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GUEST
EDITORIAL



Eastward Ho: phylogeographical perspectives on colonization of hosts and parasites across the Beringian nexus

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ABSTRACT

The response of Arctic organisms and their parasites to dramatic fluctuations in climate during the Pleistocene has direct implications for predicting the impact of current climate change in the North. An increasing number of phylogeographical studies in the Arctic have laid a framework for testing hypotheses concerning the impact of shifting environmental conditions on transcontinental movement. We review 35 phylogeographical studies of trans-Beringian terrestrial and freshwater taxa, both hosts and parasites, to identify generalized patterns regarding the number, direction and timing of trans-continental colonizations. We found that colonization across Beringia was primarily from Asia to North America, with many events occurring in the Quaternary period. The 35 molecular studies of trans-Beringian organisms we examined focused primarily on the role of glacial cycles and refugia in promoting diversification. We address the value of establishing testable hypotheses related to high-latitude biogeography. We then discuss future prospects in Beringia related to coalescent theory, palaeoecology, ancient DNA and synthetic studies of arctic host–parasite assemblages highlighting their cryptic diversity, biogeography and response to climate variation.

Keywords

Arctic, Beringia, biogeography, host–parasite relationships, phylogenetics, phylogeography, refugia.

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INTRODUCTION

The Arctic is one of the best examples of a long-term natural experiment related to the effects of global temperature change in structuring biodiversity (ACIA, 2004). Dramatic fluctuations in climate during the Pleistocene led to large ice sheets covering considerable expanses of the Arctic during glacial maxima (Andersen & Borns, 1994) and affecting large-scale movement of terrestrial organisms. Despite massive glacial advances at high latitudes, a large ice-free region extended from Far East Russia to Alaska and north-western Canada (Fig. 1). Called Beringia, this region is notable from a biogeographical perspective. First, as an ice-free region, Beringia was one of the largest northern refugia for terrestrial organisms and has been hypothesized to have played a critical part in the diversification of arctic taxa (Sher, 1999). Secondly, the Bering Land Bridge of central Beringia served as a filter for terrestrial organisms, allowing selective exchange of Nearctic and Palearctic biotas. We focus on the latter role and review a growing body of phylogeographical literature on Holarctic organisms and their parasites to identify molecular perspec-

tives on long-standing hypotheses related to exchange between Asia and North America during the Quaternary.

Phylogeography, at the intersection of the fields of population genetics and phylogenetics, promises to provide new opportunities to test hypotheses related to how diversity has been structured across these high-latitude landscapes (reviewed in Avise, 2000). One particularly powerful model that spans this intersection is coalescent theory (reviewed in Hudson, 1990; Wakeley, 2006), an approach that is already providing new perspectives on more generalized hypotheses of Beringian biogeography (Table 1). Coalescent theory has allowed researchers to estimate specific evolutionary and biogeographical parameters not previously obtainable under classical population genetics models, including migration and population growth (Kuhner *et al.*, 1998; Kuhner, 2006). These and other genetic parameters (e.g. nucleotide diversity) estimated across extant populations can provide novel views of historical and present-day biotic movement. For example, we might predict that relatively high genetic diversity will occur in populations that have persisted in refugia, while lower diversity will be found in recently expanding populations (Hewitt, 1996,

