The concept of biodiversity encompasses aspects of biology ranging from large-scale ecosystems down to the molecular level, where genetic variability is used to characterize diversity within and among populations of species. The genetic component of biodiversity is often not distributed evenly across the geographic range of species, but instead is spatially structured. The primary cause for such structure in the Arctic may be due to evolutionary history and processes related to geography, variable climate, and strong ties to seasonally available resources [e.g., 1]. Exceptions to this generalized pattern of geographic structure may include migratory species such as some birds [2, 3], but intensive research into this key aspect of biodiversity needs to be completed across a wide range of marine and terrestrial Arctic organisms.

In the Arctic, historical events have left distinctive signatures on the gene pools of individual species and these signatures must be understood if we hope to predict the impact of future changes on the genetic component of Arctic biodiversity. The Pleistocene glacial – interglacial periods (roughly 20 events every 100,000 years) during the last 2 million years played a primary role in structuring genetic variation in Arctic organisms. An understanding of genetic variability sets the stage for enlightened management of high latitude organisms in light of rapid environmental change. Molecular genetic approaches are now used in a wide range of applications from tracing the history of species dispersal and diversification across the Holarctic to evaluating the conservation status of high latitude species of concern so that wildlife populations can be sustained. Documenting the prior response of the Arctic biota provides a framework for interpreting the influence of different life history traits (e.g., migratory vs. sedentary) on genetic diversity and ultimately, will allow us to more effectively respond to future impacts on biodiversity under various climate warming scenarios.
Pleistocene climatic change had two main effects on genetic diversity of existing species. First, glacial advances created geographic barriers, leading to genetic divergence within species. Second, species responded to climatic change by adapting, moving, or suffering local extirpation or eradication. These episodic contractions and expansions of Arctic species altered their effective population size, evolutionary processes, and ultimately the geographic distribution of genetic diversity. Paleoecology and fossil records show that, in contrast to temperate species, cold-adapted Arctic species persisted in the north and expanded their ranges thousands of kilometers southward during glacial periods in Eurasia [4] and North America [5]. Ranges of many Arctic species subsequently retracted during warming phases, such as that currently under way, and retraction likely led to reduced genetic variability. Arctic-adapted populations now at the southern extreme of the species range may be isolated and most vulnerable to loss of genetic diversity. Loss of genetic variability may have important consequences for individual fitness and long-term persistence of species.

The concept of glacial refugia (i.e., areas isolated by glaciers) is appropriate for Arctic species only in the high latitude regions where development of ice sheets prevented persistence of biota during glacial periods. However, recent paleogeographical data show limited extent of the Pleistocene ice sheets in the Eurasian Arctic [6]. In contrast to Eurasia, the North American Arctic was extensively glaciated [7] with the Laurentide ice sheet covering much of Canada. These formerly glaciated Arctic regions were colonized from ice-free areas, so that understanding the nature of these colonization events provides key insight into the current distribution of genetic diversity.

Strong correspondence between evolutionary relationships and geographic distribution of genes (i.e., phylogeographic structure) has been found in the Arctic that reflects substantial endemism in many terrestrial free living and parasitic animals that have been sampled at continental and circumpolar scales [8–12]. The geographic locations of major evolutionary splits are largely similar across different species and coincide around mountain ranges that were formerly glaciated such as the Ural, Verhoyanskiy, Anuiskiy, and Richardson Mountains. In addition, cryptic northern refugia were identified [13–15].

Figure 9.1: Nucleotide diversity estimates based on the complete sequences of mitochondrial genome in the collared lemming [19] indicate how past climate has structured the genetic component of biodiversity. Lower diversity in regions (green) affected by the northward forest expansion during the Holocene warm climatic events [20] compared to Western Beringia, where there was no forest expansion, suggests a reduction of effective size due to regional range contractions during warming events in the Holocene [18].
and recently supported by palaeoecological lines of evidence [16, 17]. These refugia were important sources for colonization of formerly glaciated Arctic regions in Scandinavia and Canada. Genetic diversity of cold-adapted Arctic species also was influenced by warm climatic events during interglacials and the Holocene (the last 11 thousand years). Arctic specialists, such as the collared lemming, *Dicrostonyx torquatus*, experienced a reduction in effective population size due to range contraction (Figures 9.1 and 9.2) during warming events that expanded forest cover [18].

