The mirid bug *Chlamydatus pullus* feeding in a flower head of the dandelion *Taraxacum croceum* in the preserved herb field of Østerlien near Arctic Station at Godhavn/Qeqertarsuaq on Disko Island, W Greenland. Photo: Jens J. Böcher.

Chapter 7

Terrestrial and Freshwater Invertebrates

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Contents

> **Big new insects have appeared, beetles that fly.**
>
> [American buring beetle]
> Jolene Nanouk Katchatag an Inupiaq from Unalakleet, Alaska;
> Mustonen & Mustonen 2009.

> **Now the black flies appear before the mosquitoes, this is something new.**
>
> Komi Irina Kaneva from the Krasnochelye wilderness village on the Kola Peninsula;
> Mustonen 2011.

> **Judging by the last year there are almost no mosquitoes left in Lovozero [Luujavre]. It can be real evidence that climate is changing. Even some species of southern bugs and spiders appeared in tundra.**
>
> Vladimir Galkin, a member of the Sámi community Piras on Lovozero Lake in the Murmansk region of Russia;
> Mustonen & Zavalko 2004.

SUMMARY

The known terrestrial and freshwater invertebrate faunas of the Arctic comprise several thousand described species, representing over 16 major phyla. Many other species remain to be discovered and/or described. Arctic endemic species occur in many invertebrate groups. A significant proportion of Arctic species have circumpolar distributions. By comparison with better known groups such as vertebrates and plants, the invertebrates exhibit much higher biodiversity at all taxonomic levels and attain greater population densities in favorable habitats. Springtail (Collembola) numbers, for example, sometimes exceed $0.5 \times 10^6/m^2$ and eelworm (Nematoda) populations reach over $7.0 \times 10^6/m^2$ in areas of Taimyr.

Little is know about the detailed distribution and biology of most species, and good long-term population data on individual species, sufficient to indicate population trends, are almost entirely lacking. Predictions of how Arctic invertebrate communities may respond to climate change are, of necessity, based on extrapolations from experimental and/or distributional studies based on a few selected species or species groups in a restricted range of habitats.

This chapter brings together, and highlights for the first time, baseline information on the biodiversity of all Arctic terrestrial and freshwater invertebrates. It evaluates the importance of habitat diversity, climatic severity and biogeography, particularly historic patterns of glaciations, as determinants of invertebrate biodiversity. The significance of the Beringia refugium for biodiversity in several groups is stressed. Invertebrates are key players in a range of ecosystem services within the Arctic, including herbivory, decomposition, nutrient cycling, pollination, parasitism and predation.

Changes in invertebrate communities, perhaps involving new invasive species, may have important impacts on several of these processes, particularly through interactions with other groups of organisms. The key environmental factors (drivers) determining species success in an era of climate warming are likely to be mean summer and winter temperatures, soil-moisture availability, length of growing season and the frequency of freeze/thaw events that may disrupt preparation for and emergence from the overwintering state.

Several recommendations for future action are listed. Highest priority should be given to establishing an inventory of Arctic invertebrate species, including their distribution, habitat preference and ecological function. This list should be used to identify true Arctic endemic taxa, classify species according to IUCN Red Book criteria and identify the vulnerability of species and their habitats. Key indicator species that are responsive to habitat change should be identified and monitored. For a group as diverse as the invertebrates, conservation action should focus on the maintenance of habitat diversity coupled with the selection of ecologically important flagship species that can provide a focus for raising the profile of invertebrates as a whole.

7.1. INTRODUCTION

The observations by indigenous peoples given on the title page of this chapter, often made in association with traditional activities such as reindeer herding, hunting and fishing, clearly suggest that profound changes are occurring in the invertebrate faunas of the Arctic regions. This chapter attempts to set a baseline for invertebrate biodiversity within the Arctic, to document the scientific evidence for such change and to provide a prognosis and recommendations for the future.

Even within the scientific community, the biodiversity of invertebrates inside the Arctic is poorly understood by non-specialists and is thus frequently underplayed or sometimes ignored. The CAFF Habitat Conservation Report No.4 (Principles and Guidelines), for example, states that “invertebrate fauna in the Arctic is scarce” (CAFF 1996), a statement far removed from reality. Collectively, the number of Arctic invertebrate species greatly exceeds that of all other non-microbial eukaryotic species groups combined, including the plants and the vertebrates. Furthermore, invertebrates are often found at densities of several hundred thousand, and occasionally several million, per square meter. Arctic invertebrate faunas are thus far from simple, but their complexity is less overwhelming than for many tropical ecosystems, and their diversity is perhaps more readily understandable (Danks 1990, Vernon *et al.* 1998).

The mistaken idea of an overly ‘simple’ Arctic invertebrate food web almost certainly owes its origin to a summarizing diagram of the nutrient flow pathways through the ecological community of Bjornøya, Svalbard, published by Charles Elton in 1923 (Hodkinson & Coulson 2004). This diagram, erroneously interpreted as a ‘simple’ food web, still holds sway in several modern ecology textbooks. In such diagrams, it is assumed that individual species within related invertebrate groups are ecologically interchangeable, performing similar ecological functions or responding in similar ways to environmental change. They are in consequence usually consigned together, for example to a ‘box’ labeled ‘ciliates’ or ‘Collembola’. This assumption of species equivalence is mistaken, and important components of biodiversity become hidden when species are aggregated and compartmentalized in this way. Take for example the unicellular ciliates, a group whose biodiversity is poorly known within much of the Arctic. Despite their relatively simple body form, the freshwater ciliates of Svalbard fall into eight different trophic groups, each feeding on different microscopic prey categories representing various trophic levels and with individual species performing different ecological roles (Petz 2003). Similarly, species within several of the larger groups of Arctic invertebrates such as eelworms (Nematoda), springtails (Collembola), mites (Acari), flies (Diptera) and ground beetles (Coleoptera), to name but a few, display a similarly wide range of multi-trophic feeding specializations and adpatations (Chernov 1996, Rusek 1998, Chernov 2002, Makarova & Böcher 2009, Peneva *et al.* 2009). Trophic, behavioral and physiological divergence among related species is thus an important yet frequently overlooked component of invertebrate biodiversity within the Arctic.

Many invertebrate species are endemic to the Arctic and display highly restricted distributions. However, being small and lacking the charisma of their vertebrate and floral counterparts, few have received special conservation status, despite their vulnerability to climate change. A notable exception is the round spine tadpole shrimp *Lepidurus couesii* found in the American Arctic and listed as 'endangered' in the IUCN Red Data List. By contrast, many other Arctic invertebrate species are broadly distributed across a wide circumpolar range and display unusually wide within-species genetic diversity, or differences in their methods of reproduction, throughout their geographical range (Hobaek & Weider 1999, Reiss *et al.* 1999, Hessen *et al.* 2004, Wheat *et al.* 2005). Because of their small size and mobility, terrestrial and freshwater invertebrates are well-adapted to the multiplicity of different microhabitats generated by macro- and microtopographic variations in the landscape, interacting with climatic differences and the contrasting biotic environments created by different plant species and communities (Coulson 2000). Many species show strict fidelity to particular restricted microhabitat types, whereas others are more generally distributed across a range of habitats. Such variation in habitat occupancy is an important facet of biodiversity within the Arctic.

This chapter seeks to present a balanced assessment of invertebrate biodiversity and population trends within the Arctic regions. The quantitative data presented represent the best estimates available, but it should be recognized from the outset that our knowledge of Arctic invertebrates is far from complete, especially for many of the microscopic soil-dwelling forms. Our current understanding of their biodiversity rests on the extent and quality of available data and the reliability of the methods used to obtain those data. For many invertebrate groups, our knowledge of their distribution is based on a few samples taken from selected habitats at a few well-studied sites. Often these inadequacies are compounded by taxonomic problems, particularly a lack of critical comparison of species across different regions of the Arctic. Furthermore, large areas of the Arctic remain under-sampled for many invertebrate groups. Current sampling methods may also fail to record all species present, as evidenced by divergence between studies of soil fauna using traditional extraction techniques coupled with morphological taxonomy versus those based on the direct extraction of animal DNA from soil (Wu *et al.* 2009). Among ciliates and testate amoebae, for example, the number of described species may represent only a fraction of the total number of species present (Foissner *et al.* 2008, Smith *et al.* 2008). Even in relatively well-known groups such as the springtails, molecular techniques are also beginning to reveal the presence of sibling species not discernible by traditional taxonomy based on morphology (Hogg & Hebert 2004).

Species abundance distributions for invertebrate communities normally follow patterns in which the community is dominated by a few common species supported by a long tail of less common species, as for example in the Arctic testate amoebae on Richards Island, Canada (Dallimore *et al.* 2000). From a biodiversity perspective, this tail is highly significant but is rarely adequately sampled. The Arctic can also still produce surprises, as evidenced by the relatively recent discovery of *Limnognathia maerski*, a representative of an entirely new Class of animal, the Micrognathozoa, in a cold spring on Disko Island, W Greenland (Kristensen & Funch 2000). This species has subsequently been found on the sub-Antarctic Crozet Islands and is probably much more widely distributed than is currently recorded (De Smet 2002).

Population density estimates exist for many terrestrial and freshwater Arctic invertebrates in a variety of habitats (e.g. Hammer 1944, Coulson 2000, Sorensen *et al.* 2006), but these are often spot estimates, and there are few if any data sets that reliably indicate population trends over extended recent time periods. Even the more detailed population studies, with repeated sampling, rarely extend for periods greater than 3-5 years (e.g. Addison 1977, Hodkinson *et al.* 1998, Søvik 2004). Frequently such population estimates have been made for taxonomic groups combined, such as for the total springtails or oribatid mites, rather than for individual species. It is thus difficult to identify shorter term trends in individual species populations associated with environmental change, and it is here that manipulation experiments are important. Such experiments, measuring experimentally the response of invertebrate populations to climate manipulation and ideally linked to laboratory-based physiological studies, probably give us the best clues as to the direction of potential future change (Hodkinson *et al.* 1998). The woolybear caterpillar *Gynaephora groenlandica* in Canada provides a good example of such a study (Kukal & Dawson 1989, Morewood & Ring 1998, Bennett *et al.* 1999). However, where a vertebrate ecologist might regard a drop of 25% in a species population density as significant, invertebrate ecologists struggle to estimate mean population densities of even the commoner species with an associated statistical error of less than 25%. Furthermore, invertebrate populations are often highly aggregated and frequently display wide natural fluctuation over short time scales and across topographically diverse landscapes (e.g. Høye & Forchhammer 2008). Their densities and the associated fluctuations are thus normally expressed on the logarithmic rather than the more sensitive linear scale. Invertebrates are also capable, within limits, of shifting their population center to more suitable habitat in response to deteriorating conditions. Several species of springtails, for example, track optimum soil moisture status across a drying landscape within a given season, confusing population estimates at any one fixed point (Hayward *et al.* 2001).

Despite the limitations listed above, the stratigraphy of subfossil remains of invertebrate groups within the Arctic such as beetles, chironomid midge (Chironomidae) larvae, testate amoebae and ostracod crustaceans (Ostracoda) have successfully been used to indicate past climatic conditions and the way these conditions have changed over time (e.g. Bobrov *et al.* 2004, Wetterich *et al.* 2005, Zinovjev 2006, Thomas *et al.* 2008, Porinchu *et al.* 2009, Elias 2000a, 2000b, 2009a, 2009b). Comparison of the species composition of these subfossil assemblages with the known distribution and environmental preferences of the same species today indicates the likely conditions that prevailed when the subfossil invertebrates were deposited. Examination of the different temporal assemblages in successive strata permits the reconstruction of changing palaeoclimatic conditions at a given locality over historical time.

Large areas of the Arctic are occupied by mesic and wet tundra, grading into shallow pools, ponds and lakes where the transition between terrestrial and aquatic habitats becomes blurred. Several important groups of organisms, notably ciliates, testate amoebae, rotifers (wheel animals), tardigrades (water bears), nematodes (eelworms) and enchytraeid worms, are commonly found in both terrestrial and aquatic habitat types and several nominally terrestrial arthropod species are typical of the marine littoral zone. Some Arctic taxa, usually thought of as aquatic, such as chironomid midge larvae, contain terrestrial species, as in the genus *Smittia*. Similarly, the predominantly 'terrestial' springtails contain 'aquatic' species such as *Heterosminthurus aquaticus*, *Podura aquatica* and *Sminthurides aquaticus* (Babenko & Fjellberg 2006, Deharveng *et al.* 2008). For these reasons the non-marine Arctic invertebrates are considered here as an integrated whole rather than split artificially into terrestrial and aquatic groups. Invertebrates that are endoparasites of other terrestrial, freshwater and marine animals are considered by Hoberg & Kutz, Chapter 9.

Emphasis within this chapter is, of necessity, placed on documenting, essentially for the first time, the true biodiversity and abundance of the entire terrestrial Arctic invertebrate fauna and the driving factors that determine that diversity. Available knowledge of these organisms is sparse, precluding prediction of future population trends for the majority of species. Nevertheless, potentially important indicator groups are highlighted wherever possible and recommendations for future action are given.

7.2. STATUS OF KNOWLEDGE

To appreciate fully the biodiversity of invertebrates within the Arctic and how it might respond to environmental change, we initially need to

- Comprehend the wide diversity of life forms that are likely to be present in any one area at a given time.
- Appreciate how and why the Arctic fauna varies in composition and abundance among habitat types and across the different geographical regions of the low and high Arctic.
- Consider how and why invertebrate diversity in the Arctic differs from that of other life zones and the potential for colonization of the Arctic by invertebrates from further south.

The following sections address these issues.

