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Phylogeography and arctic biodiversity: a review

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Current concerns over the impact that anthropogenic global climate change will have on levels of biodiversity have focused mainly on tropical and temperate systems. Recently, attention has turned to polar systems, and the potential impacts these climatic changes might have on polar flora and fauna. Polar organisms have been subjected to dramatic fluctuations in environmental conditions during the Holocene and Pleistocene, so one might expect these systems to be resilient. However, little is really known of how such global climate changes will impact biodiversity in the arctic. What is known, particularly through the use of molecular markers, is that glacial cycles have impacted the evolutionary trajectories of many extant polar species. By studying these organisms, particularly those found across the Holarctic, one can examine the dynamic interaction between deterministic forces (e.g. selection) and historical processes (e.g., vicariance event) in order to better understand how these processes have impacted the phylogeography and genetic divergence among taxa. Keeping with the "northern dimensions" theme of this symposium, we review results obtained from a variety of phylogeographic studies that have examined the importance of dispersal, vicariance, and selection in shaping the distributions of arctic biota, especially among closely-related species complexes. In particular, we examine the recent debate over the importance of Pleistocene glacial cycles in influencing population genetic differentiation and speciation. Finally, we provide an assessment of how studying these arctic systems will benefit the global perspective on climate change research.

Introduction

Why is it so important to study boreal and arctic systems? After all, only a very tiny fraction of the earth's inhabitants, both human and otherwise, are found in these very northern regions, so why should we be bothered studying them? Chapin and Koerner (1994) discussed some of the main reasons why the study of arctic (and alpine) systems are very important for our understanding of global ecosystem issues, particularly related to anthropogenic climate changes. First, arctic (and for that matter, Antarctic) ecosystems are generally "simpler" having fewer species present (Freckman & Virginia 1997) and often trophic interactions are reduced to a few dominant species-species interactions, when compared to temperate or tropical systems. Second, these systems are extremely "fragile" in the sense that even minor environmental perturbations will have an immediate and long-lasting effect (Kevan *et al.* 1995). Finally, during the past 2–3 million years, the waxing and waning of Pleistocene glacial cycles have impacted the evolutionary dynamics and trajectories of many Holarctic taxa (Hewitt 1996), leading to evolutionary divergence among populations and ultimately, to speciation (Klicka & Zink 1997, 1999, Avise & Walker 1998, Avise *et al.* 1998). The arctic has experienced numerous episodes of being covered by kilometers-thick glacial sheets of ice and snow, followed by periods of glacial retreat, which have opened up new habitats for (re)colonization. Therefore, these formerly glaciated polar regions are "younger", and thus, presumably further from an equilibrium state than more equatorial regions. This glacial history has created a natural "laboratory", where one can examine the interplay between deterministic and stochastic mechanisms that influence the phylogenetics and phylogeography of not only individual species, but intraspecific lineages.

The purpose of this present paper is to summarize what is known about the effects that these glacial cycles have played on the phylogeography and biodiversity of arctic species complexes. We will focus first on a brief look at arctic species richness and diversity, and will follow up our review with a more in-depth look at phylogeographic patterning and bio(genetic) diversity of a variety of arctic taxa at the intraspecific level. Specifically, we will examine the recent debate about the relative importance that Pleistocene glacial cycles have played in the speciation process (Klicka & Zink 1997, 1999, Avise & Walker 1998, Avise *et al.* 1998). Primarily, we will focus on those studies that have employed molecular markers to differentiate between distinct lineages in these arctic complexes, and we will compare and contrast patterns of phylogeographic patterning between very disparate taxa. Finally, we will place these data into the context of why it is important to maintain a "northern perspective" in biodiversity research.

Arctic biodiversity: interspecific comparisons

A general observation that has been made during the past 150 years of biogeographic study, has been the perceived inverse relationship between levels of species diversity and latitude; i.e., species diversity decreases with increasing latitude (Fischer 1961, Rosenzweig 1995). This relationship seems to hold for most terrestrial or freshwater groups of organisms (Rosenzweig 1995), however, recent evidence suggests that such a simple relationship does not exist in the marine realm, particularly among marine benthic invertebrates (Dunton 1992, Kendall & Aschan 1993, Crame 1997).

If we focus our discussion primarily on terrestrial fauna and flora and those that inhabit inland water bodies, few would argue with the observation, that for most taxonomic groups, one sees an attenuation of taxon diversity, as one proceeds from the tropics to the temperate zone on into the boreal and arctic regions (Rosenzweig 1995). For example, Beyens and Chardez (1995) detected a total of 220 species of testate amoebae observed across a wide expanse of arctic habitat, stretching from the Bering Sea, across arctic Canada and Greenland, to Svalbard. In comparison, Chardez (1987) detected 379 species from Belgium, alone. Likewise, Pugh and McInnes (1998) detected 154 species of tardigrades across the polar regions of the Holarctic, compared to 279 species detected in temperate regions. Further, Hebert and Hann (1986) observed that freshwater microcrustacean species richness was

3–4 times greater in low versus high arctic regions of Canada. Among plants, by latest count, there are only about 1500 species of all arctic plants known (Chapin & Koerner 1994), as compared with estimates of 15 000–16 000 species of vascular plants in the United States and Canada, combined (Qian 1999).

