Siberia.

In the marine realm, biodiversity tends to be high in the vicinity of the Arctic gateways from the North Atlantic and North Pacific Oceans (Christiansen & Reist, Chapter 6). This is true for such diverse taxa as mammals, fish and invertebrates. Diversity of marine fish (mainly teleosts and cartilaginous fishes) is particularly high in the Bering and White Seas (Christiansen & Reist, Chapter 6). Similarly, marine invertebrates have high species richness in Arctic areas close to the two gateways, with the highest diversity occurring in the Barents, Kara and White Seas (Josefson & Mokievsky, Chapter 8). For both fish and invertebrates, high diversity in the vicinity of the Arctic gateways is largely the result of mixing of sub-Arctic and Arctic fauna. Among marine mammals, the gateways provide corridors for seasonal migrations from temperate seas. The gateways are not true biodiversity hotspots, however, in that there are few endemic species present.

Figure 2.2. Beringia and other glacial refugia in the Arctic distribution of ice cover (white shading) and ice-free areas in the Northern Hemisphere during the last glacial maximum, 18,000 years ago (after Ray & Adams 2001). Beringia is enclosed within the red oval.

2.3. Origins of Arctic biodiversity

It is evident that general conditions such as environmental harshness can only partially explain observed patterns of Arctic diversity. Although the proportion of Arctic biota comprising endemics is relatively low, there exist many examples of endemic species well adapted to harsh conditions. In the marine realm, for example, about 20% of mollusks and echinoderms are considered endemic (Briggs 2007). Endemic Arctic mammals include polar bear Ursus maritimus and two monotypic genera of whales belonging to the family Monodontidae, the beluga Delphinapterus and the narwhal Monodon. The degree of endemism at the level of both genera and species, however, is far lower than in the Antarctic, which has a similarly harsh environment. One likely explanation is the difference in geological age of the two systems. While Antarctic biota have evolved over about 25 million years with cold conditions persisting for the last 10-17 million years (Clarke & Johnston 1996, DeVries & Steffensen 2005, Patarnello et al. 2011; see also Box 1.3 in Meltofte et al., Chapter 1), the corresponding elapsed time for Arctic biota is generally considered to be < 3.0 million years (Murray 1995, Briggs 2007). However, recent findings suggest that the modern circulation in the Arctic Ocean actually dates back 17 million years, with perennial sea ice cover formed about 13 million years ago (Krylov et al. 2008), so the difference may not be as great in the marine environment. The lower degree of endemism in the Arctic Ocean may also be a function of less isolation from adjacent oceans compared with the Antarctic seas, which are effectively isolated by the Antarctic Circumpolar Current (e.g. Hassold et al. 2009).
Within the Arctic, regional variation in rates of endemism appears to be related to elapsed time for speciation. For example, the opportunity for speciation has persisted longer in deep-sea areas than shelf and coastal marine areas, which have been free from bottom-covering glacial ice for a relatively short time (Weslawski et al. 2010). This is consistent with the observation that there are few endemic species in continental shelf and coastal areas (Dunton 1992, Adey et al. 2008).

Recent work in molecular phylogenetics suggests that some lineages of contemporary Arctic species adapted to cold, polar conditions as early as the Oligocene (34–23 million years ago), during the first Tertiary polar chill, although the precision of these estimates has been debated (Dornburg et al. 2012). For example, right whales (Balaenidae) may have originated as early as 27 million years ago (Sasaki et al. 2005). The Pluvialis sandpipers can be traced even further back, to 34 million years ago (Baker et al. 2007), and the divers Gavia represent a lineage that dates back > 65 million years to the late Cretaceous (Jetz et al. 2012), although it is not known when these birds adapted to Arctic conditions. See also Section 12.3.1 in Ims & Ehrich, Chapter 12.

### 2.3.1. Terrestrial and freshwater

Throughout most of the Tertiary Period (65–2.6 million years ago), high-latitude regions were forested (Murray 1995, McVeer & Basinger 1999). Tundra first appeared during the late Pliocene in response to global cooling (Matthews & Ovenden 1990). Tundra communities were initially distributed discontinuously, then expanded to occupy a circumpolar belt by three million years ago (Matthews 1979). The early Quaternary flora of the Arctic included species that evolved from high-latitude forest vegetation of the late Tertiary by adapting to colder conditions, along with others that immigrated from alpine habitats in temperate regions of Asia and North America (Hultén 1937, Hedberg 1992, Murray 1995, Schönswetter et al. 2003, Ikert-Bond et al. 2009). Dramatic climatic shifts subsequently occurred throughout the Pleistocene, with more than 20 cycles of glaciation punctuated by warm interglacial periods.

The Pleistocene glacial periods had a profound impact on Arctic biodiversity at all levels. Species had to migrate, adapt or go extinct. Many species occupied southern refugia during glacial maxima and recolonized northward following retreat of the ice sheets (Stewart et al. 2010). Ice-free refugia also persisted within the Arctic proper, including areas in eastern Europe, Siberia and North America. As mentioned above, the most significant Pleistocene refugium for Arctic and boreal biota was Beringia (Fig. 2.2; Hultén 1937).

Additional glacial refugia included exposed continental shelves and nunataks protruding above ice sheets in mountain ranges of the northern hemisphere (Abbott & Brochmann 2003). The existence of these refugia and their significance in structuring Arctic biodiversity has been supported by evidence from paleoecology, ecological niche modeling and molecular genetics (Cook, Chapter 17). Populations became fragmented and isolated in these ice-age refugia, which has likely promoted diversification in the Arctic (Fedorov et al. 2003).