7.2.1. Terrestrial Arctic invertebrate biodiversity

7.2.1.1. An invertebrate biodiversity profile for a high Arctic region, Svalbard

Probably the most complete inventory of the invertebrate fauna for any Arctic region is for the high Arctic Svalbard archipelago (Tab. 7.1) (Coulson 2000, 2007, Coulson & Refseth 2004). This list illustrates the taxonomic profile of diversity across all invertebrate groups and carries a number of caveats. It is primarily based on a literature survey, which is prone to problems of misidentifications and synonymies (Danks 1981). Sampling on Svalbard, moreover, has historically been concentrated around accessible sites along the west coast, whereas the more remote eastern islands tend to be undersampled. Nevertheless, despite the fact that the climate of Svalbard is relatively warm for its latitude, the inventory is highly typical and displays the general taxonomic profile observed throughout the Arctic regions.

The terrestrial and freshwater invertebrate fauna of Svalbard, while containing fewer individual species than the equivalent faunas of the low Arctic and of the temperate and tropical regions, is still complex. It currently contains 1308 species and 556 genera spread across 16 phyla and 27 classes. For those unfamiliar with invertebrate classification, the insects, perhaps the most familiar group, represent a single Class within the Phylum Arthropoda. The dominant groups in terms of species representation are amoebae, ciliates, rotifers, tardigrades, nematodes, mites, springtails and insects, particularly those belonging to the order of flies (Diptera). Chernov (2002) highlights the dominance of the more 'primitive' groups of invertebrates within such faunas, at the expense of more advanced forms. He argues that the more 'primitive' (phylogenetically basal) forms are better able to adapt to the severe conditions and that the more advanced groups such as the insects, because of their evolved specialisms such as close dependence on specific host plants, find adaptation to Arctic conditions more difficult. He notes that worldwide there are 130 and 16 times more species of insect than of springtails and Arachnida (spiders, mites etc.), respectively. In the low Arctic, however, these ratios shrink to eight and three, and in the high Arctic numbers of springtails and Arachnida species often equal or exceed those of the insects. Similarly, only slightly more than half of the insect orders are represented in the low or high Arctic. In large insect orders like the flies and ground beetles, family representation is only 40 out of 130 and 17 out of 170, respectively (Chernov 2002). Even within speciose groups like the dipteran flies, which may make up 75% of the insect fauna of polar deserts, the dominant families/superfamilies such as the chironomid midges and craneflies (Tipuloidea) tend to fall within the less specialized lower dipteran flies, although some higher Diptera, e.g. house flies (Muscidae) and root-maggot flies (Anthomyiidae), are also well represented (Brodo 1990, Chernov 1996). The most abundant dipteran flies are almost invariably species with aquatic or semi-aquatic stages. Chernov (2002) argues that the Arctic invertebrate fauna results not merely from a gradual species impoverishment occurring as part of a latitudinal trend in diversity among higher taxa, but also from the realization of the adaptive potentials of certain, albeit more 'primitive' or basal, phyletic lineages that increase in dominance. The Arctic fauna, he contends, should be considered distinctive, with its own characteristic composition related to the adaptive success of some of the constituent taxa.

A striking feature of high Arctic faunas that reflects this adaptational trend is the greatly reduced numbers of above-ground herbivores, particularly insects, feeding on the higher terrestrial plants and the decreasing proportion of terrestrial versus aquatic insects (mainly dipteran flies) (Fig. 7.1) (Danks 1992). On Svalbard, for example, the invertebrate herbivores are dominated by 2-3 aphid (plant lice; Aphididae) species, a few sawflies (Tenthredinidae) and a single weevil (Curculionoidea) (Hodkinson & Coulson 2004). The great majority of the invertebrate species, at least during their immature stages, inhabit the soil surface or live variously within soil or aquatic habitats.

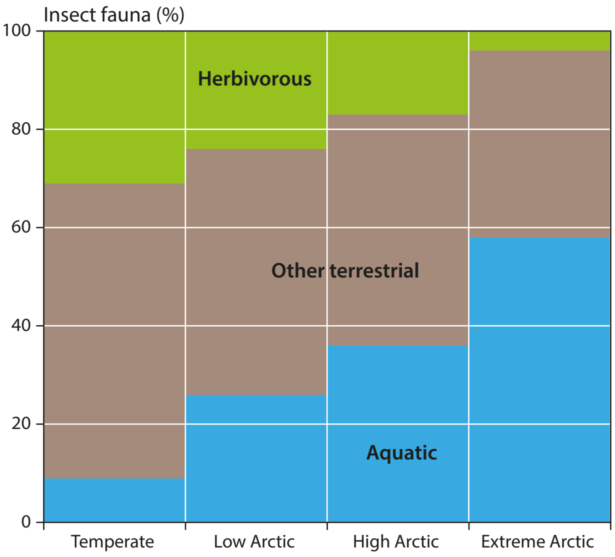

Figure 7.1. The changing relative percentages of herbivorous, aquatic and other terrestrial insect species groups with respect to increasing climate severity within the Arctic regions of North America. Note that the aquatic species are predominantly dipteran flies with larval aquatic stages and water beetles (redrawn from Danks 1992).

7.2.1.2. A biodiversity profile for a selected group, Arctic insects within the Nearctic region

Having established the general composition of a typical Arctic fauna across all taxa, we will examine the diversity *within* an example of one of the most widely represented taxa, the insects. The most wide-ranging and complete inventory of Arctic arthropods and their distribution is Danks's monumental work on the Arctic arthropods of North America (Danks 1981, Danks & Smith 2009). While this is inevitably dated with respect to both nomenclature and species completeness, the information it contains allows a more detailed analysis of major patterns of general biodiversity within an important component of the Arctic fauna over a wider area. Tab. 7.2 summarizes the diversity for insects, arranged by families with the number of genera and species indicated. There are 143 families spread over 14 orders. The large number of families represented indicates that the Arctic fauna is a derived assemblage of species representing many major evolutionary lines. There are no endemic Arctic orders or families. Many of the families, which are highly speciose in temperate/tropical regions, are represented by a single genus, and many of the genera are represented by a single or just a few species. This suggests that a wide diversity of insect taxa reach their limits of distribution and adaptational tolerance within the low Arctic. Over 60% of the families present in the low Arctic are absent from the high Arctic. There is a proportionate reduction in the average number of species per family present from 11.0 in the low Arctic to 5.8 in the high Arctic. This reduction, however, is not uniform across families. If we set a criterion of a minimum of 20 species per family, the most speciose insect families present in the low Arctic are lice (Philopteridae), aphids, ground beetles, water beetles (Dytiscidae), rove beetles (Staphylinidae), craneflies, black flies (Simuliidae), chironomid midges, empid flies (Empididae), thick-headed flies (Dolichopodidae), hover flies (Syrphidae), house fly type groups (Muscidae and Anthomyiidae), looper-moths (Geometridae), noctuid moths (Noctuidae), sawflies and ichneumon parasitoid wasps (Ichneumonidae).

The generality of these trends is reinforced by data from Svalbard, Greenland and the Palearctic region in general (Coulson 2000, Konstantinov *et al.* 2009, Böcher & Kristensen 2011 in press). For example, beetles of the families Carabidae (ground beetles), Staphylinidae (rove beetles) and Dytiscidae (water beetles) are the dominant beetle groups in Arctic mainland Norway and Russia, but Latridiidae (minute scavenger beetles) and Chrysomelidae (leaf beetles) become more significant elements in the fauna at the highest latitudes (Chernov *et al.* 2000, 2001, Olsvik *et al.* 2001, Chernov 2002, Chernov & Makarova 2008). Craneflies (inc. Limoniidae), chironomid midges, empid flies, thick-headed flies, hover flies and house flies are listed by Chernov (1996) as the most common Arctic dipteran fly families.

Table 7.1. A typical biodiversity profile across invertebrate taxa for a high Arctic region: the diversity of the terrestrial and freshwater invertebrates of Svalbard, listing the number of families, genera and species for each known group. Data are based on revised versions of Coulson (2000, 2007) and Coulson & Refseth (2004). The list includes occasional presumed vagrants and introductions. The table retains the animal classification used in the original work: more recent updates of the classification for some groups, such as the rotifers, are given in Tab. 7.3.

Phylum	Class	Order	Families	Genera	Species
Sarcomastigophora (flagellates)	Heliozoea		3	3	3
	Zoomastigophorea		1	1	2
Rhizopoda (amoebae)	Filosea	Gromiida	5	11	53
	Lobosea	Amoebida	1	1	1
		Arcellinida	13	23	145
Ciliophora (ciliates)	Kinetofragminophorea	Colpodida		4	4
		Cyrtophorida		2	2
		Nassulida		3	3
		Pleurostomatida		2	2
		Prostomatida		7	7
		Suctorida		1	1
		Synhymeniida		1	1
	Oligohymenophorea	Hymenostomatida		4	6
		Peritrichida		5	7
		Scuticociliatida		3	3
	Polyhymenophorea	Heterotrichida		3	3
		Hypotrichida		6	9
		Oligotrichida		4	5
Apicomplexa (sporozoans)	Sporozoea	Coccidea		3	3
Rotifera (rotifers)	Digononta	Bdelloidea	3	8	38
	Monogononta	Collothecacea	1	1	5
		Flosculariacea	2	2	3
		Ploimida	12	30	122
Gastrotricha (gastrotrichs)		Chaetonotida	1	1	1
Nematoda (eelworms)	Adenophorea	Enoplia	3	3	5
	Penetrantia	Dorylaimida	4	8	24
		Enoplida	4	4	10
	Secernentia	Ascaridida	2	4	5
		Rhabditida	4	11	18
		Spirurida	1	3	3
		Strongylida	1	6	11
		Tylenchida	5	13	16
	Torquentia	Araeolaimida	2	5	19
		Chromadorida	3	3	3
		Monohisterida	1	3	6
Acanthocephala (spiny-headed worms)	Palaecanthcephala	Polymorphida	1	1	1
Platyhelminthes (tapeworms & flukes)	Cestoda	Cyclophyllidea	5	10	16
		Proteocephalidea	1	1	1
		Pseudophyllidea	2	2	4
	Trematoda	Opisthorchiida	1	1	1
		Plagiorchiida	1	1	3
		Strigeata	1	1	3
Annelida (whiteworms)	Oligochaeta	Haplotaxida (all Enchytraeidae)	1	9	42

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Phylum	Class	Order	Families	Genera	Species
Tardigrada (tardigrades)	Eutardigrada	Apochela	1	1	1
		Parachela	3	16	74
	Heterotardigrada	Arthrotardigrada	1	4	16
Bryozoa (moss animalcules)	Phylactolaemata	Parachela	1	1	1
Chelicerata (mites & spiders)	Arachnida	Acari:Acariformes	38	76	133
		Acari:Parasitiformes	10	14	27
		Araneae	4	14	21
Hexapoda (springtails & insects)	Collembola	Arthropleona	7	27	65
		Neelipleona	1	1	1
		Symphyleona	2	3	6
	Insecta	Phthiraptera (Anoplura+Mallophaga)	3	14	38
		Ephemeroptera	1	1	1
		Hemiptera (all aphids)	2	4	4
		Thysanoptera	1	1	1
		Mallophaga	2	12	36
		Coleoptera	12	18	21
		Diptera:Chironomidae	1	25	92
		Diptera:other	19	39	69
		Hymenoptera:Symphyta	1	4	10
		Hymenoptera:Parasitica	4	20	21
		Lepidoptera	6	12	12
		Siphonaptera	1	2	2
		Trichoptera	1	1	1
Crustacea (water fleas, ostracods and shrimps)	Branchiopoda	Cladocera	4	7	9
		Ctenopoda	1	1	1
		Notostraca	1	1	1
	Copepoda	Calanoida	2	2	2
		Cyclopoida	1	3	4
		Harpacticoida	3	3	3
		Siphonostomatoida	1	1	2
	Malacostraca	Amphipoda	1	1	2
		Mysidacea	1	1	1
	Ostracoda	Podocopida	4	8	10
Total				**556**	**1308**

Among the dominant low Arctic families, most are still represented in the high Arctic. However, number of species is greatly reduced, with only lice, chironomid midges, house flies and ichneumon parasitoid wasps still meeting the 20 species criterion. The black flies, whose larvae live in flowing water, are lost from the fauna and ground beetle numbers are reduced from 85 to one species. The most successful insect families (i.e. those with species numbers in the high Arctic > 50% of those in the low Arctic) are the bird lice (Philopteridae), which are parasites of warm-blooded vertebrates, and the chironomid midges that breed in aquatic habitats and wet soils.

The relative abundance of ichneumonid parasitoid wasps is perhaps surprising at first, given their dependence on the availability of particular invertebrate prey species, the susceptibility of their life cycles to disruption through the direct effect of lethal cold temperatures and the potential breakdown of temporal synchrony with their host species (Hance *et al.* 2007). However, it is the other abundant species groups, notably dipteran flies, spiders (Araneae), aphids and sawflies that provide the majority of hosts for these parasitoids. Parasitism also probably takes place on other species *within* the family Ichneumonidae (parasitoid wasps) (Danks 1981, Roininen *et al.* 2002, Hodkinson & Coulson 2004).

Table 7.2. Number of genera and species of insect within each family across the Nearctic region illustrating further the taxonomic biodiversity within a selected class of Arctic invertebrate. Data are from Danks (1981) and should be viewed with the caveats noted in the text. Note also that the boundary between the high and low Arctic in the Canadian Archipelago differs slightly from that used in other sections of the Assessment.