Role of Pleistocene glaciations in the speciation process

A recent debate in the literature (Klicka & Zink 1997, 1999, Avise & Walker 1998, Avise *et al.* 1998) has centered on whether Pleistocene glacial cycles have played a role in the promotion of speciation events among Holarctic (primarily vertebrate) taxa. More specifically, the debate has asked whether the available data support the notion of a Late Pleistocene Origins (LPO) model (i.e. within the past 100 000 to 250 000 years) for the evolution of a number of taxonomic groups, most notably, modern North American songbird species (Klicka & Zink 1997). Klicka and Zink (1997, 1999) have argued that such speciation events predate the Pleistocene, having primarily late Pliocene origins (2.5 million years ago). This recent debate seems to have focused on the "duration of speciation" events; i.e. protracted speciations from Pliocene origins to Pleistocene completions (Avise & Walker 1998), and really seems to be a debate that is asking somewhat different questions. Klicka and Zink (1997, 1999) are interested in addressing the more specific question — do molecular data support a recent late Pleistocene (past 100 000–250 000 years) history of speciation events among North American songbirds? Their data suggest that the answer to this question is a resounding no. In contrast, Avise and Walker (1998), and Avise *et al.* (1998) view Pleistocene speciation events (not just of songbirds, but also other taxa) as a very protracted process, and ask the question: was the Pleistocene a key period of time with respect to promoting the continued differentiation of avian (and other) populations to the species level? They argue that the molecular (i.e. predominantly mtDNA) data support a main role for Pleistocene effects in influencing differentiation among avian forms (and presumably other forms as well). What cannot be answered by current data — was the Pleistocene, itself, an unusual period in earth's history compared with similar-length earlier geological periods?

Two main questions that we would like to address in the present paper are: (i) has it been possible to initiate and complete speciation events in Holarctic taxa within the time-frame of the Pleistocene (i.e. within the past 2.0–2.2 million years)? (ii) have such (allopatric) speciation events (Mayr 1970) been mediated by the isolation of lineages in separate glacial refugia during the late Pleistocene? In the following sections, we will use a comparative phylogeographic approach in addressing these questions.

Results

Arctic biodiversity: intraspecific comparisons

In a recent article, Taberlet (1998) reviewed a total of eight phylogeographic studies that were available to date, from North America, Europe, and Australia. Three of these studies were continent-wide surveys, while the other five were more restricted geographically in their study areas. Taberlet (1998) detected two very interesting trends: (i) there was an attenuation of the level of intraspecific genetic polymorphism at higher latitudes, and this was particularly true in regions that were formerly-glaciated during the Pleistocene; (ii) the evidence for concordance of phylogeographic patterns among taxa remains equivocal, with the five studies conducted in limited geographic areas suggesting concordance of patterns, while the three continent-wide surveys indicate non-concordant patterns. Taberlet (1998) suggests that special attention and additional effort should be focused on conducting macrogeographic studies in those regions that served as putative glacial refugia during the Pleistocene.

What can be immediately gleaned from Taberlet (1998) is that there does appear to be strong support for a reduction in intraspecific biodiversity as one heads toward the poles, and that levels of genetic variation in extant polar species have been undoubtedly impacted by Pleistocene glacial cycles, similar to what has been observed in interspecific comparisons (Fischer 1961, Rosenzweig 1995).

We would now like to take a closer look at various phylogeographic studies conducted on fauna and flora that extend into the boreal and arctic regions (*see* Appendix for summary information), and examine the extent of phylogenetic differentiation and phylogeographic structuring among these taxa.

Marine taxa

Organisms inhabiting the arctic marine realm might be expected to exhibit long-distance dispersal capabilities, which would lead to greater gene flow, less population differentiation, and would obscure any phylogeographic patterning. Surprisingly, among large, vagile marine mammals such as the walrus (Cronin *et al.* 1994, Andersen *et al.* 1998), beluga whale (Brown-Gladden *et al.* 1997), and harbor seal (Stanley *et al.* 1996), distinct subgroups have been observed, with clear evidence for stock differentiation among different oceanic basins. For example, Cronin *et al.* (1994) used mitochondrial (mt)DNA restriction fragment length polymorphism (RFLP) analysis to examine population genetic structuring and phylogenetic divergence between the two subspecies of walruses: Atlantic walruses (*Odobenus rosmarus rosmarus*) and Pacific walruses (*O. r. divergens*). Each subspecies has distinct mtDNA haplotypes and sequence divergence estimates of 1.0%–1.6% place the time since divergence at between 500 000–785 000 years ago (using a rate of 2% per million years; Brown *et al.* 1979). There was evidence of subgrouping within the Atlantic walrus, and the authors suggested that mtDNA could be useful for walrus stock identification.

As a follow up to the Cronin *et al.* (1994) study, Andersen *et al.* (1998) confirmed the distinct subgrouping of mtDNA haplotypes of *O. r. rosmarus*, whereby individuals from Svalbard, Franz-Joseph Land, and E Greenland clustered together and were distinct from northwestern Greenland stocks. The former group may have been derived from a common ancestral population that persisted south of the ice cap approximately 30 000 years ago. A further subdivision into three groups (NW Greenland, E Greenland, Svalbard/Franz-Joseph Land) was observed when the authors examined microsatellite variation among these populations.

Similarly, Brown-Gladden *et al.* (1997) detected distinct mtDNA lineages of the beluga whale, *Delphinapterus leucas*, in arctic waters of North America. Two distinct lineages consisting of a western/central arctic clade and an eastern Hudson Bay–St. Lawrence clade were detected, and appear to have diverged from a common ancestor very recently (12 000–8 000 years ago). Further, the authors suggested that high philopatry in this species may help explain this differentiation.