From a circumpolar perspective, an important historical event for the Arctic terrestrial and marine biota was the existence of the Bering Land Bridge connecting Eurasia and North America. Lowered sea levels during the glacial periods exposed the continental shelf and formed a single ice-free land mass, Beringia, that extended from the Kolyma River in north-eastern Siberia to the Mackenzie River in northwestern Canada. Apart from its importance for the transcontinental migration of plants and animals, Beringia is traditionally considered the main source for multiple recolonizations of deglaciated regions in the Arctic [21]; however, preliminary genetic analyses are equivocal on this point. Beringia represents an area of endemism (i.e., divergent DNA lineages are specific to only this region [9]). Separation of Eurasia and North America by the Bering Strait generally is not reflected in genetic analyses, which suggests that this recurring barrier to terrestrial species dispersal (most recently formed 11,000 years ago) has had a minor influence on genetic structure or divergence within many free-living and perhaps parasitic organisms [22]. In Arctic terrestrial species that are ecologically associated with dry environments, however, this barrier delineates significant genetic breaks [12, 18]. These findings are consistent with palaeoecological evidence suggesting that the Bering Land Bridge represented a moisture barrier to the dispersal of steppe-tundra biota indicative of arid environments [23]. For marine organisms, the Bering Land Bridge was a barrier to exchange between populations in the Arctic Ocean and those in the North Pacific. Hence major historical events such as formation of the Bering Land Bridge significantly altered the distribution of genetic diversity within Arctic species and ultimately the composition of biotic communities in marine and terrestrial ecosystems [24].

Figure 9.2: The collared lemming is an Arctic mammal that is providing insight into the location of refugial areas or areas that tend to support the highest levels of genetic diversity in Arctic species versus areas of recent expansion of species (generally lower genetic diversity).
Concerns for the future

Far too little is known about the distribution of genetic variability in natural populations across the Arctic. In part, past political subdivisions have hampered international collaborative efforts and there have been few coordinated efforts to survey biotic systems (and archive genetic specimens) that would allow us to assess spatial and temporal changes. Prediction of responses of individual organisms, biotic communities, or entire ecosystems to future events relies on an understanding of past responses to environmental change. Molecular genetic analyses can provide key insights into future responses because these data can be used to model the impact of various climate scenarios on population structure and ultimately species viability [1]. The contemporary distribution of genetic diversity in the Arctic points to potential areas of long-term persistence and diversification or areas that served as corridors for colonization following environmental change. These areas should be protected [25], but studies of Arctic genetic diversity are based on far too few regions and organisms. Genetic data are beginning to reveal the dynamics of how biotic communities are assembled and whether communities remained intact or, instead, species responded idiosyncratically to environmental change. Molecular genetic approaches will help identify areas where distinct biotic communities may come into contact, mix and potentially exchange pathogens and these contact zones need to be carefully monitored [26]. Fine-scale sampling of wild populations in these zones is needed to rigorously track these events, so that we can respond quickly to emerging pathogens.

The Arctic is an exceptional system for examining the influence of climatic events on the patterns and processes of both genetic differentiation as well as loss of genetic variability [27]. These details are essential to determining the prospects for long-term persistence of a diverse set of organisms adapted to Arctic terrestrial and marine environments. Loss of individual populations that harbor novel genetic variability decreases the overall adaptive potential of a species that will be necessary to respond to novel challenges. Ultimately loss of variability within species becomes a significant contributor to the extinction process and loss of species diversity contributes to ecosystem collapse. A detailed map of genetic structure is a crucial first step for conservation efforts that should be followed by renewed emphasis on identification and conservation of regions of high evolutionary potential. In extreme cases, this blueprint can be used for rescue efforts for declining species in the face of changing climate and increasing anthropogenic impacts in the Arctic.