Order	Arctic Families	Arctic Genera	High Arctic Species	Low Arctic Species
Ephemeroptera	Metretopodidae	1	0	1
	Baetidae	1	0	7
	Heptageniidae	1	0	1
	Leptophlebiidae	1	0	1
	Ephemerellidae	1	0	1
Odonata	Aeshnidae	1	0	4
	Coenagriidae	1	0	1
	Corduliidae	1	0	1
Plecoptera	Pteronarcidae	1	0	1
	Chloroperlidae	3	0	3
	Perlodidae	5	0	5
	Perlidae	2	0	2
	Capniidae	1	0	6
	Nemouridae	3	0	5
Orthoptera	Acrididae	3	0	4
Phthiraptera	Philopteridae	21	23	37
	Trichodectidae	1	0	1
	Menoponidae	7	5	10
	Ricinidae	1	2	2
	Echinophthiriidae	2	2	2
	Linognathidae	1	0	1
	Pediculidae	1	0	1
	Hoplopleuridae	2	1	2
	Polyplacidae	1	0	2
Hemiptera	Lygaeidae	1	0	1
	Miridae	4	0	8
	Anthocoridae	1	0	1
	Saldidae	4	1	9
	Corixidae	2	0	3
	Cicadellidae	7	0	9
	Delphacidae	1	0	1
	Psyllidae	2	0	9
	Aphididae	17	3	20
	Coccidae	1	0	1
	Orthezidae	1	0	1
	Pseudococcidae	3	1	2
Thysanoptera	not stated	3	1	2
Neuroptera	Chrysopidae	1	0	1
	Hemerobiidae	1	0	2
Coleoptera	Carabidae	16	1	85
	Halipliidae	1	1	2
	Dytiscidae	7	2	24
	Hydrophilidae	2	0	6
	Silphidae	3	0	3
	Staphylinidae	17	4	23
	Byrrhidae	3	0	5
	Bupestridae	1	0	1
	Elateridae	2	0	7
	Cantharidae	2	0	2
	Dermestidae	1	0	1
	Cucujidae	1	0	1
	Coccinellidae	5	0	6
	Lathridiidae	2	1	2
	Cerambycidae	5	0	5
	Chrysomelidae	6	0	13
	Curculionidae	9	1	14
Diptera	Trichoceridae	1	2	5
	Tipulidae	13	9	52
	Dixidae	1	0	1
	Chaoboridae	2	0	2
	Culicidae	2	3	17
	Simuliidae	6	0	28
	Ceratopogonidae	4	3	4
	Chironomidae	62	93	159
	Bibionidae	1	0	1
	Scatopsidae	2	0	3
	Mycetophilidae	9	9	17
	Sciaridae	4	5	3
	Cecidomyiidae	2	2	2
	Rhagionidae	2	0	2
	Tabanidae	1	0	4
	Empididae	4	7	20
	Dolichopodidae	7	2	31

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7.2.1.3. Biodiversity of Arctic invertebrates, the best collective estimates

Tab. 7.3 lists the numbers of species for each of the main groups of invertebrates recorded from the low and high Arctic regions of the Nearctic and Palearctic regions, together with the number of known endemics. This table is based on our collective knowledge derived from literature and museum collections. Greenland data, where possible, are disaggregated from the Nearctic region, as the zoogeographical origins of the Greenland invertebrate fauna remain uncertain. This list is our best current estimate of invertebrate biodiversity within the Arctic, although there may be omissions, taxonomic uncertainties and other inadequacies. Data for many groups are absent, unreliable or unavailable in a form that can easily be mapped onto the table format. Some groups present particular problems. The eelworms, for example, are one of the most numerically abundant groups of Arctic invertebrate and are undoubtedly species diverse within the Arctic regions, but most studies record biodiversity at the generic rather than the species level. For example, generic diversity associated with hair grass tussocks *Deschampsia sukatschewii* ssp. *borealis* across sites on Bol'shevik Island, Severnaya Zemlya and the Putorna Plateau, Taimyr, ranged from 18 to 28

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Order	Arctic Families	Arctic Genera	High Arctic Species	Low Arctic Species
Diptera (continued)	Platypezidae	1	0	1
	Phoridae	2	1	4
	Syrphidae	13	6	21
	Pipunculidae	1	0	1
	Micropezidae	2	0	3
	Piophilidae	4	5	7
	Acartophthalidae	1	1	1
	Agromyzidae	7	5	18
	Milichiidae	1	1	2
	Sciomyzidae	4	0	6
	Heleomyzidae	5	1	9
	Sphaeroceridae	2	0	3
	Drosophilidae	2	0	2
	Ephydridae	5	2	10
	Chloropidae	2	0	2
	Scathophagidae	9	5	28
	Anthomyiidae	19	7	138
	Muscidae	25	21	166
	Calliphoridae	12	4	12
	Oestridae	2	0	3
	Sarcophagidae	1	0	1
	Tachinidae	8	6	8
Siphonaptera	Pulicidae	1	1	1
	Leptopsyllidae	2	0	2
	Ceratopsyllidae	5	3	9
Lepidoptera	Incurvariidae	1	0	1
	Gelechiidae	1	0	1
	Plutellidae	1	0	1
	Tortricidae	10	3	19
	Hesperiidae	2	0	2
	Papilionidae	2	0	3
	Pieridae	4	2	13
	Lycaenidae	5	2	5
	Satyridae	3	0	17
	Nymphalidae	7	3	12
	Pterophoridae	3	1	3
	Pyralidae	7	0	7
Lepidoptera (continued)	Geometridae	16	2	24
	Sphingidae	1	1	1
	Lymantriidae	1	2	2
	Arctiidae	4	0	5
	Noctuidae	15	5	28
Trichoptera	Ryacophilidae	1	0	1
	Glossosomatidae	1	0	1
	Hydroptilidae	1	0	1
	Phryganeidae	2	0	2
	Brachycentridae	1	0	2
	Limnephilidae	9	1	15
	Leptoceridae	1	0	1
Hymenoptera				
Symphyta	Tenthredinidae	9	8	39
	Siricidae	2	0	2
Parasitica	Braconidae	10	3	14
	Ichneumonidae	78	35	131
	Mymaridae	1	0	1
	Eulophidae	1	1	1
	Encyrtidae	3	2	2
	Ptermomalidae	4	2	2
	Chalcidae	1	1	0
	Figitidae	1	0	1
	Alloxystidae	3	0	4
	Cynipidae	1	0	1
	Proctotrupidae	2	0	2
	Diapriidae	1	0	1
	Scelionidae	1	0	1
	Platygastridae	1	0	1
	Ceraphronidae	1	0	1
Aculeata	Formicidae	1	0	1
	Vespidae	1	0	2
	Megachilidae	1	0	1
	Apidae	1	3	12
Total		**677**	**330**	**1567**

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genera, comparable with the 29 and 40 genera listed for Cape Chelyuskin, Taimyr, and the Devon Island Plateau, Canada (Peneva *et al.* 2009). At least 73 genera have been recorded from within the whole Arctic region (Tab. 7.3). Where specific studies of small regional areas have been made, such as for Lake Hazen, Canada, and the low Arctic tundra on Taimyr, species numbers range from 60 to 162 (Danks 1981, Kuzmin 1976).

7.2.1.4. Variation within species

Modern molecular techniques are beginning to reveal high levels of genetic variation within Arctic populations of several of the invertebrate taxa named above, both across their geographical range and within local populations. These variations often provide strong evidence for genetic polymorphism within species populations and provide insights into the local adaptation and dispersal history of species. Studies have focused particularly on genetic variation at different spatial scales within and among metapopulations of aquatic species, notably the waterfleas *Daphnia* spp. (Cladocera), tadpole shrimps (Notostraca) and ostracod crustaceans, in the mosaic of lakes, ponds and pools scattered over the landscape (Dufresne & Hebert 1995, 1997, Van Raay & Crease 1995, Weider *et al.* 1996, 1999a, 1999b, 2010, Little

Group	**Palearctic low Arctic**	**Palearctic high Arctic**	**Total Palearctic**	**Nearctic low Arctic**	**Nearctic high Arctic**	**Total Nearctic**	**Greenland**	**Total Arctic**	**Arctic endemic**
Testate amoebae	190	185	229	210	121	243	128	319	9
Rotifera (rotifers)									
Monogononta	97	137	191	220	97	191		327	12
Bdelloidea	0	68	68	10	6	15		80	
Micrognathozoa							1	1	
Tardigrada (water bears)	132	126	182	106	70	123		215	10
Cladocera (water fleas)	85	16	86	74	17	79	32	110	6
Copepods (copepods)									
Calanoida	19	8	19	35	12	35	4	39	11
Cyclopoida	7	2	7	14	3	12	8	19	0
Harpacticoidea	5	3	15	14	1	14	9	21	2
Anostraca (shrimps etc)	5	8	9	5	4	6	2	12	6
Notostraca (tadpole shrimps)	1	1	1	1	1	1	1	2	0
Ostracoda (ostracods)	34	30	34	40	27	40	12	47	4
Enchytraeidae (white worms)			73			48	32	85	16
Nematoda (eelworms)								73+ (genera)	
Araneae (spiders)	250	100			50	200		450	50
Acari (mites)									
Mesostigmata	182	37	188	68	33	80	63	231	72
Prostigmata			94			111	72+		
Oribatida	271	97	283	174	46	177	110	372	69
Astigmata			8				10		
Collembola (springtails)	347	132	348	162	49	174	94	425	14
Insecta (insects)									
Plecoptera								72	0
Hemiptera									
Psylloidea	7		7	11		11	3	14	6
Aphidoidea[2]				21	6	27	23	(407)[2]	> 12
Coleoptera									
Carabidae		10			4				
Staphylinidae		28			9				
Dytiscidae		2			6				
Chrysomelidae		5			4				
Curculionidae		5			1				
Diptera									
Tipuloidea			131	128	53	139			32 (Nearctic)
Chironomidae	235 (695)	155 (235)	235 (695)	165 (450)	81 (165)	235 (695)		360 (760)	?
Culicidae						36	2		
Anthomyiidae	98	15	98	141	22	142	32	143	c10
Muscidae	140	37	145	224	21	224	35		
Lepidoptera (total)			105			165		270	25
Butterflies[1]			91[1]	21	7	61[1]		106[1]	6
Hymenoptera									
Symphyta	17	25	37	46	5	46		71	8
Parasitoidea				see Tab. 7.2					

Table 7.3. Number of species in the dominant or relatively well-studied groups of invertebrates in the major biogeographical regions of the low and high Arctic. Greenland, in addition to being included within the traditional Nearctic region, is also considered as a separate unit as its fauna cannot be considered as being solely derived from the Nearctic region. Data are partly compiled from Babenko & Fjellberg (2006), Chernov & Makarova (2008), Chernov & Tatarinov (2006)1 and Stekolshchikov & Buga (2009)2, but mainly from original data assembled by the contributing authors. Data on butterflies and Anostraca (shrimps, etc.) are for the whole of the Arctic region including the sub-Arctic zone and may, in the case of the butterflies, include some migrant species – about 40% of the 106 species of butterflies numbered are typically Arctic. For the midge family Chironomidae the first number in each cell is an estimate of the total number of species present, the figure in parentheses is the total number of species known to occur north of the Arctic Circle, many of which are likely to be found in the low Arctic. Within this highly diverse group a revised and updated species list is only currently available for the subfamilies Podonominae, Tanypodinae, Diamesinae, Prodiamesinae and Telmatogetoninae within the Arctic (see Ashe & O'Connor 2009). The ratio of Arctic to total Holarctic species in these taxa has been extrapolated to arrive at a revised estimate of the number of species in the remaining subfamilies. For the aphids, the Nearctic data are reliably compiled from published accounts, whereas the data given for the Total Arctic (inluding the sub-Arctic and thus placed in parenthesis) are taken from Stekolshchikov & Buga (2009), but the original source is not known. A major omission is the parasitoid Hymenoptera wasps (predominantly Ichneumonoidea), which are relatively diverse but for which up to date data in the required format are not easily accessible. Tab. 7.2 should be consulted for older data on their biodiversity in the Nearctic region.

& Herbert 1997, Weider & Hobaek 2003, Hessen *et al.* 2004). More limited data are available for terrestrial groups such as ground beetles (Ashworth 1996, Reiss *et al.* 1999), sulfur butterflies *Colias* spp. (Wheat *et al.* 2005) and selected springtails (K. Hedlund pers. com.).

Several species of Arctic invertebrates, e.g. Svalbard aphids, show diversity in their method of reproduction, switching between sexual and parthenogenetic modes. The seed bug *Nysisus groenlandicus* exists as both parthenogentic and sexually reproducing populations at Zackenberg (74° 30’ N, 20° 30’ W), NE Greenland (Böcher & Nachman 2011). Other invertebrates, e.g. some waterfleas and chironomid midge species, may be obligatorily parthenogenetic (Armitage *et al.* 1995, Dufresne & Hebert 1995, Strathdee *et al.* 1995, Gillespie *et al*. 2007). Parthenogenetic reproduction leads to the creation of genetically distinct clones or haplotypes whose distinctness is frequently reinforced by polyploidy (Dufresne & Hebert 1995, Van Raay & Crease 1995). The waterflea *Daphnia middendorfiana* in Canada appears to have evolved polyploidy independently in several separate geographical areas, possibly as a result of nuclear introgression between haplotypes or hybridization with haplotypes of related species (Dufresne & Hebert 1997, Weider *et al.* 1999b). By contrast, high genetic similarity occurs in some species that display high levels of morphological plasticity, such as the tadpole shrimp *Lepidurus arcticus* (Hessen *et al.* 2004).

Waterflea species show a high clonal diversity within the Arctic, contradicting the assumption that genetic variation in Arctic species is limited and suggesting a high degree of population fragmentation and isolation (Weider *et al*. 1996, Weider & Hobaek 2000). The tadpole shrimp, by contrast, had just two haplogroups (A and B), identified by mitochondrial 12SrDNA, across 48 populations. The distribution of these haplogroups, nevertheless, provides intriguing insights into species disperal. Both haplogroups occur over wide geographic ranges, including northern Norway, suggesting efficient long distance dispersal. However, populations on Svalbard consisted entirely of haplogroup A, while those on neighbouring Bjørnøya were almost all of haplogroup B (Hessen *et al.* 2004).