In a related cetacean species, the narwhal (*Monodon monoceros*), Palsbøll *et al.* (1997) examined mtDNA control region sequence variation in populations from the north-west Atlantic, and found extremely low nucleotide diversity (0.0017 — one of the lowest ever recorded for cetaceans), with low average pair-wise genetic distances, suggesting recent (i.e., past several tens of thousands of years) expansion from a small bottlenecked population. Despite the low levels of genetic variation, they still found frequency differences among the most common haplotypes between areas. These data suggest some site philopatry, with the possibility of mixing of pods with different haplotypic compositions in a single breeding ground.

Stanley *et al.* (1996) examined mtDNA sequence variation in yet another marine mammal example, the harbor seal *Phoca vitulina*. They determined that Atlantic stocks were distinct from those in the Pacific (i.e. divergence time estimates in the early Pleistocene 2.2–1.7 million years ago). In addition, west coast and east coast stocks in each of these ocean basins also were distinct, with intra-oceanic divergence time estimates ranging from 540 000–340 000 years ago. The authors postulated that the ancient isolation of Atlantic and Pacific stocks was due to arctic sea ice serving as a barrier to dispersal among basins, which matches up quite nicely with paleoglaciological evidence related to the opening of the Bering Strait, thus permitting colonization of the Arctic Ocean from a Pacific refugium.

Among arctic marine mammals that rely on both terrestrial and marine systems, the best-studied example to date is that of the polar bear, *Ursus maritimus* (Paetkau *et al.* 1999). Using a suite of 16 highly variable microsatellite loci, Paetkau *et al.* (1999) found no large genetic discontinuities that would suggest significant periods of isolation among *U. maritimus* populations, circumarctically. However, they did detect some population differentiation and discontinuities among a number of populations in the Canadian arctic. So, despite the ability of polar bears to move/range long distances (thousands of kilometers), relative rates of gene flow were still insufficient to eliminate (totally) population-level differentiation. In an earlier study, Shields and Kocher (1991) used mtDNA cytochrome *b* and control region sequences to estimate an average sequence divergence of 0.37% among Alaskan polar bears ($N = 8$). Based on a substitution rate of 2.0% per million years for primates (Brown *et al.* 1979), the net divergence time among these Alaskan polar bears was estimated at approximately 185 000 years ago.

A final marine example comes from a quite different organism, the red alga, *Phycodrys rubens* (van Oppen *et al.* 1995). van Oppen *et al.* (1995) examined ribosomal (r)DNA internal transcribed spacer (ITS) sequence variation among Atlantic and Pacific strains, and concluded that multiple invasions of the north Atlantic from Pacific stocks was facilitated by openings in the Bering Strait. Further, they estimated that the Pacific lineage and the European lineage (i.e. NE Atlantic lineage) diverged from a common ancestor in either the Pliocene or early Pleistocene (5.3–2.1 million years ago). In addition, they also concluded that isolated and divergent lineages of this alga exist along the European coast, which could represent the remnants of glacial refugial populations. Finally, they detected evidence of a recent long-distance trans-Atlantic (anthropogenic?) transport of lineages from Europe to the Canadian Atlantic provinces (i.e. Newfoundland).

Birds

As mentioned above, the vagility of organisms may be counter-balanced by specific behavioral mechanisms such as site philopatry. Quinn (1992) examined mtDNA control region sequence variation in the lesser snow goose, *Chen caerulescens caerulescens*, in arctic North America. He uncovered the presence of two distinct clades, one existing in eastern Beringia (i.e. Alaska), the other found in the western–central Canadian arctic. He observed that the Beringian clade exhibited higher mtDNA genetic diversity than the Canadian clade, and he estimated the time since divergence of these two clades at approximately 350 000 years. He also detected two distinct subclades within the Canadian lineage, and estimated divergence time at approximately 110 000 years ago.

In a second avian example, Wenink *et al.* (1993) surveyed mtDNA control region sequence variation in the long-distance migratory shorebird, the dunlin (*Calidris alpina*). This species exhibits a circumarctic distribution and the authors were able to detect at least five distinct haplotype groups (Alaska, W Coast North America, Gulf of Mexico, W Europe, Taymyr Peninsula in Siberia). Evidence suggests that these lineages survived in distinct glacial refugia, show limited gene flow, and high philopatry. Divergence time estimates ranged from 440 000 years (i.e. Gulf of Mexico group compared with all others), to 350 000 years (W Europe group compared with Taymr and Alaska groups), to 90 000 years ago (W Coast of N.A. compared with Alaska).

Further, Holder *et al.* (1999) examined phylogeography of the rock ptarmigan, *Lagopus mutus,* one of only a few bird species that spend their entire life cycle in the arctic tundra. Using mtDNA and nuclear (nuc)DNA markers, Holder *et al.* (1999) determined that previously recognized morphologically distinct subspecies were also clearly differentiated genetically into distinct refugial lineages, most of which diverged from each other prior to the last glacial maximum (range of divergence times:135 000 to 11 000 years ago). Their data support the notion that isolated populations of arctic organisms diverged in multiple refugia during the Wisconsinian glaciation and that present geographic distributions reflect recolonization patterns from these multiple refugia.