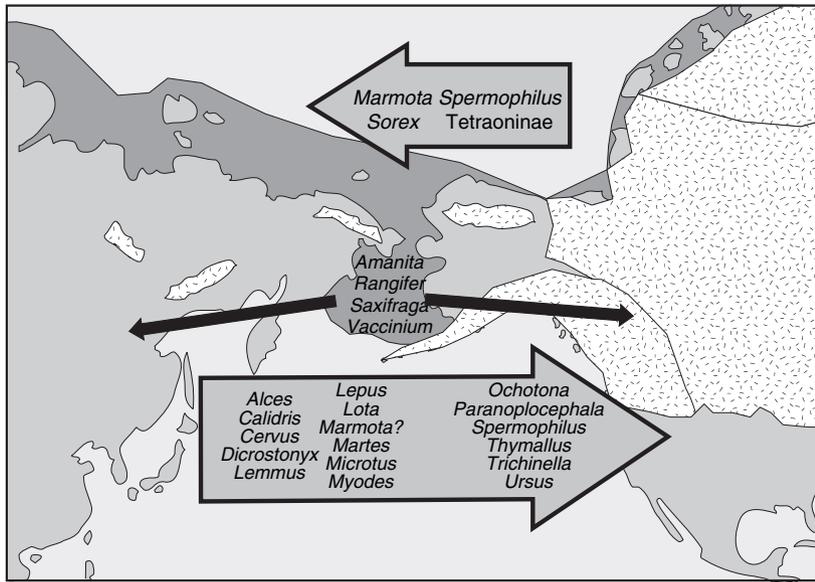


Figure 1 Beringia during the Last Glacial Maximum. Darker areas indicate sea floor exposed during the glacial maximum. Genera are listed next to the arrow indicating their movement across, or from, the Beringian refugium. The extent of ice sheets and glaciers is taken from Andersen & Borns (1994), Brigham-Grette (2001), Clark & Mix (2002), Dyke *et al.* (2002), Miller *et al.* (2002), the PALE Beringian Working Group (1999) and Siegert *et al.* (2001).

Table 1 Beringian hypotheses, predictions, expectations, and implications.

Beringia has been noted for its importance as a:

(1) Refugium (e.g. Hultén, 1937)		
Centre of endemism (Sher, 1999)		<i>Prediction:</i> Beringia has higher endemism than surrounding regions that were ice-covered during glacial maxima <i>Expected result:</i> organisms will show endemic clades within Beringia
(2) Corridor for transcontinental exchange (colonization)		
Predominant direction of colonization		<i>Prediction:</i> primarily eastward (Hopkins <i>et al.</i> , 1982) due to ice sheet coverage <i>Expectation:</i> phylogenies with ancestral Eurasian clades, recent North American clades <i>Implication:</i> historical community assemblage and faunal evolution
Number of colonization events		<i>Prediction 1:</i> no exchange: Beringia as filter preventing exchange of some taxa (Hopkins <i>et al.</i> , 1982) <i>Implication:</i> Beringian habitat unsuitable (Guthrie, 2003) <i>Prediction 2:</i> single colonization <i>Expectation:</i> single clade endemic to opposite side of Bering Strait from ancestral clade <i>Prediction 3:</i> multiple colonizations <i>Expectation:</i> multiple clades distributed on opposite sides of Bering Strait <i>Implications:</i> epidemiology (e.g. Yates <i>et al.</i> , 2002), co-evolution (Hoberg <i>et al.</i> , 2003; Hoberg, 2005)
Timing of colonization		<i>Prediction 1:</i> pre-Pliocene colonization most important (Kurtén & Anderson, 1980; beyond bounds of most phylogeographical studies) <i>Prediction 2:</i> Pliocene, Pleistocene colonization more important (e.g. Weir & Schluter, 2004) <i>Expectation:</i> molecular clock indicates Old World–New World divergence is specific to Pliocene or Pleistocene <i>Implication:</i> Quaternary glaciations important in current biotic distribution and diversity <i>Are colonization events temporally concordant across taxa or independent?</i> <i>Implication:</i> Community assemblage and dynamics

1999). Thus, we can use these measures to explore colonization dynamics for particular species. Genetic diversity, however, may simply reflect differences in extant population sizes. Fortunately, coalescent theory allows estimation of historical changes in population size, such as those expected in association with colonizations from refugia. Unlike populations that show restricted variation simply because of small population size, recently expanded populations should not show equilib-

rium between mutation and drift. These contrasting expectations can be used to examine the directionality of colonization events, as recently colonizing populations should have a genetic signal of expansion from one or more population genetics tests, for example significantly negative Fu's F_S and Tajima's D values (Lessa *et al.*, 2003; Fig. 2).

We further propose that an integrative model linking phylogeography and parasitology can provide novel interpretations