Studies of waterflea mitochondrial DNA and allozyme variation have also provided insights into the phylogeography of species complexes within the Arctic and evidence for relationships between waterflea clone distributions and the position of old Pleistocene glacial refuges. The highest levels of haplotype diversity within the waterflea *Daphnia pulex* complex have been found in areas that were within the unglaciated Beringian refuge during the Pleistocene, namely NE Siberia and NW North America. The contrast is most striking in N Canada where haplotype diversity is highest along the eastern edge of the Beringian refuge, reaching a maximum on Banks Island. The more recently deglaciated parts of the eastern Canadian Arctic support a much lower diversity of haplotypes, with diversity decreasing significantly with distance from the edge of the Beringian refuge (Weider & Hobaek 1997, 2003). These data suggest a longer uninterrupted period of haplotype development within the refuge followed by only limited dispersal into the surrounding geographical areas as the ice sheets retreated. A similar pattern is found in the ground beetle *Amara alpina* as indicated by DNA restriction-site variation, which is greatest in the Beringian regions of Alaska and northern British Columbia and lowest in the area of Hudson Bay (Reiss *et al.* 1999).

On the more local scale, genetic studies are beginning to reveal shifts in the parameters of genetic diversity over short time intervals. For example, allozymic studies on waterfleas in 131 rock pools at Churchill, Manitoba, Canada indicate dynamic changes in the clonal structure of populations occurring over time intervals as short as 20-25 years (Dufresne & Hebert 1995, Weider *et al.* 2010). The number of populations with melanic clones fell from 131 to 90, 59% had an unchanged clonal structure, 33% showed some clonal replacement and 8% showed total clonal replacement (Weider *et al.* 2010).

It is often assumed that species generally show reduced genetic diversity with increasing latitude as a result of population extinction followed by limited recolonization events associated with expanding and retreating ice sheets. Evidence for three genes that code for the metabolic enzymes phosphoglucose isomerase, phosphoglucomutase and glucose-6-phosphate dehydrogenase in sulfur butterflies, however, suggests that, at least for some genes, high heterozygosity is maintained into the highest latitudes (Wheat *et al.* 2005).

7.2.2. Historical overview

Changes in subfossil Arctic invertebrate assemblages, in conjunction with pollen and diatom stratigraphy, have been widely used as proxies for past climatic conditions within the Arctic (e.g. Andreev *et al.* 2004, Sher *et al.* 2005). They illustrate the magnitude and time scales for past changes of the Arctic climate and provide a baseline for assessing future trends in both climate and biodiversity (Kaufman 2009). Key indicator taxa for particular climatic regimes can be identified and the boundaries of shifting climatic zones can be mapped.

Subfossil beetle assemblages in permafrost provide some of the earliest proxy evidence for Arctic climate conditions across a wide region, with many identifiable beetle species surviving virtually unchanged since the late Miocene (Elias *et al.* 2006). Changes in such assemblages have been particularly useful in resolving the past climates of N Greenland, E and W Beringia, and the Bering Land Bridge (Böcher 1995, Elias 2000a, 2000b, Elias & Mathews 2002). Elias (2000a, 2000b), for example, identified 147 Pleistocene species of predatory or scavenging beetles (mainly ground beetles, water beetles and rove beetles) that were particularly important for climate reconstruction in Alaska and the Yukon Territory. For each species, he described Mutual Climatic Range, a climate envelope defined by the mean temperature range of the warmest (TMAX) and coldest (TMIN) months at sites where the species occurred today. This allowed species to be classified with respect to the breadth/narrowness of their TMAX and TMIN ranges and grouped according to their likely distributional responses to climate change. Species assemblages from other sites representing more recent stages within the Holocene could then be compared with this species preference list to gain an idea of the likely climate under which they existed. Cold-adapted beetles, such as ground beetles, have tracked climate change since the Pleistocene, through dispersal and differential survival (Ashworth 1996).

Freshwater ostracod crustaceans and soil testate amoeba species assemblages, similarly preserved in permafrost, provide examples of the longest continuous data sets for the climate within Arctic regions. On the Bykovsky Peninsula, Siberia, near the mouth of the Lena, the ostracod crustaceans and testate amoeba record extends over nearly 60,000 years. Six ostracod crustacean zones, based on 15 species within seven genera, track stadial-interstadial variations in climate from the Late Quaternary through to the Late Holocene, reflecting repeated changes from cold to warm and/or wet to dry (Wetterich *et al.* 2005). Variations in the testate assemblage, totaling 86 taxa, were less indicative but suggest cold, dry conditions during the Late Pleistocene and warm wet conditions throughout most of the Holocence (Bobrov *et al.* 2004). Presence/absence of rare amoeba species, e.g. those of the genus *Argynnia*, and shifts in dominance among the commoner groups such as species in the genus *Difflugia* are useful indicators of change.

Available data series for freshwater chironomid midge communities, based on head capsule analyses, are usually of shorter duration, from < 10,000 BP to the present, although much earlier spot samples exist for lakes in NW Greenland (Brodersen & Bennike 2003). Care is needed in extrapolating data from single sites, however, as local climates may differ from regional averages or there may be a lag in community response to climate change (Wooller *et al.* 2004, Rolland *et al.* 2008). Chironomid assemblages for lakes on Southampton Island in the eastern Canadian Arctic, for example, provide evidence for recent cooling, contrary to the general trend of Arctic warming (Rolland *et al.* 2008). Stable isotope $\delta^{18}O$ values derived from chironomid head capsules within sediment cores taken from Fog Lake, Baffin Island, and Qipisarqo Lake, S Greenland, correlate strongly with mean annual temperature. Such data can be used further to support observations on changes in species assemblages associated with shifting climate (Wooller *et al.* 2004).

Chironomid data from the Canadian Arctic Islands exemplify identifiable trends during the late Holocene deglaciation. Three major stratigraphic zones that reflect variations in temperature and productivity have been recognized in a core sample from Lake V57 on Victoria Island (Porinchu *et al.* 2009). The basal zone (0-1600 AD) is characterized by high abundance of the genera *Heterotrissocladius*, *Tanytarsus* and *Micropsectra*, with narrowly cold-adapted taxa such as the genera *Pseudodiamesa*, *Abiskomyia*, *Sergentia* and *Zalutschia*, and a species of the *Parakiefferiella nigra* type also present at low densities. The second zone (1600 – c. 1850 AD) is dominated by a species of the *Corynocera ambigua* type, a *Psectrocladius sordidellus* type and *Micropsectra*; several of the narrowly cold adapted taxa named above have disappeared. From 1850 onwards the community is characterized by high proportions of *Tanytarsus* and a *C. ambigua* type, by increases in a *C. olivieri* type, *Hydrobaenus/Olivieridia*, *Orthocladius* and Pentaneurini, and a decline in *Heterotrissocladius*, *Paracladius* and *Paratanytarsus*. Chironomid data from Lake CF8 on northeastern Baffin Island similarly forms part of multi-proxy evidence for very rapid climate change within the last 200 years, during which time productivity increased 20-fold. The chironomid communities show the most marked changes post 1950. Two narrowly cold-adapted genera *Oliveridia* and *Pseudodiamesa* declined rapidly, disappearing from the community by 1980, while other taxa with higher temperature optima, especially *Abiskomyia* and Tanytarsini, increased in abundance (Thomas *et al.* 2008). These four genera had formed part of the community continuously for over 5000 years. Changes in testate amoebae assemblages in cores from Richards Island, Canada similarly suggest shifts in local climate within the last 3000 years (Dallimore *et al.* 2000).

7.2.3. Regional considerations

The overwhelming diversity of invertebrate species, many of which display circumpolar distributions, coupled with the influence of microclimate and habitat type on species distribution and diversity, makes any strict compartmentalized analysis of regional invertebrate faunas relatively uninstructive. Here we examine how various driving factors influence the biodiversity of invertebrate communities on different spatial scales, from the local to the circumarctic.

7.2.3.1. Habitat specificity and its implications for biodiversity

Many Arctic invertebrate species have specific requirements that restrict their distribution to particular habitats within their broader geographical range. Other related species may be more broadly distributed across habitat types. This ensures that different habitat types tend to support communities of differing species composition, an important consideration when measuring total biodiversity. It is, however, impractical to list all habitat types that support characteristic species assemblages; examples will suffice to illustrate the general principles.

Testate amoebae communities of soil, moss, water and lichen habitats on Devon Island, Canada, have been classified into 18 separate species assemblages based on 75 species in 19 genera (Beyens & Chardez 1994). Six of these assemblages are linked to specific habitats, notably soil (*Plagiopyxis callida* association), moss (*Assulina-muscorum-Corythion dubium* and *Euglypha rotunda* assemblages) and water (*Trinema lineare* and *Paraquadrula irregularis-P. penardi*); the remaining assemblages occupy more than one habitat. Fig. 7.2 shows the generality of this trend, illustrating the percentage of testate amoeba species that are unique to these habitats throughout Svalbard, Jan Mayen, Greenland and the North American Arctic combined (Beyens *et al.* 1986a, 1986b, Beyens & Chardez 1994). Even among common aquatic testates, species such as *Centropyxis aerophila*, *Paraquadrula irregularis* and *Trinema lineare* are characteristic indicators of acid-oligotrophic, alkaline-mesotrophic and waters of intermediate pH conditions, respectively (Beyens *et al.* 1986a). Ciliate species similarly show differences in habitat choice, resulting in clear differences in biodiversity between habitats. On Svalbard, diversity was higher in stagnant versus running water. Highest species numbers were associated with cyanobacterial mats and aquatic moss beds; lowest diversity occurred in sediments and among species associated with encrusting plants or filamentous green algae (Petz 2003).

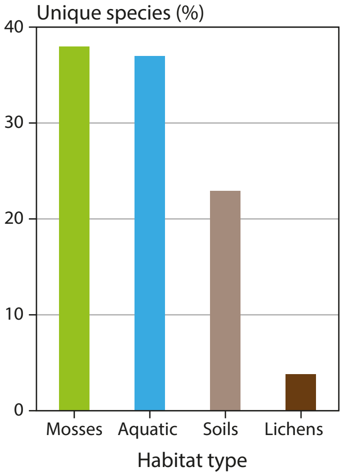

Figure 7.2. The number of species of testate amoebae unique to particular habitat types, expressed as a percentage of the total species found within that habitat. Data are from several sites spread across the Arctic compiled by Beyens & Chardez (1995).

The influences of water chemistry, temperature, and lake size and depth are important determinants of species composition for communities of chironomid midges in Arctic water bodies (Brodersen & Anderson 2002, Walker *et al.* 2003, Nyman *et al.* 2005, Gajewski *et al.* 2005). Differences in the characteristics of surrounding bedrock, soil and plant community combine to determine the invertebrate species assemblages present. Nitrogen, phosphorous and organic matter content, together with water temperature and pH, are frequently the important explanatory variables. For lakes in W Greenland, midges of the genera *Heterotrissocladius*, *Micropsectra*, *Ablabesmyia* and *Chironomus* are those most strongly influenced by such differences in environmental conditions, making them the best predictors of lake nutrient status. They are, however, not necessarily the most abundant taxa (Brodersen & Anderson 2002). Among stream-dwelling chironomids, water origin, distance from source and level of disturbance, including channel stability and sediment load, are major influences shaping communities at the landscape scale (Lods-Crozet *et al.* 2007).

Terrestrial and freshwater tardigrades are another group that contains both habitat specialists and generalists. Several species are typically associated with homothermal springs, notably on Disko Island, W Greenland. The area around the warmest (c. 17 °C) of these springs, Puilassoq, supports 18 species of Eutardigrada and three Heterotardigrada, with species variously associated with wet soil, mud, algae, hydrophilic mosses and moss-on-stone habitats (Heide-Jørgensen & Kristensen 1999). Comparison of the soil-dwelling tardigrade communities at three separate locations on Disko Island showed a distinctive community at each, with only four of 13 species common to all three locations (Stark & Kristensen 1999). A separate study along two transects, however, showed little evidence that altitude and bedrock type strongly influenced species composition (Peters & Dumjahn 1999).

Perhaps the most unique habitats supporting invertebrate life, including tardigrades, are the water-filled dust holes (cryoconites) that form on the surface of Arctic glaciers. White Glacier at 79 °N on Axel Heiberg Island, Canada supports a mixed cryoconite community of unidentified flagellates, ciliates, rotifers and tardigrades (Mueller *et al.* 2001). Tardigrades and sometimes rotifers occur frequently in cryoconites on Disko Island, Greenland, and Svalbard glaciers (De Smet & Van Rompu 1994, Grøngaard *et al.* 1999, Séméria 2003). Invertebrates in eight cryoconite holes on Hyrnebre, Svalbard, included seven rotifer species in six genera, the tardigrades *Diphascon recamieri* and *Isohypsibius granulifer* and at least four species of ciliates (De Smet & Van Rompu 1994). Most of the species involved are not unique to cryoconites but are often widely distributed elsewhere in non-glacial habitats and some are cosmopolitan (McFatter *et al.* 2007).

Higher plant species are often good indicators of soil conditions, particularly the depth and content of organic matter and water availability. These same factors strongly influence soil invertebrate biodiversity. At Zackenberg, NE Greenland, different assemblages of testate amoebae species are associated with polargrass *Arctagrostis* sp. and bilberry *Vaccinium* sp. (high soil moisture, thicker active layer), mountain heather *Cassiope* sp. and willow *Salix* sp. (low soil moisture) and meadow-grass *Poa* sp. (high organic content, shallow active layer) (Trappeniers *et al.* 2002). Enchytraeid worm communities in the same area show comparable changes in species composition between vegetation/soil types (Sorensen *et al.* 2006), and even within individual species there may be diversity in life cycle duration between vegetation types (Birkemoe *et al*. 2000). There are similar differences in community structure of springtail and mite communities in soils beneath willow, saxifrage *Saxifraga*, mountain avens *Dryas*, wood-rush *Luzula* and mountain heather growing together in a mixed vegetation mosaic on Svalbard (Coulson *et al.* 2003b). Even within ostensibly similar plant communities, parameters of diversity may shift along short environmental gradients. Microathropod communities on Svalbard associated with a *Dryas*-dominated plant community changed along a snow-melt transect of 135 m in response to differences in temperature, annual heat accumulation and soil moisture characteristics (Dollery *et al*. 2006). Furthermore, over greater latitudinal distances there is often little overlap at the species level in springtail communities occupying similar vegetation, as demonstrated by comparing areas such as Severnaya Zemlya in the high Arctic with areas farther south in Siberia (Babenko 2000).