Terrestrial mammals

The best-studied examples of the phylogeography of arctic terrestrial mammals are those of Fedorov (1999) and Fedorov *et al.* (1999a, 1999b), who examined the distributions of mtDNA haplotypes in true lemmings, *Lemmus* (Fedorov 1999, Fedorov *et al.* 1999a) and the collared lemming, *Dicrostonyx* (Fedorov 1999, Fedorov *et al.* 1999b, Fedorov & Goropashnaya 1999). Fedorov *et al.* (1999a) screened populations of *Lemmus* sp. from across northern Eurasia for variation in mtDNA RFLPs and mtDNA cytochrome b sequence variation and uncovered the presence of three distinct lineages (west, central, east). Interestingly, the Kolyma River delta in eastern Siberia serves as a pronounced geographic barrier between the central and eastern lineages (divergence time estimates of approximately 2 million years), while the Lena River to the west serves as a divide between the central and western lineages (divergence time estimated at 115 000–10 000 years ago). In addition, the authors were unable to detect any significant differences in levels of genetic variation between non-glaciated and formerly glaciated regions, in contrast with the results obtained for other organisms (e.g. *Daphnia*, Weider *et al.* 1999a, 1999b, *see* below).

Phylogeography of the collared lemming, *Dicrostonyx* (Fedorov *et al.* 1999b, Fedorov & Goropashnaya 1999) was also examined using mtDNA RFLPs, DNA sequencing, and karyotyping of different chromosomal races across its arctic range. Fedorov *et al.* (1999b) found the main split in mtDNA phylogeny at the Bering Strait, which also corresponds with the main chromosomal division between the Beringian and the Eurasian karyotype groups. This split between these Palearctic and Nearctic lineages was estimated to have occurred approximately 1 million years ago, during the mid-Pleistocene. They detected five distinct phylogenetic groups, most of which exhibited low nucleotide and haplotype diversities, suggesting that these populations experienced severe bottlenecks during the recent past (possibly during the Holocene). In addition, there was good congruence between mtDNA haplotype group and chromosomal race, with 69% of the total mtDNA variation allocated to different karyotypic races.

Likewise, Ehrich *et al.* (2000) using mtDNA sequence data detected two phylogeographic groups of the North American collared lemming, *Dicrostonyx groenlandicus*, which showed limited divergence across the MacKenzie River delta of the Northwest Territories, Canada. Their data suggest separation of these two clades into more than one glacial refuge during the late Pleistocene (100 000 years ago). Further, they found no significant differences in levels of genetic variation between formerly-glaciated and ice-free regions, and their data provide strong evidence for the existence of population bottlenecks, most likely due to range contraction during the Holocene, thus supporting the earlier results of Fedorov *et al.* (1999b).

Fedorov and Goropashnaya (1999) examined mtDNA cytochrome *b* sequence variation in *Dicrostonyx* sp., circumarctically, and concluded that four species exist in the genus: *D. torquatus* is restricted to Eurasia, while three distinct species (*D. groenlandicus, D. hudsonius, D. richardsoni*) are found across the Nearctic. Interspecific divergence estimates suggest that radiation took place during the Pleistocene (i.e. divergence time between *D. torquatus* and *D. groenlandicus* estimated at 500 000 years ago), indicating that indeed speciation events can and do occur within the time-frame of the mid-late Pleistocene, a result which appears to be somewhat at odds with other arctic vertebrate fauna (i.e. North American passerine songbirds, Klicka & Zink 1997). Further, Fedorov and Goropashnaya (1999) found evidence to support Ehrich *et al.*'s (2000) claim that *D. groenlandicus* is divided into two clades with limited divergence across the MacKenzie River delta dating back to the late Pleistocene (approximately 100 000 years ago). Finally, their data support the notion that the Asian parts of Beringia served as a refugial area for the tundra specialist, *D. torquatus*, during one of the late Pleistocene interglacials.

In a more restricted study of the wood lemming, *Myopus schisticolor*, in Scandinavia, Fedorov *et al.* (1996) detected very low levels of mtDNA diversity in Norwegian and Swedish populations, with much higher values found for Finland and western Siberia. These low values are most likely the result of founder effects. Further, their results provide strong evidence that postglacial colonization (10 000–8 000 years ago) of Norway and Sweden was primarily from a northeasterly (western Siberia) direction.

A final terrestrial mammal example involves the work of Conroy and Cook (2000), who used mtDNA sequencing data to examine phylogenetic relationships and phylogeographic patterning in the long-tailed vole, *Microtus longicaudus*. These authors found that populations of this species from northwestern North America (including Alaska), underwent a strong northern postglacial expansion (mostly likely via multiple colonization pathways) following retreat of the Laurentide & Cordilleran ice sheets during the past 10 000–20 000 years. The authors observed close relationships among haplotypes in northern subclades due to recent (Holocene) colonization, with some genetic differentiation among subclades due to prolonged isolation dating back to the mid/late Pleistocene. Net divergence time of *M. longicaudus* from other *Microtus* species was estimated at approximately 920 000 years. Divergence of the main southern clade from all other clades was estimated at 340 000 years ago (during the Kansan glaciation), while the central clade diverged from the others at approximately 250 000 years ago. Finally, divergence among the NW coast and island clades was estimated to have occurred about 90 000 years ago.

Fishes

Bernatchez and Wilson (1998) presented an extensive comparative study of the influence of Pleistocene glaciations on levels of genetic diversity and phylogeographic patterning in 42 species of Holarctic fishes. They observed a clear difference in the phylogenetic signature of species found in formerly-glaciated regions versus unglaciated regions; in particular, they found much deeper intraspecific phylogenies among fishes from unglaciated regions versus formerly-glaciated regions. Furthermore, they detected a significant decrease in nucleotide diversity going from the temperate to the boreal and to the arctic zone.