An interesting example of the diversity-promoting effects of recurrent glaciations followed by interglacial periods is found in vascular plants of the Arctic. Arctic plants have a particularly high incidence of polyploidy, the presence of more than two sets of chromosomes. These polyploids have arisen through recurrent episodes of population fragmentation associated with glaciations followed by range expansions and hybridization during interglacials (Abbott & Brochmann 2003). New species resulting from this process (allopolyploids) are more successful than diploids in colonizing ice-free areas after deglaciation due to the buffering that their fixed-heterozygous genomes provide against inbreeding and genetic drift. Further, polyploids have broader ecological tolerances than diploids, and are thereby able to more readily adapt to diverse ecological niches and better cope with changing climate (Brochmann et al. 2004).

Beringia provided a land bridge between Eurasia and North America during most of the Tertiary, until it was severed by the Bering Strait at the shift between the Miocene and the Pliocene about 3.5 million years ago. The Bering Land Bridge repeatedly reformed throughout the Quaternary when sea levels fell during major glaciations (Hopkins 1973, Clark & Mix 2002), providing opportunities for biotic interchange between Eurasia and North America. This interchange included both terrestrial and freshwater species. An example of the latter is the Arctic grayling, which apparently originated in eastern Siberia (Froufe et al. 2003, Weiss et al. 2006) and dispersed to Arctic North America via freshwaters of the Bering Land Bridge. The importance of this alternation between opportunities for dispersal and isolation is also well documented from fossil rodent faunas (Repenning 2001) and from phylogenies for other small mammals of the region (Hope et al. 2013).

### 2.3.2. Marine

Many marine mammals, invertebrates and algae of the Arctic Ocean appear to have an evolutionary origin in the Pacific at the time of the opening of the Bering Strait, about 3.5 million years ago (Adey et al. 2008). Throughout most of the Tertiary, the Arctic Ocean region supported a temperate biota, although intermittent polar sea ice formed as early as 47 million years ago and perennial sea ice was probably present by 13 million years ago (Krylov et al. 2008, Polyak et al. 2010). Harsh Arctic conditions developed only during the latter part of this period, however, beginning approximately three million years ago (Jansen et al. 2000).

Several endemic Arctic lineages started to develop during the glaciated periods of the Tertiary. For example, the bowhead whale diverged from the right whale 16
For example, the Pacific boreo-Arctic echinoderms have a limited bathymetric range in the Arctic (often < 100 m), while the Atlantic boreo-Arctic species are mostly eurybathic (capable of tolerating a wide range of ocean depths). This is believed to be the result of substantial shelf glaciation on the Atlantic side that caused primarily eurybathic species to escape to great depths for survival, and later re-invade the shelves when conditions changed (Nesis 1983).

2.4. Future prospects for Arctic biodiversity

Over the last 2.6 million years, throughout the cycles of Pleistocene glaciations, Arctic species have shifted their distributions, become extirpated or extinct, persisted in glacial refugia, undergone hybridization, and evolved in situ. Although the last 10,000 years have been characterized by a relatively high degree of climatic stability, the Earth has now entered a period of rapid anthropogenic climate change. Global temperatures have been warmer than today’s for less than 5% of the last three million years (Webb & Bartlein 1992) and are within 1 °C of the maximum over the last one million years (Hansen et al. 2006). Further, the rate and magnitude of warming is amplified in the Arctic (McBean 2005, IPCC 2007, AMAP 2009, AMAP 2011). This trend of accelerating climate change and Arctic amplification is expected to continue (Overland et al. 2011). Global warming has caused species distributions to shift northward and to higher elevations for a wide range of taxa worldwide (Walther et al. 2002), including species occupying the Arctic (e.g. Sturm et al. 2001, Hinzman et al. 2005). The Arctic, being a region with high ORD and therefore populated by species that have experienced selection pressure for generalism and high vagility (Jansson & Dynesius 2002), should have inherent resilience in the face of climate change. Some extant Arctic species have survived population bottlenecks driven by climatic change, including cetaceans (e.g. narwhal [Laidre & Heide-Jørgensen 2005]) and waders (Kraaijeveld & Nieboer 2000), further suggesting some degree of climate-change resiliency. However, the rapid rate of change occurring now and the amplification of this change at high latitudes pose unique challenges for Arctic species. The Arctic has experienced less anthropogenic habitat change and fragmentation than lower latitudes, which favors the ability of species to track shifting habitats. However, because of the limited area available in the polar regions, terrestrial Arctic biota have limited ability to respond to warming by northward displacement (MacDonald 2010). Kaplan & New (2006) predicted that Arctic tundra will experience a 42% reduction in area if global mean temperature is stabilized at 2 °C above pre-industrial levels. Although the rate of change is debated (e.g. Hofgaard et al. 2012), there is general agreement that area of tundra will be significantly reduced in this century.

In addition to rapid and accelerating climate change, Arctic species are experiencing anthropogenic stressors that did not exist during past periods of warming,
including human habitation, overharvest, industrial and agricultural activities, anthropogenic contaminants, altered food webs, and the introduction of invasive species (Meltofte et al., Chapter 1). The many migratory species that occur only seasonally in the Arctic face additional and potentially cumulative anthropogenic stressors on migration routes and in overwintering areas that could further impact their ability to adapt. The suite of stressors experienced by Arctic species today is therefore novel, making past periods of climatic change an imperfect analogue for the challenges now facing Arctic biodiversity. Future efforts to preserve Arctic biodiversity must be similarly novel and broad-reaching.

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