At the highest latitudes, local invertebrate biodiversity may be linked to restricted microtopographical features that create slightly more favorable microclimatic conditions that extend the growing season, e.g. well-drained slopes, raised areas and river terraces. The chrysomelid beetle *Chrysolina septentrionalis* and the latridiid beetle *Dienerella elegans*, for example, are found only in turf growing on lemming mounds on Severnaya Zemlya and Ellef Ringnes Island, respectively (Chernov & Makarova 2008). Populations of the rove beetle *Micralymma brevilingue* are also highest on these mounds (Makarova *et al.* 2007). Similarly, springtail communities associated with the different microhabitat topographies created during different stages of the frost-boil cycle in Taimyr, Russia, differ markedly in their species composition over short distances (Babenko 2009).

Table 7.4. Habitat preferences of common Arctic springtail species selected to illustrate variation in the range of habitats utilised, often by related species. Data are from Fjellberg (1994) with nomenclature updated from Babenko & Fjellberg (2006).

Species	Habitats
Hypogastrura viatica	Wet areas rich in organic matter
Hypogastrura tullbergi	Dry upland, grassy meadows, lichen heath
Hypogastura concolor	Moss, lichens, grass tussocks
Anurida polaris	Wet mossy areas
Megaphorura arctica	Bird colonies, sea shore
Oligaphorura groenlandica	Wet mossy sites, bird cliffs
Tetracanthella arctica	Beach meadows, bird cliffs, lagoon edges
Folsomia sexoculata	Salt meadows, littoral
Folsomia quadrioculata	Ubiquitous across a wide range of habitats
Isotoma anglicana	Both wet and dry areas
Isotoma tshernovi	Wet meadows, moss by ponds, snowfields
Lepidocyrtus lignorum	Dry meadows, bird cliffs
Sminthurides malmgreni	Very damp habitats
Sminthurinus concolor	Rocky dry sites

Tab. 7.4 illustrates diversity in habitat usage by springtails and shows the habitat preferences of selected common species on Svalbard. Most notably the springtails occupy a multiplicity of habitats from marine littoral through wet tundra to dry polar desert, with several species commonly associated with seabird colonies. Mites almost invariably co-occur with springtails and selectively occupy the same wide range of habitats, including association with nesting birds and/or lemming mounds and burrows (Lebedeva *et al.* 2006, Makarova 1999, 2002b). Furthermore, mesostigmatid mites are among the main predators of springtails and other invertebrates and several Meso- and Astigmata mite species show phoretic associations with flying insects such as flies (Diptera) of the families Anthomyiidae (root-maggot flies), Muscidae (house flies) and Trichoceridae (winter craneflies) across a variety of habitats (Makarova 1999, Makarova & Böcher 2009). Prostigmata mites, by contrast, are usually associated with spiders of the family Linyphiidae. As a consequence of habitat specialization by constituent species, the composition of springtail and mite communities varies between habitats. For example, mesic and dry heath at Zackenberg, NE Greenland, share several species in common, but their relative densities often differ widely between habitats, and some species are unique to each habitat type (Sorensen *et al.* 2006).

Some taxa show a shift in their habitat preference with latitude, perhaps in response to reduced competition. For example, species of oribatid mite of the widely distributed genus *Ameronothrus* are typical of marine intertidal habitats. However, the Arctic species occupy an uncharacteristically wide range of habitats from supralittoral to terrestrial, with one Arctic species, *A. dubinini*, found only in terrestrial habitats (Marshall & Convey 2004). Compared with temperate regions, most species of oribatid mite within the Arctic are associated with soil surface, moss and lichens, rather than living deep within the soil (Behan-Pelletier 1999).

The general conclusion to be drawn from these examples is that extensive sampling in a wide range of habitats is necessary to establish the true invertebrate biodiversity even at a single location. When the whole of the Arctic is considered, the task becomes immense. The level of variation in habitat selection and usage among taxa makes generalization across the invertebrates exceedingly difficult.

7.2.3.2. Biodiversity changes along latitudinal gradients

The broad general trend of decreasing biodiversity with increasing latitude described previously for many insect groups has often been, as might be expected, correlated with decreasing temperature, which acts progressively to limit the northern distributions of species, many of which occur south of the low Arctic (Gaston 1996). Fig. 7.3 shows an example of this trend among the well-studied ground beetles along a north-south transect through the low Arctic tundra of the Taimyr Peninsula, Russia. As mean July temperature declines from 12.5 to 4.0 °C, the number of ground beetle species declines from 59 to three (Chernov 1995, Chernov & Makarova 2008). Equivalent data showing similar trends are available for spider and butterfly assemblages in Middle Siberia and Russian Beringia (Chernov 1995). The pattern is repeated, if less dramatically, among ground beetles in Arctic Alaska and Norway (Nelson 2001, Olsvik *et al.* 2001) and leaf beetles (Coleoptera: Chrysomelidae) in the Palearctic tundra (Chernov *et al.* 1994, Medvedev 1996, Makarova *et al.* 2007).

The ground beetles appear more strongly temperature restricted than the other group of smaller predatory/scavenging beetles, the Staphylinidae (Chernov & Makarova 2008). Among the 341 spider species of the Russian Arctic tundra, 41 are restricted to the Arctic zone, 34 are Arctic-alpine and 266 are also found in zones farther south (Marusik & Eskov 2009). In addition, as for many invertebrate groups, the family composition of spiders changes with latitude. At high Arctic sites such as Svalbard, Linyphiidae make up 93% of the species. This percentage declines to 59% at Kevo, N Finland and 36% in W Germany (Koponen 1993). A similar trend occurs within mesostigmatid mites, with the family Ascidae becoming progressively more dominant with increasing latitude (Makarova 2002a, 2009). Nearly all known Arctic species of sawflies (Symphyta) belong to the family Tenthredinidae, and all the high Arctic species fall within the subfamily Nematinae. Apart from Nematinae, the ranges of only a very few species of other tenthredinid subfamilies such as Selandriinae, Allantinae, Heterarthrinae, Tenthredininae and Cimbicidae reach into the low Arctic.

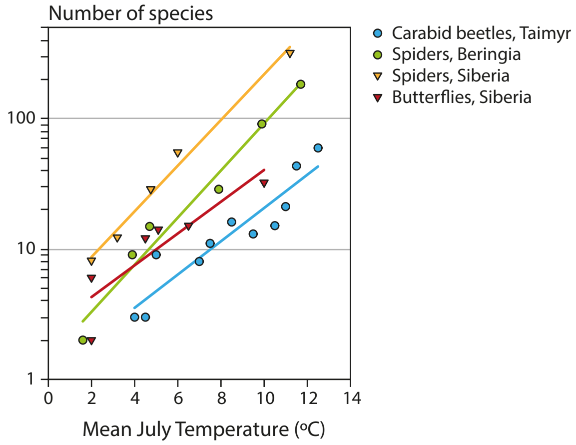

Figure 7.3. Relationship between numbers of spider, carabid beetle and butterfly species and mean July temperature at sites along south to north transects in Taimyr, Middle Siberia and Beringia (based on data from Chernov 1995, Chernov *et al.* 2000, Chernov & Makarova 2008).

Among many other groups that are poorly represented in the Arctic, e.g. thermophilous bumble bees *Bombus* spp., the few Arctic species represent the extreme northern branches of much larger and more broadly distributed phylogenetic lines (Pekkarinen & Teräs 1993, Hines 2008). The 27 Arctic *Bombus* species are scattered thinly across the subgenera *Bombus* sensu stricto, *Pyrobombus*, *Alpinobombus*, *Melanobombus*, *Thoracobombus*, *Tricomibombus*, *Psithyrus*, *Megabombus* and *Subterraneobombus* (Hines 2008).

A detailed analysis of the distribution of the abundant and well-adapted springtails along a north-south transect through the central Siberian Arctic reveals a far more complex picture. At first sight the pattern appears similar to the ground beetles, with a decline in number of species from the northern taiga/southern tundra zone to the polar desert, albeit at a slower rate (Babenko 2003a, 2003b, 2009). This trend, however, masks greater subtleties with important consequences for biodiversity. At each point along the transect the fauna is made up of varying proportions of different faunal elements, each with a different characteristic distribution pattern. Important elements include high Arctic species associated with polar desert, separate faunal elements typically occupying the northern and mid zones of the low Arctic tundra, and a faunal element typical of the southern tundra and forest-tundra zones. Only a small proportion of species occurred across all zones. Unlike the ground beetles, the number of species across the entire transect greatly exceeded the number of species within the more southerly zones (Babenko 2003a, 2003b, 2009).

Some groups show an opposite trend in diversity. Host-plant-specific sawflies, for example, exhibit increasing species richness into the low Arctic, before declining in the high Arctic (Kouki *et al.*1994, Kouki 1999). This appears to be associated with the diversity and abundance of suitable host-plants, especially willows, on which the majority of Arctic sawflies feed in the larval stages (Viitasaari 2002). Willows are themselves unusual, reaching their highest species diversity in high northern latitudes.

Enchytraeid worms, a group particularly associated with the abundant wet organic soils of the low Arctic tundra, exhibit a similar inverse trend in diversity with increasing latitude. Species richness in the Palearctic tundra is only marginally lower than in the temperate regions. Only 13 of the 56 species known from Palearctic tundra occur further south (Christensen & Dózsa-Farkas 1999). Four genera, *Mesenchytraeus*, *Henlea*, *Cognettia* and *Bryodrilus*, exhibit higher species diversity in the tundra than in temperate regions. This general pattern is repeated among enchytraeids in NE Greenland and the Canadian Arctic Archipelago (Christensen & Dózsa-Farkas 2006).

Lumbricid earthworms, by contrast, are strictly temperature limited and scarce, with only two freeze-tolerant species, *Dendrobaena octaedra* and *Eisenia nordenskioldi*, found in areas with permafrost. *D. octaedra* is widespread in W Greenland up to Disko, but also found on Novaya Zemlya and low areas of W Siberia. *E. nordenskoldi* occurrs relatively commonly at sites at Maria Pronchitsheva Bay and Tareya on the Taimyr Peninsula (MacLean 1981, Holmstrup *et al.* 2007, Overgaard *et al.* 2007). However, in sub-Arctic, permafrost free soils of southern Greenland several other earthworm species occur quite frequently, some of them probably introduced with Nordic settlers (M. Holmstrup pers. com.). Among the oribatid mite species of North America, nearly 50% of species are known only from boreal and Arctic areas, suggesting a distinctive high latitude faunal element with its own provenance (Behan-Pelletier 1999, Behan-Pelletier & Schatz 2009). Genera of the tiger moth family Arctiidae of the Arctic tundra are similarly relatively distinct from those of the adjacent areas of the Palearctic and Nearctic regions, albeit based on a small number of species present (Dubatolov 2008).

Freshwater and terrestrial tardigrades (Tardigrada) in the North American Arctic form another characteristic species assemblage distinct from that of the remaining Nearctic region (Meyer & Hinton 2007). Chironomid midges show a parallel trend along a north-south transect through the Yukon, Canada, with genera such as *Abiskomyia, Mesocricotpus*, *Pseudochironomus* and *Polypedilum* being restricted to the Arctic tundra section of the transect (Walker *et al.* 2003). Chironomid community composition also tracks apparent north-south temperature anomalies. For example, in the Canadian high Arctic islands chironomid communities of the relatively warmer northern and southern islands are more similar than those of the cooler intervening central areas, notably Devon and Cornwallis Islands (Gajewski *et al.* 2005).

In several groups of herbivorous insects the effects of temperature along latitudinal transects in the Arctic are mediated through their host plant's range and phenology. Jumping plant lice (Hemiptera: Psylloidea), for example, are host-plant specific and develop on a number of woody shrubs, including many willow species, dwarf birch *Betula nana* sensu lato and Labrador tea *Rhododendron tomentosum* ssp. *decumbens* across a broad distribution within the low Arctic, including Alaska, the Chukotka Region of NE Russia and Scandinavia. Numbers of species decline with increasing latitude within the low Arctic but in nearly all cases the host plant extends further north than the insect (Hodkinson & MacLean 1980, MacLean & Hodkinson 1980). Furthermore, several psyllid species drop out at a similar point along the transect. Their disappearance appears to result from a breakdown of phenological synchrony with their host, resulting from a failure to develop sufficiently quickly to complete their usual annual life cycle within a prescribed developmental window set by the plant (Hodkinson *et al.* 1979). One W Greenlandic species, *Cacopsylla groenlandica*, progressively sheds willow host-plants in this manner with increasing latitude before itself disappearing from its last surviving host grayleaf willow *Salix glauca* at the northern limit of its distribution (Hodkinson 1997). It is thus the differential effect of temperature on interacting insect and plant development that limits distribution, rather than the direct effect of cold temperature *per se*.

Such phenological limitation of distribution within the Arctic probably applies to many phytophagous groups with annual life cycles, including many of the sawflies (Høye & Forchammer 2008). However, more polyphagous herbivores with the ability to extend life cycle duration such as chrysomelid beetles and some Arctic moths (Lepidoptera) such as woolybear caterpillars *Gynaephora* spp. are unlikely to be restricted in this manner (Chernov *et al.* 1994, Medvedev 1996, Morewood & Ring 1998, Chernov & Makarova 2008). Among Finnish butterflies the proportion of species capable of overwintering in the extendable larval stage increases significantly at the highest latitudes (Virtanen & Neuvonen 1999).