Some specific examples that were reviewed by Bernatchez and Wilson (1998) included the work of Bernatchez and Dodson (1994), who examined mtDNA lineage differentiation among whitefishes (*Coregonus* sp.) using RFLPs. They detected distinct differences between Nearctic and Palearctic lineages, and determined that Beringia (i.e. trans-Bering Strait region) represents a zone of secondary contact between a Nearctic lineage, and one with a Eurasian origin. Also, this region harbors greater mtDNA variation, which could very well be a consequence of this secondary contact. Further, they were able to determine that Europe was colonized by two distinct groups of whitefish: a northern clade that stretches across the breadth of northern Europe and Eurasia into eastern Beringia (i.e. Alaska and the Yukon), and a central European lineage, that may have existed in refugial populations in the Alps during the Pleistocene. These two clades diverged from each other approximately 18 000 years ago.

A second example (Taylor & Dodson 1994) compared anadromous and freshwater populations of smelt, *Osmerus* sp., and detected trans-arctic faunal exchange of mtDNA haplotypes. A north Pacific–Arctic group clustered with a northwest Atlantic group, and was very distinct from a northeast Atlantic (European) clade (i.e. divergence time estimates between the N Pacific–Arctic clade and the European clade range from 2.5–2.0 million years ago). The authors interpret this phylogeographic structuring as indicating vicariance events (i.e. Bering Strait opening and closing) during the mid-Pliocene to early Pleistocene.

Finally, Wilson *et al.* (1996) examined mtDNA RFLP haplotypes in arctic charr, *Salvelinus alpinus*, from across northern and arctic North America. Three divergent lineages were detected, with the most divergent lineage (termed "Arctic") found from Alaska eastward to Labrador. The two other lineages, both Laurentian (i.e. northeastern North America) in origin, show somewhat distinct phylogeographic patterns, with one Laurentian lineage found across Quebec, New Brunswick, and New England, while a second Laurentian lineage colonized Labrador. The

Arctic lineage is highly differentiated from these two eastern North American lineages, as well as European haplotypes, and the authors estimate that it diverged from the others some time in the early to mid-Pleistocene (1.6–1.0 million years ago), while the two Laurentian lineages most likely diverged from each other during the Wisconsinian glaciation (90 000–60 000 years ago). These latter two lineages appear to have diverged from W European–Iceland lineages approximately 600 000–300 000 years ago.

Freshwater invertebrates

Most of the previous discussion has centered on fairly mobile organisms, many of which might be considered good long-distance dispersers. We will now focus our attention on some less vagile taxa. For example, Väinölä et al. (1994) examined the genetic structure of a glacial relict species, the opossum shrimp, *Mysis relicta*. Using allozymes, they determined that *M. relicta* actually represents a species complex, with at least four species present. One of the four was found to be unique to North America, with apparent post-glacial colonization from two separate (east and west) refugia. The other three "species" are found in Europe, two of which were extremely widespread, while the third was restricted to a single subarctic lake. The authors conclude that post-glacial colonization of Fennoscandian lakes was primarily from proglacial lakes east of the Scandinavian ice dome. Further, the authors provide evidence to suggest that the distribution patterns of the two widespread European "species" may be modulated by differences in ecophysiological tolerances to fluctuating environmental parameters such as salinity.

Terrestrial plants

We now look at results from studies of other passively-dispersed arctic organisms — terrestrial plants. There have been some recent studies (Abbott *et al.* 1995, Gabrielsen *et al.* 1997, Tollefsrud *et al.* 1998) using molecular markers that have focused on the notion of whether certain organisms (e.g. terrestrial plants) might have been able to survive within the arctic in localized glacial refugia (i.e the "nunatak" hypothesis; Dahl 1987) versus the opposing "tabula rasa" hypothesis (i.e. postglacial colonization of the arctic; Nordal 1987). Abbott *et al.* (1995) examined chloroplast (cp)DNA variation in two arctic plant species, *Silene acaulis* and the purple saxifrage, *Saxifraga oppositifolia* collected from Svalbard, Norway, Iceland, and Scotland, as well as allozyme variation in *S. acaulis* alone. Allozyme results from *S. acaulis* revealed that populations from the high arctic Svalbard archipelago contained high levels of genetic diversity and were genetically similar to populations from more southerly locales, with evidence of extensive gene flow between Svalbard and mainland Norway. They found very low cpDNA haplotype diversity (i.e. all populations contained a single identical haplotype with the exception of one population from mainland Norway, which contained a second haplotype).

In contrast, they found five different cpDNA haplotypes in *S. oppositifolia* spread across Svalbard, northern and southern Norway, and Scotland, with one of two populations on Svalbard containing all five haplotypes. Abbott *et al.* (1995) interpret these contrasting cpDNA results as suggesting that high arctic (Svalbard) populations of *S. acaulis* are most likely derived from post-glacial colonists which arrived from more southerly locations, while the *S. oppositifolia* results suggest that these high arctic populations may have been derived (in part) from ancient northern lineages which survived the last glacial cycle in high arctic refugia.

Gabrielsen *et al.* (1997) and Tollefsrud *et al.* (1998) reexamined molecular genetic diversity in *Saxifraga oppositifolia* and *S. cespitosa* (a closely-related congener) using random amplified polymorphic DNA (RAPDs) nuclear markers from populations from mainland Norway, Svalbard, and the high arctic Russian archipelago, Novaya Zemlya. Gabrielsen *et al.* (1997) found that there was an attenuation of intrapopulational RAPD variation in *S. oppositifolia* as one proceeded from southern Norway to northern Norway and further to Svalbard, suggesting greater inbreeding towards the north, possibly due to lower pollinator activity. Further analyses suggest that there is strong intermingling of genotypes among populations from the different regions, suggesting extensive gene flow among regions. Tollefsrud *et al.* (1998) found similar results for *S. cespitosa*, with both sets of authors concluding that these high arctic plants, particularly on Svalbard, did not necessarily survive in high arctic refugia, but are most likely post-glacial colonists, which happened to spread northward after the recession of the Weichselian glaciers. They conclude that the nunatak hypothesis is superfluous and is not needed to explain present day high arctic distributions of these (and possibly other) arctic plant species.