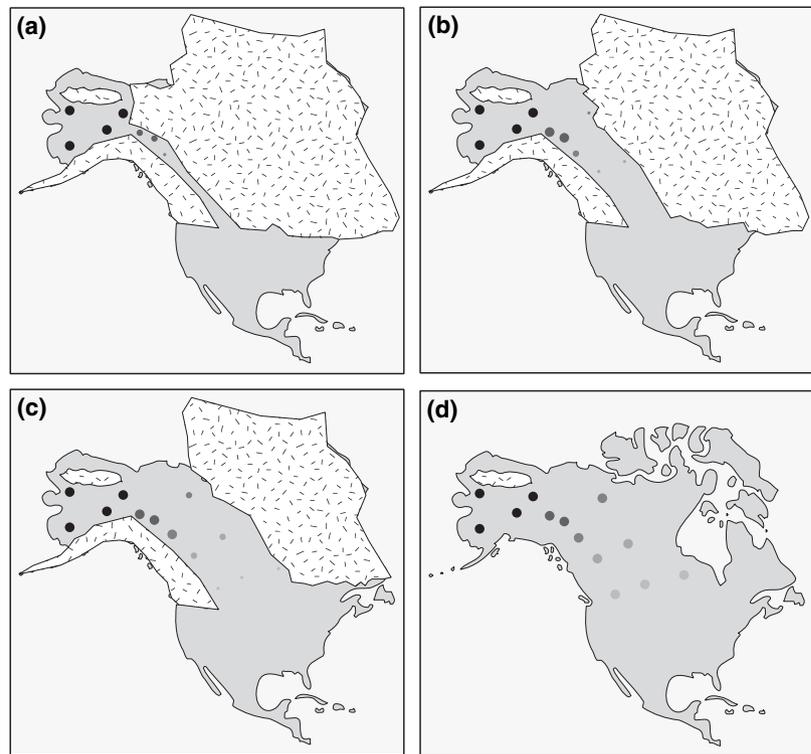


Figure 2 Theoretical schematic of post-glacial population growth into northern North America. (a, b) Successive colonization bouts with few population founders result in reduced genetic variation (lighter shading) compared to source populations (darker shading). (c, d) As deglaciation and colonization continues, colonized populations grow in size (larger circle diameter), but maintain low genetic diversity relative to source populations.

for the faunal history of Beringia on varying temporal and spatial scales (Hoberg, 2005). In Beringia, research emphasizing parasite and host biology, historical biogeography, and co-evolution has a long tradition linked to a foundation of survey and inventory extending over the past 50–60 years in terrestrial (e.g. Rausch, 1952, 1957, 1994) and marine environments (Hoberg, 1992, 1995; Hoberg & Adams, 2000). Parasitology has figured prominently in the articulation of core hypotheses for the history and structure of the Beringian and Holarctic biotas (Rausch, 1994; Hoberg *et al.*, 1999, 2003; Haukisalmi *et al.*, 2001, 2002; Hoberg, 2005). Although high-latitude systems have been characterized by relatively minimal diversity, recent collections have served to dispel this misconception. Geographically extensive and site-intensive surveys, as well as molecular-based analyses, are documenting previously unrecognized cryptic diversity, dramatically changing our perspective about species richness in arctic and subarctic parasite faunas (Hoberg *et al.*, 1995, 1999; Wickström *et al.*, 2003; Haukisalmi *et al.*, 2006). Concurrently this process of integrated survey and discovery contributes to substantial insights about ecological and evolutionary mechanisms that structure faunal assemblages (Hoberg *et al.*, 2003; Cook *et al.*, 2005).

We review arctic phylogeographical studies of free-living and parasitic organisms with trans-Beringian distributions, conducted over various spatial and taxonomic scales. Our aim is to summarize and evaluate the new molecular views on the direction, number and timing of events of geographical colonization across Beringia, and highlight promising prospects for further study of the biotic exchange at high

latitudes, with a particular focus on complex host–parasite systems.

MATERIALS AND METHODS

Review of Beringian phylogeography

We examined 35 studies, collating the number, direction and timing of trans-continental colonizations as inferred in the original publications (Table 2). These include 20 investigations of mammals (18 taxa), four of freshwater fishes (four taxa), four of birds (three taxa), three of cestode parasites (two taxa), two of flowering plants (two taxa), one of nematode parasites (one taxon) and one of fungi (one taxon). We divided the taxa studied into two categories: 15 of the groups include phylogenetic data for multiple closely related species within a single genus, and one of species within a subfamily (Interspecific studies; Table 2); 16 additional taxa were examined at or within the species level (Intraspecific studies; Table 2). We did not consider phylogenetic results at higher taxonomic levels. All studies include taxa with trans-Beringian distributions.

RESULTS

Beringian phylogeography

Of the 15 interspecific phylogenetic studies, five taxa were inferred to have one trans-Beringian colonization, nine had two or more colonizations and a single taxon (marmots) either had one or two colonization events (Table 2). The direction of

Table 2 Summary of findings for 31 trans-Beringian taxa, including number of trans-Beringian colonizations and direction and timing of colonization. Note that this summary is limited to taxa with trans-Beringian distributions.