Some Arctic insects exhibit restricted distributions relative to those of their host-plant along local rather than latitudinal microclimatic gradients, sometimes over relatively short distances. The aphid *Acyrthosiphon svalbardicum*, for example, feeding on eight-petal mountain-avens *Dryas octopetala* on W Spitsbergen, Svalbard is absent from its host at colder sites on the outer Kongsfjord but becomes progressively more abundant at warmer and more sheltered sites on the inner fjord. The distribution is related to the availability of sufficient 'degree-days' for the aphid to complete its life cycle (Strathdee & Bale 1995).

7.2.3.3. Geographical and regional variations in biodiversity

The present compositions of the regional invertebrate faunas of the Arctic are determined by a multitude of factors. They represent an amalgam of taxa that survived the Pleistocene glaciations in Arctic glacial refuges, such as Beringia, intermixed with taxa that have at various times and with varying degrees of success colonized the Arctic from different geographical source areas lying farther to the south. Different taxa have dispersed at different rates, with climatic and geographical barriers to dispersal, such as mountain ranges, proving more effective for some taxa than others (Varga & Schmitt 2008, Ávila-Jiménez & Coulson 2011). The overall outcome is expressed as differences and similarities in faunal biodiversity among different regions of the Arctic and groups of invertebrates.

Danks (1981) predicted that invertebrate species with Holarctic distributions would tend to form a greater proportion of the fauna in the boreal/Arctic zones than elsewhere. Transholarctic, circumboreal, northern circumpolar and cosmopolitan species do indeed comprise a significantly large proportion of most Arctic faunas. Some Arctic bug species (Hemiptera) exemplify such wide-ranging and common northern Holarctic species. These include the seed bug *Nysius groenlandicus* (Lygaeidae) and the shore bugs *Chiloxanthus arcticus* and *Calacanthia trybomi* (Saldidae) (Danks 1981, Makarova & Makarov 2006, Böcher & Kristensen 2011). However, even though some large taxa often contain several Holarctic species they may also contain other, often closely related, species that display widely disjunct distributions. Such distributions, as found in many springtail species, are often more difficult to interpret (Babenko 2005). Furthermore, the proportion of Holarctic species within the fauna may vary among the different regions of the Arctic and across invertebrate groups. Oribatid mites, for example, generally contain a high proportion of Holarctic species, with the majority of species found in the North American high Arctic and eastern low Arctic having Holarctic distributions (Behan-Pelletier 1999). Similarly, several important dipteran fly families within the Arctic, such as the winter craneflies (Trichoceridae), mosquitoes (Culicidae), root-maggot flies (Anthomyiidae) and blow-flies (Calliphoridae), contain at least 68% Holarctic species (Danks 1981). By contrast surprisingly few (28%) Holarctic species of spider have Arctic or boreal ranges (Marusik & Koponen 2005). A similarly low proportion of Holarctic species also occurs in some aquatic insect groups, such as the stoneflies (Plecoptera), which tend to be largely restricted to the low Arctic. The declining percentage of Holarctic species with decreasing latitude is illustrated by moths of the family Noctuidae (noctuid moths) in which the percentage falls from 100%, in the high Arctic, to around 42% at lower latitudes in Iceland and the Yukon (Mikkola *et al.* 1991). For Arctic lepidopterans as a whole, the proportion of Holarctic species is around 13%.

Table 7.5. The number of species of springtail and butterfly species recorded from the different sectors of the Arctic (from Babenko 2005 and Chernov & Tatarinov 2006). Data for the high Arctic springtails alone are given in parentheses. Note that not all sectors have been sampled with equal thoroughness. For butterflies, the Ural and Western Siberian sectors are combined.

Sector	Collembola	Butterflies
A Western European	201 (71)	51
B Eastern European	97 (14)	74
C Ural	65 (51)	57
D Western Siberian	178 (37)	
E Eastern Siberian	105 (43)	60
F Northeastern Siberian	152 (62)	59
G Western American	155	59
H Eastern American	115 (49)	47
I Greenland	89	6

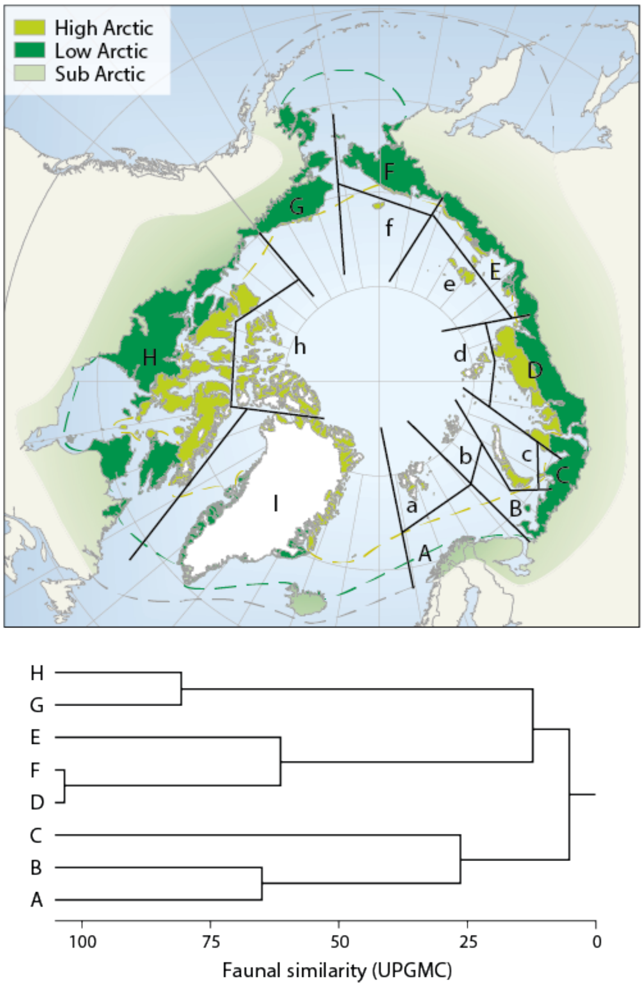

Figure 7.4. Biodiversity of springtail species within and among biogeographic sectors of the low (upper case letter) and high Arctic (lower case letter). Data in Tab. 7.5 are based on the divisions in the map: A Western Europe, B East Europe, C Ural, D West and Middle Siberia, E Eastern Siberia, F North East Asia, G Western America, H Eastern America, I Greenland. The lower dendrogram summarises the similarity of the faunas in eight of the different sectors (from Babenko 2005, Babenko & Fjellberg 2006). Clustering was carried out using the Unweighted Pair Group Method with Centroid Averaging (UPGMC).

Differences in biodiversity across geographical regions are well illustrated by a comparison between a well-adapted and diverse but flightless group, such as the springtails, and an assemblage, such as the butterflies, in which species are capable of flight but are more strongly restricted by climate and consequently contain a smaller proportion of high Arctic species. The overall patterns of diversity also differ in that for Arctic butterflies over 50% of species belong to just four genera *Colias* (sulfur butterflies), *Boloria* (fritillaries), *Oeneis* (graylings) and *Erebia* (mountain ringlets), a pattern most accentuated at higher latitudes (Chernov & Tatarinov 2006). Springtail species are, by contrast, more widely spread across a wider set of genera (Babenko & Fjellberg 2006). Tab. 7.5 shows the distribution of the 425 species (102 genera in 16 families) of springtails and 106 species of butterflies (36 genera in six families) across nine sectors of the low and high Arctic as defined in Fig. 7.4 (Babenko 2005, Babenko & Fjellberg 2006, Chernov & Tatarinov 2006). The numerically most important groups of springtail species present within the high Arctic, based on their known geographical distributions, are, in descending importance, Transholarctic and cosmopolitan > TransPalearctic > European and W Palearctic > E Palearctic > Beringian > Nearctic > Amphi-Atlantic species (Babenko 2005).

Patterns of glaciation have left strong residual effects on the biodiversity of invertebrate communities in different regions of the Arctic. Zooplankton crustaceans, for example, display higher diversity in lakes that remained unglaciated during the Pleistocene such as on the Chukotski Peninsula, Russia; Point Barrow, Alaska; and Disko Island, Greenland, compared with lakes in recently glaciated areas such as the Canadian Shield and parts of E Siberia (Samchyshyna *et al.* 2008). The old Beringian refuge still casts its shadow today on invertebrate biodiversity, with many invertebrate species exhibiting an Amphi-Beringian distribution and the Beringian region being a diversity hotspot for several Arctic invertebrate groups such as chrysomelid beetles, weevils, craneflies, noctuid moths, spiders and particular groups of oribatid mite, such as the Ceratozetoidea (Danks 1981, Chernov & Makarova 2008, Behan-Pelletier & Schatz 2009, Elias 2009a, 2009b). Wrangel Island and the adjacent Chukotka Region are particularly rich in spider species, although Novaya Zemlya is also a hotspot for spider diversity.

The Bering Strait generally represents a less significant faunal disjunction than certain physiographic barriers within continental North America. For many arthropod groups, there is a strong faunal disjunction between the western and eastern sectors of the North American Arctic (Danks 1993). Several groups show a progressive decline in biodiversity as one moves from the Arctic west of the Mackenzie through the region between the Mackenzie and Hudson Bay to the area east of Hudson Bay (Danks 1981, Danks & Smith 2009). The reason for this is unclear. Notable examples include spiders; beetles of the families Carabidae (ground beetles) and Chrysomelidae (leaf beetles); flies of the families Tipulidae (craneflies), Anthomyiidae (root-maggot flies) and Muscidae (house flies) and butterflies of the families Pieridae (whites and sulfurs) and Nymphalidae, including the Satyrinae (fritillaries and browns). Several groups of Hymenoptera with strongly contrasting biologies, such as the leaf-eating sawflies Tenthredinidae, the parasitoid wasp family Ichneumonidae and the social bees Apidae, follow a similar trend (Danks 1981). Likewise, the number of mite species in the low Arctic of western North America is almost double that of the eastern part of the continent and the high Arctic combined (Behan-Pelletier 1999). There are also significantly more springtail species in NE Siberia and the western North American Arctic than in adjacent areas of W Siberia and eastern North America (Babenko 2005).

By contrast with the higher invertebrate groups, many of the lower invertebrate taxa within the Arctic are much more cosmopolitan in their distribution. This has been attributed to their small size and abundance facilitating dispersal and the maintenance of persistent populations (Segers & De Smet 2008). Of the 70 species of rotifers collected in ponds on Devon Island, Canada, only two species, *Notholca latistyla* and *Proales kostei*, are restricted to the Arctic, and a significant majority are cosmopolitan (De Smet & Beyens 1995). This dominance by cosmopolitan species is repeated in the 69 species from samples collected in W (Kangerlussuaq) and E (Ammassalik) Greenland (De Smet & Beyens 1993). The ciliates similarly contain high proportions of cosmopolitan species (Foissner *et al.* 2008). Forty-four of the 210 ciliate species found on Svalbard are also found in Antarctica, although other species have a more restricted distribution (Petz 2003, Petz *et al.* 2007). Around 13% of species in Petz's Arctic samples were new to science, and some may represent rare endemics (Petz *et al.* 2007).

Greenland forms an especially interesting sector of the Arctic as it is geologically a part of the North American continent and has traditionally been included within the Nearctic zoogeographical realm. However, Greenland presents a good example of how typical Arctic invertebrate faunas comprise an admixture of several biogeographical elements. It has long been recognized that the Greenland invertebrate fauna is not exclusively and typically Nearctic (Danks 1981). Some have suggested that it might represent a distinct zoogeographical unit containing characteristic faunal elements that survived the Pleis-

Table 7.6. Wider distribution patterns of species within selected arthropod taxa from Greenland, showing affinities with the Holarctic, Nearctic and Palearctic regions (from Makarova & Böcher 2009).

Taxon	Species in Greenland	Holarctic+ Semicosmopolitan + Cosmopolitan	Nearctic + Nearctic-W Beringian	Palearctic + European
Oribatid mites	109	78	15	11
Mesostigmatid mites	59	28	5	21
Areneae	74	37	25	8
Collembola	89	50	7	31
Coleoptera	37	20	1	15
Lepidoptera	42	14	22	6
Diptera: Muscidae	37	26	10	0
Trichoptera	8	1	6	1

tocene glaciations in addition to the later colonizers from various geographic sources (Böcher 1988, Bergersen 1995). The presence of endemic species, often associated with the homothermal springs, lends some weight to this argument (Bergersen 1995). Tab. 7.6 shows that for several important arthropod groups, three distinctive elements can be recognized within the Greenland fauna (i.e. Holarctic, Nearctic and Palearctic), in addition to the endemic and cosmopolitan species. These data suggest that Greenland has been repeatedly colonized from the north, east and west. Even among closely related taxa within groups such as the mites there may be differences in the geographical origins of different subgroups. The moss mites (Oribatida), for example, show the strongest affinities with Nearctic faunas, whereas the Mesostigmata mites display clearer affinities with the Palearctic fauna (Makarova & Böcher 2009).

7.2.3.4. Endemic species

Despite the widespread presence of transholarctic and cosmopolitan invertebrate species within the Arctic fauna, many other species are apparently endemic (Tab. 7.3). Some of these endemics are widespread within the Arctic, such as the springtails *Ceratophysella longispina* and *Bonetogastrura nivalis*, but others are restricted to small specific regions (Babenko & Fjellberg 2006). Even among primarily cosmopolitan groups, e.g. testate amoebae and rotifers, eight and twelve Arctic endemics, respectively, have been identified (e.g. De Smet & Beyens 1995). Interestingly, centers of endemism of some groups, e.g. rotifers (Monogononta), tardigrades and testate amoebae, include Svalbard and NE Canada, areas not noted for high endemicity among arthropods.