If evidence for the role of nunataks as refugia for arctic plant species (as well as other organisms) is wanting, as suggested above, there is evidence that post-glacial colonization of the arctic from multiple refugia either along the ice-sheet margins or from Beringia has occurred. Tremblay and Schoen (1999) used cpDNA RFLPs to examine the roles that glacial refugia and post-glacial colonizations have played in influencing the present-day phylogeography of the widespread, arctic perennial, *Dryas integrifolia*, across arctic North America. They found ample evidence that Beringia served as a primary refugium, while additional evidence points to a refuge in the high central Arctic of Canada (most likely in the Canadian arctic archipelago), as well as putative refugia to the southeast (i.e. New Jersey to Quebec) and east (i.e. Labrador coast, west Greenland) of the former ice-margin of the Laurentide ice-sheet.

Clonal species complexes

Vandel (1928, 1940) described the phenomenon of geographic parthenogenesis — the observation that one often sees a shift in breeding mode from predominately sexual reproduction at lower latitudes, to an increase in asexual reproduction (i.e. apomictic parthenogenesis) as one moves to higher latitudes. This phenomenon has been observed in numerous plant and invertebrate taxa in the arctic, and indeed, numerous arctic biota incorporate at least some means of asexual propagation into their life cycles. Given this shift in breeding mode, one would expect to see a concomitant attenuation in genetic (clonal) diversity as one moves into higher latitudes.

A recent series of papers (Colbourne *et al.* 1998, Weider *et al.* 1999a, 1999b) has provided an unprecedented circumarctic view of levels of genetic (clonal) diversity and phylogeography of members of the asexual freshwater microcrustacean *Daphnia pulex* species complex. Seven distinct clades distributed within two major groups (*tenebrosa* and *pulicaria*) have been detected within this complex (Colbourne *et al.* 1998), with clear differences in the distribution of lineages. The *tenebrosa* and *pulicaria* groups diverged sometime during the Pliocene (5.0–2.2 million years ago; Colbourne *et al.* 1998), while radiation within groups occurred during the Pleistocene. Combining the mtDNA sequencing results of Colbourne *et al.* (1998) with a widespread survey of mtDNA RFLP variation in this complex, Weider *et al.* (1999b) demonstrated that *pulicaria* group lineages were restricted primarily to the Nearctic, with some limited colonization of northern Fennoscandia. In contrast, *tenebrosa* group lineages were widespread across the circumarctic, with evidence of considerable intercontinental divergence between North American and Eurasian lineages. Strong evidence for the long-distance dispersal of certain lineages indicates that passively dispersed arctic organisms may be much more vagile than previously believed. Conservative estimates of clonal diversity in this asexual species complex (Hobæk & Weider 1999, Weider *et al.* 1999a), based on a suite of six allozyme loci, revealed that, on average, one finds 2.1 clones per population (i.e. pond habitat) within the *pulicaria* group, while clonal richness is nearly doubled (4.1 clones per population, on average) within the *tenebrosa* group, a result that might be partially explained by the sporadic presence of sexual reproduction in this group, in certain regions of the arctic (i.e. Beringia, Weider & Hobæk 1997). These levels of clonal richness/diversity are comparable with what is often found in temperate zone populations of obligately parthenogenetic *Daphnia* (Hebert *et al.* 1988). In a more limited (in scope) geographic study of clonal diversity in the eastern Canadian arctic, Weider *et al.* (1987) showed that pockets of high clonal diversity can occur in the arctic, with diversity values equal to or greater than temperate zone values. Subsequent work (Dufresne & Hebert 1997, Weider *et al*. 1999a, 1999b) has shown that high clonal diversity in these areas is at least partially the result of secondary contact between lineages from distinct glacial refugia.

However, secondary contact does not necessarily explain why one often sees high intrapopulational clonal diversity; the mechanisms are unclear, since there is no evidence for (cryptic) sexual reproduction in the vast majority of these populations. However, in a similar study of another aquatic invertebrate group, Little and Hebert (1997) showed that high clonal diversity in arctic populations of two asexual ostracods, *Prionocypris glacialis* and *Candona reticulata*, was common. Associated with obligate parthenogenesis is the prevalence of polyploid lineages, both in ostracods (Havel *et al.* 1990) and *Daphnia* (Beaton & Hebert 1988). Little and Hebert (1997) found evidence for autopolyploids in *P. glacialis*, and they speculate that genomic recombination associated with polyploidy in these arctic invertebrate taxa may play a role in generating at least local clonal diversity following the transition to obligate parthenogenesis.

In another study of a clonal organism, Bayer (1991) examined latitudinal shifts in clonal diversity within the apomictic plant, *Antennaria rosea.* He found that subarctic populations of *A. rosea* show relatively low amounts of clonal diversity, when compared with more temperate populations, and he found an overall negative correlation between levels of clonal diversity with latitude. He speculated that founder-effects, perhaps associated with glacial advances, have undoubtedly played a role in decreasing levels of clonal diversity at higher latitudes in this plant species.