Taxon examined	Trans-Beringian colonization results			References
	No.	Direction	Timing	
Interspecific studies				
True lemmings (<i>Lemmus</i> spp.)	1	E	EP	Fedorov <i>et al.</i> (2003)
Collared lemmings (<i>Dicrostonyx</i> spp.)	1	E	EP	Fedorov & Goropashnaya (1999)
<i>Paranoplocephala arctica</i> cestode complex	1	E	EP	Haukisalml <i>et al.</i> (2001), Wickström <i>et al.</i> (2003)
Martens (<i>Martes</i> spp.)	2	E	Early*, EP	Stone & Cook (2002)
Voles (<i>Microtus</i> spp.)	2	E	EP, LP	Conroy & Cook (2000)
<i>Paranoplocephala omphalodes</i> cestode complex	≥ 2	E	EP, LP	Haukisalml <i>et al.</i> (2004)
Red-backed voles (<i>Myodes</i> spp.)	2	E	EP, LP	Cook <i>et al.</i> (2004), Runck & Cook (2005)
Arctic hares (<i>Lepus</i> spp.)	≥ 2	E	Early*	Waltari <i>et al.</i> (2004), Waltari & Cook (2005)
Shrews – <i>Sorex cinereus</i> complex (<i>Sorex</i> spp.)	1	W	LP	Demboski & Cook (2003)
Ground squirrels (<i>Spermophilus</i> spp.)	≥ 2	E, W	Miocene, EP	Harrison <i>et al.</i> (2003)
Pikas (<i>Ochotona</i> spp.)	1	E	Pliocene	Yu <i>et al.</i> (2000)
Grouse (subfamily Tetraoninae)	3	W	Miocene, EP	Lucchini <i>et al.</i> (2001), Drovetski (2003)
<i>Trichinella</i> nematodes	2	E	Early*, LP	Zarlenga <i>et al.</i> (2006)
Whitefish (<i>Coregonus</i> spp.)	2	1st?, 2nd W	Early*, LP	Bernatchez & Dodson (1994)
Marmots (<i>Marmota</i> spp.)	1–2	1st W, if 2nd, E	Pliocene	Steppan <i>et al.</i> (1999)
Intraspecific studies				
Moose (<i>Alces alces</i>)	1	E	LP	Hundertmark <i>et al.</i> (2001)
American marten (<i>Martes americana</i>)	1	E	EP	Stone <i>et al.</i> (2002)
Dunlin (<i>Calidris alpina</i>)	1	E	LP	Wenink <i>et al.</i> (1996)
Rock ptarmigan (<i>Lagopus mutus</i>)	1	Unclear	NA	Holder <i>et al.</i> (1999)
Brown bear (<i>Ursus arctos</i>)	1	E	Miocene	Waits <i>et al.</i> (1999)
Purple saxifrage (<i>Saxifraga oppositifolia</i>)	**	**	NA	Abbott <i>et al.</i> (2000)
Tundra/root vole (<i>Microtus oeconomus</i>)	1	E	EP	Galbreath <i>et al.</i> (2004)
Northern red-backed vole (<i>Myodes rutilus</i>)	1	E	LP	Cook <i>et al.</i> (2004)
Caribou (<i>Rangifer tarandus</i>)	**	**	LP	Gravlund <i>et al.</i> (1998), Flagstad & Røed (2003)
Arctic ground squirrel (<i>Spermophilus parryii</i>)	1	Unclear	NA	Eddingsaas (2003)
Wapiti/red deer (<i>Cervus elaphus</i>)	1	E	LP	Mahmut <i>et al.</i> (2002)
Arctic char (<i>Salvelinus alpinus</i>)	1	Unclear	NA	Brunner <i>et al.</i> (2001)
Burbot (<i>Lota lota</i>)	1	E	NA	Van Houdt <i>et al.</i> (2005)
Arctic grayling (<i>Thymallus arcticus</i>)	≥ 2	E	Pliocene, LP	Stamford & Taylor (2004)
Fly agaric (<i>Amanita muscaria</i>)	**	**	Miocene	Geml <i>et al.</i> (2006)
Bog bilberry (<i>Vaccinium uliginosum</i>)	**	**	EP	Alsos <i>et al.</i> (2005)

For direction of colonization, E refers to eastward (Asia to North America) colonization across Beringia and W refers to westward (North America to Asia) colonization.