Some Arctic endemics have very highly restricted distributions. The aphid *Sitobion calvulus*, for example, despite extensive searches, is known only from a few scattered localities adjacent to the inner parts of Kongsfjord, W Spitsbergen, Svalbard (Gillespie *et al.* 2007). Another aphid, *Acyrthosiphon svalbardicum*, is more locally abundant but still endemic to Svalbard (Strathdee & Bale 1995). The primary host-plants of these aphids, polar willow *Salix polaris* and mountain-avens respectively, are however widespread within the Arctic. Endemicity is especially common among Arctic aphids, with around 37% of the Nearctic species apparently endemic to the region and a particular concentration of endemic species in the eastern Canadian Arctic (Tab. 7.3).

In general, the Arctic endemic invertebrate species tend to be scattered across a wide range of taxa. For example, the number of endemic species within numerically important groups of arthropod in Greenland is: springtails 1, aphids 9, scale insects (Coccoidea) 5, chironomid midges 13, fungus gnats (Mycetophilidae) 2, parasitic wasps of the families Braconidae 8 and Ichneumonidae 28, ground beetles 1, spiders 3, moss mites 4, Prostigmata mites 11 and Mesostigmata mites 5 (Böcher & Kristensen 2011 in press). The enchytraeid worms represent a group especially rich in Arctic endemic species, particularly within the Palearctic tundra and in the Amphi-Beringian region, with a strong dominance by species of the genera *Mesenchytraeus* and *Henlea* (Christensen & Dózsa-Farkas 1999). The Amphi-Beringean region, notably the tundra steppe region of NE Siberia, is particularly rich in endemic species in many taxa, including spiders, oribatid mites, lepidopterans, craneflies, weevils and ground beetles, chrysomelid and rove beetles (e.g. Mikkola *et al.* 1991, Ryabukhin 1999, Marusik & Koponen 2002, Chernov & Makarova 2008, Konstantinov *et al.* 2009). Arctic endemic species of flightless leaf beetles belonging to the genus *Chrysolina*, for example, are typical of eastern Siberia and adjacent islands (e.g. Wrangel Island) and northern Alaska, but are absent from the Canadian Arctic Islands and Greenland (Chernov & Makarova 2008). It is notable that several species of insect living in the eastern Siberian steppe desert today, such as the pill beetle *Morychus viridis* (Byrrhidae), are remnants of an Early Pleistocene fauna that have survived in similar unglaciated habitats for around 2.5 million years (Berman 1990, Elias 2009a).

Care is needed, however, in interpreting available data on endemicity. For example, existing data suggest that 68% of anthomyiid flies are Holarctic and the remainder is Nearctic endemics. This is unlikely to be the case and merely reflects a paucity of data on this group from the Russian Arctic (A. Pont, unpublished data).

7.3. STATUS AND TRENDS

7.3.1. Species richness and distribution

The lack of long-term studies on most invertebrate species leads to a paucity of empirical data on their response to climate change across the Arctic regions, despite some knowledge about their existing distributions. Much evidence for natural change, including that noted earlier by indigenous peoples, is primarily based on records of species that appear to have become more abundant or extended their range. For example, the moth *Apamea zeta* (= *maillairdi*) appears to have become more abundant around Longyearbyen, Svalbard, and the thrip *Aptinothrips rufus* has been recorded from Svalbard for the first time (Hodkinson 2004). The latter record, however, illustrates a further problem of knowing whether a species is newly establishing or whether it is a mere vagrant. The Greenland ladybird *Coccinella transversoguttata* appears to have recently pushed its distributional limit about 100 km northwards in E Greenland, and the aphid *A. svalbardicum*, previously thought to be apterous, is now commonly producing winged forms (Simon *et al.* 2008, Böcher 2009). Observations by indigeneous peoples, notably the Sámi in Finland, provide many records of apparent longer-term changes in insect abundance, particularly in association with reindeer herding. These involve changes in the numbers of biting flies, such as mosquitoes and black flies, and of parasites such as caribou nostril flies and gadflies. They also extend to a wider range of species, including bees, wasps, butterfly and beetle species (Salin *et al.* 2004, Mustonen 2004, Mustonen & Zavalko 2004, Mustonen & Mustonen 2009, 2011).

Probably the best quantitative evidence for change within the last hundred years comes from studies on aquatic chironomid midges, where community composition can be reconstructed from subfossil records. Chironomids in high Arctic ponds on Ellesmere Island, Canada, for example, have shown a marked increase in both population density and diversity associated with shifts in diatom populations and reduced ice cover (Quinlan *et al.* 2005).

Glacial retreat in many parts of the Arctic is exposing new habitats for colonization by invertebrates. Studies of the past chronology of colonization and community assembly indicate how and why future changes in biodiversity may take place. For example, a study of the progressive colonization of the glacier foreland of Midtre Lovénbreen, Svalbard, with respect to elapsed time since exposure, showed that colonization by pioneer species is rapid, but that it may take up to 2000 years for the full complement of species found in the surrounding non-glaciated areas to establish, particularly the species associated with deeper soils (Hodkinson *et al.* 2004). Invertebrate species fell into eight groups with respect to colonization success, based on ecophysiological tolerances, the need for facilitation, or a dependence on other species. The earliest colonizers were predators and detritus feeders, including spiders, surface-active springtails and drought resistant oribatid mites, which established before vascular plants arrived and soil developed. Later colonizers required facilitation and soil development. Equivalent data for associated glacial streams shows similar rapid early colonization by cold-adapted aquatic faunas, especially chironomid midges, followed by gradual community change as conditions become more stable (Lods-Crozet *et al.* 2007). Such glacier retreat chronosequences show that the development of biodiversity is time dependent but deterministic, and that this process is likely to accelerate within a warming Arctic.

These local changes in biodiversity should, however, be viewed against the broader background of a changing Arctic, the ability of existing species to survive change and the potential for the invasion by dispersal of 'new' species from outside. Arctic invertebrates, despite their small size and absence of specialized adaptations, frequently display highly effective dispersal mechanisms. For many of the smallest invertebrates with cold/drought resistant egg or other resting stages, often coupled with asexual reproduction (e.g. rotifers, tardigrades, ostracod crustaceans and testate amoebae), dissemination by wind or water is commonplace. The use of yellow sticky traps and water traps reveals a significant and continual dispersal of flying, wind-blown and ballooning (spider) invertebrate species across the Arctic landscape, with chironomid midges usually the dominant faunal component (Coulson *et al.* 2003a, Hawes 2008). Springtail and mite species appear to disperse effectively on the surface of, and occasionally submerged within, both fresh and salt water (Coulson *et al.* 2002a). Phoretic association of several, such as oribatid mites, with flying Diptera and birds may also enhance their wider dissemination (Lebedeva & Lebedev 2008, Coulson 2009). The sporadic mass arrival within the high Arctic of a wide diversity of living non-indigenous insect species, such as the moth *Plutella xylostella*, resulting from the movement of atmospheric depressions from lower latitudes, suggests that a mechanism is already in place for colonization by more southerly species as climate ameliorates (Coulson *et al.* 2002b). However it also indicates that conditions must become suitable for sustained activity, growth, development and reproduction before establishment can occur. For example, *P. xylostella*, which has yet to establish known self-sustaining populations within the high Arctic, has a development threshold of 7 °C and an activity threshold of 18 °C for sustained flight compared with a current maximum mean monthly temperature of 6 °C and a maximum air temperature of 17 °C at sites on Svalbard where it has been found (Coulson *et al.* 2002b). However, the successful colonization by *P. xylostella* of the sub-Antarctic Marion Island, with a similar summer climate to Svalbard, suggests that classical physiological thresholds may not always reflect true adaptational ability.

Changes in Arctic biodiversity in response to changing climate at any site will in all probability result from a re-sorting of existing Arctic species as they shift their distributions and potentially begin to interact with incomer species. Different organisms, however, will tend to move at different rates. Their success in adapting to change will depend largely on their ability to track changes in their habitat and match their ecophysiological requirements to those of their new surroundings. The key environmental factors determining their success are likely to be mean summer and winter temperatures, moisture availability, length of growing season and the frequency of freeze/thaw events that may disrupt preparation for, and emergence from, the overwintering state (Hodkinson *et al.* 1996a, 1998, Ávila-Jiménez *et al.* 2010, Bale & Hayward 2010, Ayres *et al.* 2010). While warmer summer temperatures may adversely affect some Arctic invertebrate species such as stenothermal ground beetles and spiders, many are likely to respond positively to such temperature increases, provided other conditions remain suitable. For example, populations of the aphids *A. svalbardicum* and *S. calvulus*, despite their status as high Arctic endemics, both respond rapidly and positively to increased summer temperature under experimental manipulation (Strathdee *et al.* 1995, Gillespie *et al.* 2007). The response, however, may occur differentially among ostensibly similar taxa. The larvae of tenthredinid sawflies, for example, appear to develop and molt more rapidly at low temperatures than those of lepidopterans, suggesting that their responses to increased temperature will also differ (Bogacheva 1994). Similarly, several springtail and oribatid mite species may respond positively to increased temperatures, but many springtail species are also highly susceptible to reduced moisture availability (Hodkinson *et al.* 1998). Oribatid mites, by contrast, appear more drought resistant and better able to withstand lower soil moisture, but are less responsive to increased temperature. Soil dwelling invertebrates such as enchytraeid worms, eelworms, ciliates, testate amoebae, rotifers and tardigrades, which either live in the soil water film or possess cuticles that are highly permeable to water, are the organisms that are the most likely to be adversely affected by a drying of the tundra associated with increased temperatures (e.g. Maraldo *et al.* 2009).

It is unlikely, however, that the overall effect of climate amelioration on Arctic invertebrates will be simple, with high Arctic species disappearing to be replaced in an orderly manner by species diffusing up from the south. Change will at least initially involve resorting and reordering of taxa within existing communities. Much of the terrestrial high Arctic is comprised of island archipelagos that are separated from areas farther south by marine/pack ice barriers. While many colonizing invertebrate taxa and species are easily capable of jumping these barriers, they will do so at different rates and with a significant element of stochasticity in their order of arrival and establishment (Hodkinson *et al.* 1998). A more gradual northward diffusion of species is most likely in the continental low Arctic tundra areas of northern Russia, Canada and Alaska, but even here topographic diversity should ensure that diffusion proceeds in a punctuated manner. In mountainous regions there is a strong possibility that Arctic arthopods, together with their host plants, will move to and survive at higher elevations (Hodkinson 2005). Equilibrium communities will take a long time to develop, if they become established at all.

7.3.1.1. The importance of species interactions

Arctic invertebrate species do not live in isolation, but rather interact with other species to form food chains and webs of varying complexity. Increasing biodiversity implies increased food web complexity, with implications for species interdependence, ecosystem function, resilience and stability (Wall 2009). Interactions can take many forms, including predation, parasitism and pollination, all of which are susceptible to modification in a changing climate. For interacting species to co-exist in space and time, they must share similar ecophysiological tolerances and habitat requirements. Phenological asynchrony or mismatched environmental tolerances may lead to the breakdown of interactions between the species, especially in the harsh and unpredictable climates of the Arctic (Hance *et al.* 2007).

The success of seed set in many common Arctic dicotyledenous plants, such as Arctic willow *Salix arctica*, purple saxifrage *Saxifraga oppositifolia* and entire-leaved mountain-avens *Dryas integrifolia* at Lake Hazen, Ellesmere Island, is totally or partially dependent on pollination by insects (Kevan 1972, Danks 1986). Bumblebees, the important pollinators at temperate latitudes, are generally scarce within Arctic ecosystems where a wide variety of nectar/pollen feeding dipteran flies are the main pollinators (Pont 1993, Elberling & Olesen 1999, Larson *et al.* 2001). Butterflies, e.g. the fritillaries *Boloria* spp., are less common pollinators, but parasitoid wasps are frequently associated with flowers, although their precise role in pollination is less clear (Klein *et al.* 2008).

Arctic plant-insect pollinator networks can be complex. For example, seven pollinator networks at sites located between latitudes 66-82 °N involved 15 to 31 plant species, 26 to118 insect pollinators, and 63-286 recorded insect plant interactions per site (Lundgren & Olesen 2005). However, the extent to which these networks are flexible and able to accommodate new invading species in an era of warming climate remains unclear and probably depends on the extent of the mutual specificity of the relationships among incoming species (Klein *et al.* 2008). Some plants with specialized floral anatomy, e.g. the lousewort *Pedicularis* spp. and legumes, appear more closely linked to pollination by bumblebees and hoverflies (Kevan 1972, Klein *et al.* 2008). Established pollinators may thus be unable to facilitate the establishment of such specialized plants.

Communities of Arctic arthropods contain at first sight a surprisingly high proportion of predatory and parasitic species relative to prey species (Hodkinson & Coulson 2004). Spiders, predatory mesostigmatid mites and parasitoid wasps are an abundant and ubiquitous element of faunas throughout the Arctic. Among beetles, predatory ground beetles and rove beetles often predominate, particularly in the low Arctic. The precise food/host interrelationships of many of these predators and parasitoids remain unknown, although existing data suggest that food chains are not as short as some have suggested. A four link chain, for example, springtail → spider → ichneumon wasp → bird is not uncommon (Hodkinson & Coulson 2004).

Levels of predation by beetles and predatory hover fly larvae are frequently reduced at higher latitudes as these less well adapted predator species become temperature limited and fail to exploit the full range of their potential hosts. For example, the distribution of the rove beetle, *Atheta graminicola*, in NW Spitsbergen is confined to thermally favorable microsites, and it is absent from the coldest areas despite an abundance of suitable prey. Similarly, the Greenland willow psyllid *Cacopsylla groenlandica* suffers reduced predation by hover fly larvae in the northern part of its range (Hodkinson 1997). Communities of *Eupontania* species of gall-forming sawflies in the Russian Arctic support fewer parasitoids and suffered lower overall parasitism at northern compared with southern Arctic localities (Roininen *et al.* 2002). A warming climate will begin to alter the balance of these relationships.