Summary and conclusions

One of the goals of the Northern Dimensions symposium was to examine the factors and mechanisms influencing biodiversity of boreal and arctic ecosystems, and to arrive at a better understanding of what the "northern dimension" to biodiversity research really entails. We will argue that one essential aspect of northern biodiversity research is to account for how global climatic changes and glacial cycles have impacted the evolutionary paths of so many extant taxa. Molecular techniques have opened unprecedented possibilities to unveil detailed phylogenies. Arctic taxa are of particular significance in this context, since their evolutionary trajectories through the glacial cycles are very recent and can often be related to particular Quaternary events (e.g., the Bering land bridge, periglacial drainage systems) that formed barriers to dispersal for some taxa, while opening up dispersal routes for others. Thus, northern systems allow for uniquely detailed studies of "the ecological theatre and the evolutionary play". Some key phenomena are: (i) speciation by vicariance and hybridization; (ii) the roles of dispersal, founder effects, range expansions, and secondary contacts in structuring population genetics; (iii) the importance of life-cycle and breeding system optimizations as adaptations to environmental factors. These are phenomena of broad basic scientific and applied interest, and our understanding of their significance constitutes the basic rationale for biodiversity conservation worldwide.

Furthermore, it is clear from virtually all studies to date, that latitudinal shifts in species richness, as well as shifts in intraspecific genetic variation show an attenuation of richness/diversity as one proceeds from lower latitudes into boreal and arctic regions. This attenuation of diversity and complexity of communities and food webs towards the north may serve another useful purpose — it facilitates the tracking of ecosystem responses to environmental changes (i.e. "simpler" systems are easier to "track", Freckman & Virginia 1997). Thus, these northern systems could serve as "early warning" or "sentinel" systems of present-day global change.

Yet, another important component of northern systems is that the use of molecular markers in so many of the studies reviewed here, allows one to identify taxonomic and phylogenetic affiliations among taxa, as well as reconstruct post-glacial colonization scenarios by using the comparative approach to look for phylogeographic concordance of patterns among taxa. More specifically, these arctic (i.e. northern) systems allow us to critically evaluate some very important evolutionary hypotheses. For example, we can begin to test whether indeed the Pleistocene period in earth's history has been a major factor in promoting speciation events.

As mentioned in the introduction, a controversy has centered on whether the Late Pleistocene Origins (LPO) model, as outlined above and by Klicka and Zink (1997), really is a fundamentally sound model that accurately depicts the speciation process in Holarctic taxa. The three basic steps in this model, as outlined by Klicka and Zink (1997) are: (i) fragmentation of a widespread ancestral species into (glacial) refugia during periods of glacial advance; (ii) subsequent genetic divergence among small isolated populations, followed by; (iii) range expansion during interglacials. The LPO model incorporates two glacial cycles, one beginning approximately 100 000 years ago, and a second cycle dating back to approximately 250 000 years. As argued above by Avise and Walker (1998) and Avise *et al.* (1998), the whole speciation process is a protracted one, and we believe that many of the studies that we have presented in this review, more than adequately support this contention. In particular the work of Fedorov and Goropashnaya (1999) and Conroy and Cook (2000), have clearly shown that speciation events among small arctic terrestrial mammals such as the collared lemming, genus *Dicrostonyx*, and voles, genus *Microtus*, easily fall within the time-frame of the mid-Pleistocene (920 000–500 000 years ago). Additional evidence from the studies of Cronin *et al.* (1994) on subspecies divergence (785 000–500 000 years ago) among Atlantic (*Odobenus rosmarus rosmarus*) and Pacific (*O. r. divergens*) walruses, and the work of Holder *et al.* (1999) on subspecies divergence (135 000–11 000 years ago) among rock ptarmigan (*Lagopus mutus*), further support the notion that the mid- to late Pleistocene was a period of importance in facilitating the speciation process in Holarctic taxa. Interestingly, a recent study by Klicka *et al.* (1999) of mtDNA sequence divergence between the Timberline sparrow (*Spizella taverni*) and the Brewer's sparrow (*S. breweri*), provides evidence that these two subspecies/species are reproductively isolated from each other. Divergence time estimates indicate that these two subspecies/species have diverged within the past 40 000 years, thus providing the first empirical validation of the LPO model among passerine birds.

Likewise, many of these studies (e.g Wenink *et al.* 1993, Fedorov *et al.* 1999a, 1999b, Fedorov & Goropashnaya 1999, Holder *et al.* 1999, Conroy & Cook 2000, among others) have clearly shown that divergence of taxa in separate glacial refugia indeed has played a major role in the "protracted" speciation process (Avise & Walker 1998).

Clearly, most of the phylogeographic studies (*see* Appendix) fall into the category of "incomplete" speciation events among "phylogroups" (Avise & Walker 1998). Further, most of these studies would be classified as "phylogeographic category I" studies (i.e., "significant mtDNA phylogroups exist in the matrilineal gene tree, and these phylogroups display a strong geographic orientation", Avise & Walker 1998).

In addition, a number of these studies (e.g., smelt — Taylor & Dodson 1994, red alga — van Oppen *et al.* 1995, harbor seal — Stanley *et al.* 1996, beluga whale — Brown-Gladden *et al.* 1997) have shown that divergence time estimates among lineages, coincide quite well with known glaciological events (e.g., the opening and closing of the Bering Strait during the Pleistocene). This concordance of phylogeographic patterns observed in such disparate taxa, provides a powerful tool in trying to reconstruct past (i.e., Pleistocene) climatic impacts.