For timing of colonization LP refers to late Pleistocene and EP to early or mid-Pleistocene.

*Mid-Pleistocene or earlier.

**Colonization both west and east from Beringia.

NA, not applicable.

movement across Beringia was overwhelmingly eastward into North America (11 or possibly 12 taxa), and equivocal due to the lack of resolution in one study (Fig. 1 & Table 2). Three taxa moved westward into Asia, one colonized in both directions and in one taxon the direction was equivocal in the first colonization and westward in the second. Of 23 colonization events, four were placed in the Miocene or Pliocene, 13 were dated to the mid-Pleistocene (120,000 yr BP) or earlier, and six were late Pleistocene (Table 2).

Of the 16 intraspecific taxa, 11 were interpreted to show a single colonization event; of these 11 taxa, eight were eastward into North America and three had equivocal directionality

(Fig. 1 & Table 2). A single intraspecific taxon (the arctic grayling) showed evidence for multiple colonizations, all eastward. Of 12 timed movements, three were dated to the Miocene or Pliocene, three to the early or mid-Pleistocene and six were attributed to the late Pleistocene or Holocene (Table 2).

DISCUSSION

Over the past 15 years, dramatic new insights concerning spatial and temporal structure of diversity have emerged from the field of phylogeography (Avisé, 2000; Hewitt, 2004a).

Investigations of high-latitude faunas using molecular markers are now exploring the dynamic environmental history of the late Neogene, particularly the Quaternary. Boreal phylogeographical studies often rely upon classical works of arctic biogeography (e.g. Rausch, 1952, 1953, 1994; Rand, 1954; MacPherson, 1965) to develop and test hypotheses related to the origin of this Beringian biota. Broader conceptual issues include: (1) the importance of Pleistocene glacial cycles in promoting diversification and speciation in arctic taxa; (2) the role of particular refugia (notably Beringia) in promoting diversification and speciation in arctic taxa; and (3) co-evolutionary processes including co-speciation and host colonization among arctic organisms and their parasites (Hoberg *et al.*, 2003). Research in other disciplines is also building upon classical arctic biogeography using technological advances, for example the use of stable isotope analysis for reconstructing historical ecosystems (e.g. Finney *et al.*, 2000, 2002).

Beringian molecular biogeography

Molecular studies that span the Beringian region have focused primarily on either phylogenies of congeners (interspecific scale) or within one species (intraspecific scale). Examining trans-Beringian colonization at these two scales requires somewhat different approaches (Table 3). At the interspecific scale, analyses are primarily tree-based, focusing on gene phylogenies that are presumably sufficiently resolved to allow identification of migratory events. At this level, tree topology generally provides a clear picture of the number and direction of trans-Beringian colonizations. Some approaches to interspecific biogeographical inference include: (1) vicariance biogeography through the use of area cladograms and multiple taxon trees, first assuming vicariance and then allowing for dispersal as *ad hoc* hypotheses to explain discordance across taxa; (2) parsimony reconstruction of changes in distribution

by treating areas as character states that may be mapped and optimized onto a phylogeny; (3) examining tree topology and inferring colonization patterns; for example if a clade found in one continent is nested within a broader clade found in another continent, the former is postulated to have migrated into its current area. In these approaches, the choice of outgroup may be important in rooting and, consequently, in inference of directionality. In addition, gene trees will require further testing based on additional, independent loci to corroborate that they are not different from the true species tree (Edwards & Beerli, 2000). More difficult, however, is the issue of the precise timing of colonization events due to stochastic variation surrounding the application of a molecular clock to single gene analyses (Edwards & Beerli, 2000). Although absolute timing is problematic, relative timing of colonization events may be more feasible. Local clocks calibrated with external dates may also be used instead of a single, overall clock based on a presumed rate of evolution for the genes under examination. We use broad geological periods such as Miocene and Late Pleistocene (following the peak of Eemian/Sangamon interglacial) to provide a rough summary of colonization dates (Table 2).

Phylogeographical studies primarily focus on the intraspecific scale; a scale at which phylogenetic trees are often poorly resolved and hence directionality and number of colonization events may be somewhat obscured. New analytical techniques, however, can be used to extract information about the history of these populations, including signals of population expansion (Lessa *et al.*, 2003). Population genetic analyses that use a coalescent approach (Kingman, 2000) allow for estimates of population-level parameters, such as migration and population growth or decline, from molecular data. Consequently, phylogeographers can examine populations within species to estimate historical population size and migration rates, which are often critical parameters for testing phylogeographical

Table 3 Molecular approaches for analysis of timing and direction of trans-Beringian colonization events.