Many tundra-nesting bird species depend for their reproductive success on the availability of a diverse assemblage of invertebrates on which to feed their young. A reliable and sufficient food supply, which is sustained throughout the breeding season, requires a seasonal progression of invertebrate species, particularly insects, becoming successively available through the summer. There is some evidence that, at least initially, a warmer summer may lead to accelerated emergence of insect species, notably chironomid midges and mosquitos, such that the availability of food is increased early in the season but becomes restricted later in the year (MacLean 1980, Hodkinson *et al.* 1996b, Tulp & Schekkerman 2008). Larval chironomids also provide a prime source of food for some freshwater fish species.

7.3.2. Population sizes and densities

Population densities of both individual species and higher taxa of invertebrate vary greatly among habitat types, and it is not possible to quote typical density values. Likewise it is difficult to predict future trends. It is more apposite to emphasize the variation that occurs across a range of habitats. For example, on Svalbard total springtail numbers may range from less than 2,000/m^2 in impoverished habitats to over 260,000/m^2 in damp grassland and 590,000/m^2 in enriched wet moss sites below bird cliffs (Coulson 2000). Similarly, numbers of eelworms vary between 400,000 and 7,000,000/m^2 among sites at Tereya on the Taimyr Peninsula, Russia (Chernov 1972). Proportions of individual species within the total population also vary considerably among habitats. The mite *Camisia anomia*, for example, comprises over half the total oribatid mite population in polar semi-desert communities on Svalbard but less than 10% in tundra heath (Webb *et al.* 1998). Tab. 7.7 shows the range in mean population densities recorded for some of the numerically dominant groups of soil invertebrates at selected sites throughout the Arctic. Variation among habitats within sites is frequently as great as that among sites.

Other invertebrate groups are usually present at much lower densities. However, certain groups, such as the larvae of craneflies, sawflies and butterflies can, because of their larger individual size, make highly significant contributions to total invertebrate biomass (Bogacheva 1977, MacLean 1980). Craneflies, for example, are especially important in wetter low Arctic habitats such as at Barrow, Alaska (MacLean 1980). Earthworms, although unevenly distributed, can in some hotspot areas reach moderately high densities and contribute substantially to the biomass of the soil biota. *E. nordenskioldi* populations in the Taymyr peninsula reach densities of 80 individuals/m^2, and biomass varies between 25 and 65 g fresh weight/m^2 (Matveyeva *et al.* 1975). *D. octaedra* in Greenland may attain densities of 10-20 individuals/m^2, but the distribution is patchy (M. Holmstrup pers. com.). Total Diptera larval densities across habitats ranged from 0 to 668/m^2 at Zackenberg, NE Greenland, 10 to 2,500/m^2 on Svalbard, 8 to 99/m^2 at Tereya, Taimyr, and 171 to 915/m^2 at Barrow, Alaska (Chernov 1972, MacLean 1980, Coulson 2000, Sorenson *et al.* 2006). Equivalent data for beetle numbers are 0 to 60/m^2 on Svalbard and 0 to 107/m^2 at Tereya, and for spiders 0 to 100/m^2 on Svalbard and 35.9/m^2 on the Yamal Peninsula, Russia (Danilov 1972, Coulson 2000).

The population densities of biting flies found within some areas of the Arctic, notably mosquitoes and black flies, have strong impacts on a range of human activities, particularly reindeer herding and tourism. They also have important implications for the breeding success of native mammals and birds. These may involve positive effects, such as the provision of food for birds, but also negative impacts, such as the disruption of normal patterns of behaviour in both birds and mammals. Despite their often high abundance, the biting flies are not particularly species rich. Nevertheless, they have the potential to act as vectors of disease in both humans and a range of bird and mammal species. The introduction of novel or more virulent forms of insect-borne disease may thus become more likely because of climate-change effects on biting fly distribution and density.

It is notoriously difficult to estimate accurate population densities for microscopic soil animals and data, when recorded, are usually expressed per gram of soil rather than per square meter. Testate amoebae populations ranged from 20 to 40 individuals/g soil across four vegetation types at Zackenberg, NE Greenland, while 'Protozoa' (naked amoebae + flagellates) numbered 7,000 to 11,000 individuals/g soil at sites ranging from mesic to dry heath (Trappeniers *et al.* 2002, Sorenson *et al.* 2006).

7.4. CONCLUSIONS AND RECOMMENDATIONS

7.4.1. Sensitive areas and hotspots

In addition to the known major biodiversity hotspots within the Arctic, e.g. Beringia, there are many smaller biodiversity hotspots or oases with features favorable to invertebrates. Such sites may, for example, have a particu-

Table 7.7. Mean population densities (1,000/m^2) of the numerically dominant soil invertebrate groups across a variety of habitats and dates at selected Arctic sites. Data are compiled from existing summaries, which should be consulted for more detailed information and original source references (see Chernov 1972, Bliss 1987, MacLean 1980, 1981, Coulson *et al.* 1996, Webb *et al.* 1998, Coulson 2000, Sorensen *et al.* 2006).

Site	Springtails	Mites	Enchytraeidae	Nematoda
Svalbard	0.6-592	0.3-248	0.2-100	2.3-376
Devon Island, Canada	2-30	10-20	20-30	40-50
Point Barrow, Alaska	24-171	9-83	11-93	46-723
Prudhoe Bay, Alaska	1-70	1-80	10-40	-
Tereya, Taimyr, Russia	14-119	2-45	1-24	400-76,000
Zackenberg, Greenland	30-130	39-46	0.3-3.5	65-250/g soil

larly favorable microclimate, habitat diversity or nutrient status. These sites are more likely to attract new colonizing species and to harbor source populations from which species may spread as conditions become more favorable in the surrounding areas. Several thermally favorable 'oases' are sheltered south or west facing sites, often with a reflective body of water in front and cliff behind (Mikkola 1992). Consequently, such sites occur most frequently at the sheltered heads of fjords or adjacent to sea coasts where climate is ameliorated by a warmer ocean current.

Examples of oases for invertebrates in the Canadian Arctic include Lake Hazen and Alexandra Fjord on Ellesmere Island and Truelove Lowland on Devon Island (Bliss 1987, Svoboda *et al.* 1994, Ring 2001). Greenland sites include low Arctic Disko Island with its homothermal springs, the sub-Arctic inner fjord region around Narsarsuaq on the west coast, and the high Arctic Zackenberg adjacent to Young Sund on the northeast coast (Høye & Forchammer 2008). These sites, because of their perceived diversity, have frequently been the subject of the most intensive investigations. On Svalbard, Ossinsarsfjellet oasis at the head of Kongsfjord in NW Spitsbergen supports a relatively rich flora and fauna. The moth *Pyla fusca*, a more typical denizen of temperate regions, is persistently found here. This is an excellent example of a species that has managed to establish a toehold within a Svalbard oasis, albeit at a single favorable site (Coulson *et al.* 2003c). Wrangel Island is an important biodiversity hotspot within the Russian high Arctic.

The areas on, below and in front of nesting seabird cliffs that receive high subsidies of nutrients from bird droppings, and allochthonous detritus often have greater diversity of invertebrates such as beetles. These areas may also support atypically high population densities for several invertebrate species. High total populations of mites and springtails, however, are often associated with lowered species diversity within these groups.

There is a danger that because diversity hotspots often coincide with areas of climatic favorability or historic glacial refugia, any conservation focus on such areas may result in the cold-adapted, true Arctic species with wide ranging distributions being ignored.

7.4.2. Key knowledge gaps and recommendations

Our fragmentary knowledge of the biodiversity of many Arctic invertebrate taxa and the lack of good long-term data on population trends suggests the following important priorities for Arctic invertebrate diversity research:

- There is a pressing need for an increased recognition within CAFF that the invertebrates play a significant and essential role in the functioning of Arctic ecosystems. Given their dominant contribution to Arctic biodiversity and their role in providing key ecosystem services such as energy flow, decomposition, nutrient cycling and pollination (e.g. Wall *et al.* 2008), it is surprising how little attention has been paid to them in previous syntheses on the impact of climate change on the Arctic biota. For example, the *Arctic Climate Impact Assessment* barely touches on their biodiversity and makes few suggestions as to how they might respond to changing climate (Callaghan *et al.* 2004, 2005). Furthermore, their interaction with other organism groups through pollination (higher plants), ecto- and endo-parasitism (birds, mammals and other invertebrates) and their role as food for tundra-nesting birds or fish species at critical stages of their life cycle further emphasizes their importance to the functional health of Arctic ecosystems.

- A comprehensive inventory should be compiled for invertebrate species within the Arctic, listing their known distribution, abundance, habitat preference and functional role within the ecosystem. Traditional knowledge and expertise should be incorporated wherever feasible. Initially this inventory should be based on existing literature. It is recognized that this will be fraught with difficulties and will require the resolution of many taxonomic and nomenclature problems. This latter issue might be tackled by utilizing and further developing molecular methodologies such as the DNA Barcode of Life (BOL) initiative at the University of Guelph, Canada (www.dnabarcoding.ca/).

- There is a pressing need for further field survey work throughout previously neglected areas of the Arctic to ensure that the species inventory is as complete as possible and to establish more clearly the distribution patterns of species, particularly among the neglected invertebrate groups such as the eelworms and most lower invertebrates. Potential sites for long-term monitoring should be identified within these areas.

- The inventory should be used to identify and list the number and distribution patterns of the true Arctic endemic species, spread across many higher taxa, which are most likely to be most affected by a warming climate. All species, where possible, should be classified using the IUCN Red List Categories and Criteria. The inventory should also be used to identify or confirm areas of high diversity and endemism at various taxonomic levels across the invertebrates.

- There is an urgent need to establish a longer-term program monitoring population trends for selected indicator species that are likely to show both adverse and positive reactions to changing climate. It is essential that both above-ground and soil-dwelling species are included as they are likely to respond to climate change at different rates. Lake/pond dwelling species may similarly exhibit a buffered response to temperature changes. Compared with vertebrates and plants, many species/communities of invertebrates posses the attributes to act as highly sensitive indicators of changing climate. Their often effective powers of dispersal, coupled with rapid development rates leading to short generation times, ensure that they are able to rapidly shift location and re-establish populations as conditions permit (Hodkinson & Bird 1998). The potential exists to identify key indicator species/communities that may be used, through changes in phenology and distribution, to track climate changes and their impacts over time. Such changes may have cascading effects within ecosystems. Indicator species could include generalist, temperature-limited predators/scavengers such as ground and rove beetles and cold-adapted spiders including the genus *Erigone* (dwarf spiders), or species of host-specific herbivorous insect, such as psyllids (jumping plant lice) or leaf beetles, which currently do not occupy the full range of their host plant. The former group would be particularly easy to monitor as baseline data on their distribution along north-south transects already exist, and their common and widespread host-plants are easy to locate. Monitoring should also examine longer term population/genetic trends in indicator species/communities at fixed locations. The indicator species should include both Arctic endemics and widespread Arctic species across a range of sites. Candidate species/groups might include chironomid midges and water beetles in lakes, herbivorous terrestrial species such as the aphid *Acyrthosiphon svalbardicum* on Svalbard and the woolybear caterpillar *Gynaephora* in Canada, and certain widespread springtail species such as *Folsomia quadrioculata* and *Hypogastrura tulbergi*, soil-dwelling and surface-active species respectively. Inclusion of species with a long continuous history within the Arctic, such as the Beringean pill beetle *Morychus viridis*, could provide the longer-term context for change.

- Community change in the Arctic is likely to be driven in part by newly arrived incomer species. It would be instructive to set up a sampling program to analyze the species composition and abundance of the aerial invertebrate plankton that is carried into the Arctic from farther south by northwards-moving weather systems. These are the potential colonizing species. An inventory of newly establishing species should be developed and the extent of human mediated introductions of species into the Arctic assessed.

- The effects of climate change on economically significant biting fly populations should be evaluated throughout the Arctic in relation to alterations in the hydrology of habitats and rising temperatures. This is particularly important for the indigenous peoples of the Arctic, especially with respect to reindeer herding and other traditional activities. It also has implications for the tourism industry. Assessment should be made of the potential spread of important arthropod vector-borne diseases of humans, other mammals and birds into the Arctic.

7.4.3. Recommended conservation actions

Because of the sheer number of species, it is impractical to take a species-based approach to conservation of Arctic terrestrial and freshwater invertebrates. Conservation actions should focus on the maintenance of habitat diversity and protection. Nevertheless, invertebrate conservation in the Arctic has suffered from a lack of focal species that can be used to highlight the problems of conservation. Focal species, however, must be chosen for their uniqueness or for their importance in ecological processes rather than for their aesthetic appeal. Examples of the former might include the flightless aphid *Sitobion calvulus* with its highly restricted distribution on Svalbard or chrysomelid beetles on the high Arctic islands. Examples of the latter could include a typical widely-distributed, surface-active springtail such as *Hypogastrura tullbergi* or widespread Arctic species of enchytraeid worms.

7.4.4. Other key messages

Our knowledge of the invertebrates as a group lags far behind that of higher plants, mammals and birds, yet the invertebrates represent the dominant group in terms of species-based biodiversity. This deficiency is reflected in the paucity of data concerning numerical trends, drivers and stressors presented in the preceding sections. Invertebrates are small and, to many, aesthetically unappealing, but they are almost invariably the numerically dominant group of organisms (excluding microorganisms) at sites in the Arctic, where they serve a wide variety of ecological functions and are key players in important ecosystem processes. There is danger in overstating the importance of larger, more charismatic vertebrate species with conservation appeal at the expense of those lesser invertebrates with greater functional significance for the well being of Arctic ecosystems.

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