Yet, another facet of studying these northern systems involves the increasing use of molecular methods into studies of population ecology and systematics. We have the increasing ability to estimate the incidence of cryptic speciation in northern biota, as well as measure levels of genetic variation within taxa. As has been shown by a number of studies (e.g., Hobæk & Weider 1999), levels of genetic diversity in certain taxa (e.g., clonal diversity in the water flea, *Daphnia pulex*), when taken across the entire circumarctic range, may be exceptionally high.

Finally, we can pose the question: where should we focus our attention in these arctic (northern) systems? We believe that enough data support the conclusion that studying the biota that inhabit putative or known glacial refugia may prove fruitful, as voiced earlier by Taberlet (1998). In particular, there appears to be overwhelming evidence that Beringia and adjoining regions (i.e. western and central Siberia) should be the focus of more intense study due to higher biodiversity present in these regions (Quinn 1992, Bernatchez & Dodson 1994, Weider *et al.* 1999a, 1999b).

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Appendix. Summary of phylogeographic studies conducted on arctic fauna and flora. Divergence time estimates are in millions (MY) or thousands (KY) of years.

Taxon	Marker	Divergence Times	Reference
Marine Taxa			
Atlantic (*Odobenus rosmarus rosmarus*) and Pacific (*O. r. divergens*) walruses	mtDNA RFLPs	785–500 KY	Cronin *et al*. (1994)
Atlantic walrus (*O. r. rosmarus*)	mtDNA RFLPs & microsatellites	30 KY	Andersen *et al*. (1998)
Beluga whales (*Delphinapterus leucas*)	mtDNA seq. (control region)	12.0–8.0 KY	Brown-Gladden *et al.* (1997)
Narwhal (*Monodon monoceros*)	mtDNA seq. (control region)	30–10 KY	Palsbøll *et al.* (1997)
Harbor seal (*Phoca vitulina*)	mtDNA seq. (control region)	2.2–1.7 MY 540–340 KY (intra-oceanic stocks)	Stanley *et al.* (1996)
Polar bear (*Ursus maritimus*)	Microsatellites mtDNA seq.	185 KY (among Alaskan bears)	Paetkau *et al.* (1999) Shields & Kocher (1991)
Red alga (*Phycodrys rubens*)	rDNA ITS sequence	5.3–2.1 MY	van Oppen *et al.* (1995)
Terrestrial Plants			
Dryas integrifolia	Chloroplast (cp)DNA RFLPs		Tremblay & Schoen (1999)
Silene acaulis	Allozymes (cp)DNA		Abbott *et al.* (1995)
Purple saxifrage (*Saxifraga oppositifolia*)	cpDNA		Abbott *et al.* (1995)
Saxifraga oppositifolia	Random amplified DNA (RAPDs)		Gabrielsen *et al.* (1997)
Saxifraga cespitosa	RAPDs		Tollefsrud *et al.* (1998)

Continued

Appendix. Continued.

Taxon	Marker	Divergence Times	Reference
Birds			
Snow geese (*Chen caerulescens caerulescens*)	mtDNA seq. (control region)	350 KY (clades I & II) 110 KY (subclades of clade II)	Quinn (1992)
Dunlin (*Calidris alpina*)	mtDNA seq. (control region)	440 KY (between five groups) 350 KY (W. Europe vs Tamyr & Alaska) 90 KY (W. Coast N.A. vs Alaska)	Wenink *et al.* (1993)
Rock ptarmigan (*Lagopus mutus*)	mtDNA & nucDNA sequence variation	135–11 KY	Holder *et al.* (1999)
Terrestrial Mammals			
True lemming (*Lemmus* sp.)	mtDNA RFLPs and cytochrome b seq.	2 MY (central vs east) 115–10 KY (central vs west)	Fedorov *et al.* (1999a)
Collared lemming (*Dicrostonyx* sp.)	mtDNA RFLPs	1 MY	Fedorov *et al.* (1999b)
Collared lemming (*D. groenlandicus*)	mtDNA sequencing	100 KY	Ehrich *et al.* (2000)
Collared lemming (*Dicrostonyx* sp.)	mtDNA sequencing	500 KY	Federov & Goropashnaya (1999)
Wood lemming (*Myopus schisticolor*)	mtDNA RFLPs	10.0–8.0 KY	Fedorov *et al.* (1996)
Long-tailed vole (*Microtus longicaudas*)	mtDNA sequencing	920 MY (*M. longicaudas* vs other *Microtus* species) 340 KY (southern clade vs others) 250 KY (central clade vs others) 90 KY (N.W. clade vs island clade)	Conroy & Cook (2000)
Fishes			
Whitefishes (*Coregonus* sp.)	mtDNA RFLPs	18 KY (two European groups)	Bernatchez & Dodson (1994)
Smelt (*Osmerus* sp.)	mtDNA RFLPs cytochrome b seq.	2.5–2.0 MY (N. Pacific–Arctic vs European clade)	Taylor & Dodson (1994)
Arctic charr (*Salvelinus alpinus*)	mtDNA RFLPs	1.6–1.0 MY (Arctic vs eastern lineages) 600–300 KY (eastern vs W Europe–Iceland) 90–60 KY (two eastern lineages)	Wilson *et al.* (1996)
Freshwater Invertebrates			
Opossum shrimp (*Mysis relicta*)	Allozymes		Väinölä *et al.* (1994)
Water flea (*Daphnia pulex*)	mtDNA RFLPs & seq. allozymes	5.0–2.2 MY (between major groups) 2.2–10 KY (within groups)	Weider *et al.* (1999a, 1999b) Colbourne *et al.* (1998)