Interspecific	
Direction	Examine geographical and phylogenetic location of taxa within phylogeny (e.g. colonizing monophyletic lineage nested within paraphyletic source)
Timing	If appropriate, use molecular clock (overall or local, constrained by fossil or other date estimates, e.g. Zarlenga <i>et al.</i> , 2006) Improve estimates using multiple loci Look for concordance using multiple independent taxa (e.g. Brooks & McLennan, 1993; Brooks & McLennan, 2002)
Intraspecific	
Direction	If resolution is sufficient, use geographical location and topology of phylogeny Use coalescent-based analyses (e.g. estimates of genetic diversity, evidence of population expansion) to compare putative source/colonizing populations (e.g. on separate sides of the Bering Strait; Fedorov <i>et al.</i> , 2003; Waltari & Cook, 2005) Check for evidence of migration/local drift equilibrium (e.g. isolation by distance-type pattern) or for signals of geographical expansion (e.g. lack of isolation by distance-type pattern, expected patterns for different colonization scenarios) Use coalescent-based analyses with explicit geographical framework (e.g. explicit models that include subdivision, migration and demographic change)
Timing	Estimate relevant parameters (e.g. population separation/expansion) to absolute dates If appropriate and resolution is sufficient, use molecular clock to translate relative estimates of age of events

hypotheses (Kuhner, 2006). Because of the inherent variance of intraspecific gene genealogies, such that any particular genealogy is but one realization of a broad array of possibilities, a direct interpretation of the gene tree may be misleading. Coalescent methods are useful because they model genealogical processes and their intrinsic variance. Two major sources of variance are variance in the gene genealogy (i.e. topology and time intervals between coalescent events) and variance in the mutational process that occurs along the genealogical branches (Wakeley, 2006). Other methods such as the mismatch distribution (Rogers & Harpending, 1992) may also be used to detect population expansion. Furthermore, novel methods for testing explicit hypotheses that incorporate geography now exist. Nested clade analysis (Templeton, 1998) uses parsimony networks and geographical distances to infer biogeographical patterns, although there are pitfalls in the interpretation of nested clade analysis (Knowles & Maddison, 2002; but see Templeton, 2004). More recent simulation-based approaches using the Mesquite software package (Maddison & Maddison, 2006) are also being used to address some of these concerns (e.g. Carstens *et al.*, 2005). In addition, coalescent-based models for subdivided populations and demographic change are also being developed (Wakeley, 2004a,b).

Number, direction and timing of trans-Beringian colonizations

Biotic exchange between eastern Asia and western North America has perhaps received less attention than other intercontinental connections (e.g. the Great American Interchange; Stehli & Webb, 1985); however, a diverse set of biogeographers, palaeontologists and palaeoecologists have investigated the impact of the dynamic geological history of Beringia in structuring biotic diversity (for summaries see Pielou, 1991; Rausch, 1994; Hoberg, 1995, 2005; Weider & Hobæk, 2000; Hewitt, 2004b). Beringia provides a unique arena where the recurrence of geographical colonization, biotic expansion and isolation has led to cyclical faunal interchange over the past 2–3 Myr (Hoberg, 2005). Molecular analyses build upon studies based on fossils and distributions of hosts and parasites to provide another view of colonization dynamics.

Across the studies we reviewed, 10 taxa are thought to have experienced two or more bouts of trans-Beringian colonization (Table 2). Not surprisingly, nine of these ten studies are interspecific comparisons and thus reflect deeper history. In four of the ten studies, more than two colonizations were possible, but not clearly defined. Four intraspecific studies found bi-directional colonization out of Beringia (purple saxifrage, bog bilberry, fly agaric mushroom and caribou; Fig. 1). The Bering Land Bridge was not a feasible colonization route for many temperate organisms, but these results support the idea that the long history of connectivity between Eurasia and North America (Sher, 1999) has led to multiple colonizations in some organisms.

Palaeontological evidence strongly favours eastward movement from Eurasia to North America (Kurtén, 1963, 1966;

Hopkins, 1967; Hopkins *et al.*, 1982). Molecular perspectives developed to date for a variety of high-latitude organisms are consistent with this record (Table 2). Asymmetry is probably due to differences in the extent of ice sheets in Eurasia and North America. During glacial maxima, the Cordilleran and Laurentide ice sheets sealed Beringia from the remainder of North America, but patchy glaciation in eastern Siberia created a 'leaky' boundary between Central Asia and Beringia (Hoffmann, 1981; Rausch, 1994). Differences in the relative sizes of eastern and western Beringia at times of contact may also have resulted in differing population sizes and thus contributed to differential rates of migration and persistence. Biogeographical theory would also predict that larger areas should be able to retain more species, thus turning these areas into potential sources of more emigration events.

The studies examined were conducted at interspecific and intraspecific scales. Of the estimated colonizations at the interspecific scale, four were placed prior to the Pleistocene, 13 in the early or mid-Pleistocene and six in the late Pleistocene. At the intraspecific scale, six of twelve colonizations were placed in the late Pleistocene or Holocene. Because phylogeographical studies are focused on closely related species or within single species, our review emphasizes colonization dynamics within the late Neogene (last 2 Myr). Intercontinental exchange across the land bridge connecting Asia and North America, however, was possible for much of the Tertiary (Hopkins *et al.*, 1982), so phylogenetic analyses at deeper taxonomic levels are needed to test the generality of our conclusions relating to the late Neogene (e.g. Johnson *et al.*, 2006).

Future prospects

What new avenues are available for stimulating insight into the biogeographical history of Beringia?

Establish testable hypotheses

Palaeontological evidence, parasite data and current taxon distributions have produced a large set of hypotheses (Table 1). These take the form of possible scenarios for the retention or evolution of diversity (especially during glacial phases) and subsequent colonization of newly developed habitat or across formerly precluded areas. On the other hand, intercontinental connections are hypothesized to have been stronger during glacial phases. Phylogeographical hypotheses have been tested in other regions (e.g. Lessa *et al.*, 2003; Carstens *et al.*, 2005), and the rapid advancement in molecular-based analyses are providing new opportunities for testing existing hypotheses.

Timing and directionality of trans-Beringian colonization

As molecular phylogenetics matures, studies using multiple molecular markers are becoming increasingly common. This approach substantially reduces variance surrounding estimates

of colonization events. Additional fossil calibrations (e.g. Guthrie, 2003) are also refining our understanding of trans-Beringian exchange and may be used to constrain local molecular clocks.

Multiple independent markers will also improve estimates of directionality. As the number of loci used in phylogenetic reconstruction increases, estimated phylogenies are expected to converge on the true species tree (Edwards & Beerli, 2000; but see Degnan & Salter, 2005). A multi-marker approach also improves the ability of coalescent models to estimate historical demographic parameters such as population expansion, population structure and migration (Kuhner, 2006; Wakeley, 2006). These are key parameters that reflect colonization events across the Bering Land Bridge.

Characterize palaeoenvironments

Since the initial proposal of an ice-free region spanning Eurasia and North America (Hultén, 1937), several research programmes have aimed to reconstruct the ecology of Beringia during the Last Glacial Maximum. Two competing scenarios have emerged. Palaeontologists studying large mammals concluded that Beringia was a cold but arid 'mammoth steppe', supporting a diverse fauna of horses, bison and mammoths (Guthrie, 1990). Some palaeobotanical research supports this hypothesis, as high proportions of fossil pollen of sagebrush (*Artemisia*) and grasses have been documented for eastern Beringia (Anderson & Brubaker, 1994). However, other researchers have argued for the dominance of mesic tundra throughout the Pleistocene in Beringia, based on pollen cores from the Bering Strait (Elias *et al.*, 1996).

These views were synthesized into a theory that Beringia was primarily a cold and arid steppe, but with mesic lowlands located centrally. This mesic belt was similar to extant wet tundra (Guthrie, 2001; Zazula *et al.*, 2003). Such palaeoecological reconstructions provide a framework for interpreting the apparent filtering of species that occurred across the land bridge (Simpson, 1965, p. 88). Those studies also demonstrate that a synthesis across multiple disciplines greatly improves our understanding of Beringia's dynamic geological history (Guthrie, 2006).

Parasites

Parasites, of intrinsic importance in human and animal health (e.g. Kutz *et al.*, 2004), are also excellent indicators in present-day and historical ecology and biogeography at varying temporal and spatial scales (Brooks & Hoberg, 2000; Hoberg & Klassen, 2002). Encompassing a range of microparasites (e.g. viruses, bacteria, rickettsia, protozoa) to macroparasites (e.g. helminths, arthropods), parasitic organisms reveal complex processes involved in diversification and the formation of ecosystems and provide insights about the history and structure of faunal associations in evolutionary and ecological time (Brooks & McLennan, 1993; Brooks & Hoberg, 2000; Brooks & McLennan, 2002).

While Beringian parasitology has a long and successful tradition, we now have the requisite tools and methods for integrating traditional ecological and historical approaches with molecular phylogenetics and phylogeography to pursue fine-scale questions that have previously been beyond evaluation (Riddle, 2005). In Beringia, an array of potential model systems dealing with a variety of host-parasite assemblages can directly contribute to the elucidation of Beringian history (Table 4).

Episodic processes involving biotic expansion, geographical colonization and refugial isolation at varying temporal and spatial scales have been implicated as determinants of faunal structure in host-parasite systems since the late Pliocene (Hoberg, 2005). Contrasting modes and tempos for geographical colonization, responses to habitat perturbation and fragmentation and refugial effects have been found across putative complexes of cryptic species of both nematodes and cestodes among such phylogenetically disparate mammalian hosts as artiodactyls and arvicoline rodents (Hoberg *et al.*, 1999; Haukisalmi *et al.*, 2001, 2006; Table 4).

The potential for Beringian parasite studies is illustrated by evaluations of molecular and morphological variation relative to host and geographical associations for anoplocephaline and hymenolepidid tapeworms among arvicoline rodents (e.g. Cook *et al.*, 2005; Haukisalmi *et al.*, 2006). Similarly, historical biogeography for the Nematodirinae nematodes in lagomorphs and ungulates has a strong west-east component with Beringia serving as a filter and the ultimate control on broad distributions for these parasites in the Nearctic and Neotropical regions (Hoberg, 2005). Further, *Trichinella* nematodes parasitizing an array of carnivore hosts underwent two independent events of geographical colonization to the Nearctic from Eurasia since the early Pleistocene (Zarlenga *et al.*, 2006). Such studies have found an ancestral Palearctic fauna with independent trajectories for biotic expansion from west to east across Beringia, involving processes at regional and intercontinental scales. A complex history of subsequent geographical colonization, host switching and co-speciation is now being revealed (e.g. Koehler, 2006).

Complex biogeographical patterns also emerge from protostrongylid lungworms and muscle worms among artiodactyls. For example, phylogeographical analyses indicate that *Parelaphostrongylus odocoilei* occurs in Dall's sheep as a consequence of host and geographical colonization coinciding with a rapid Holocene range expansion from south to north tracking deglaciation of the Laurentide and Cordilleran icefields (Jenkins *et al.*, 2005; Jenkins, 2005; E.P. Hoberg, I. Asmundson & E.J. Jenkins, unpublished observations). Recent expansion contrasts with hypotheses for a deeper temporal association between caprine bovids such as *Ovis dalli* and *Ovis canadensis* and an ancestral lungworm fauna typical of wild sheep in Eurasia. Thus, we predict that the history for a lungworm fauna, including *Protostrongylus stilesi*, in Nearctic species of *Ovis* will mirror that of refugial isolation and secondary biotic expansion that has been postulated for these caprines in Beringia (Loehr *et al.*, 2006). Differential histories

Table 4 Examples of Beringian host–parasite systems as models for exploring patterns of biotic expansion, geographical colonization, historical biogeography and phylogeography.

Hosts/host group	Generic groups of parasites	Distribution of species diversity*
Arvicolinae (Rodentia)	Eucestoda	
	<i>Arostrilepis</i> (Hymenolepididae)†	Holarctic to regional scale
	<i>Anoplocephaloides</i> (Anoplocephalidae)†	Holarctic to local scale
	<i>Paranoplocephala</i> (Anoplocephalidae)†	Holarctic to local
	Nematoda	
	<i>Heligmosomum</i> (Trichostrongylina – Heligmosomoidea)†	Holarctic to regional
	<i>Heligmosomoides</i> (Trichostrongylina – Heligmosomoidea)†	Holarctic to regional
	<i>Rictularia</i> (Spirurida)†	Holarctic to regional
	<i>Mastophorous</i> (Spirurida)†	Holarctic to regional
	<i>Syphacia</i> (Oxyurida)†	Holarctic to regional
Artiodactyla	<i>Raushivingylus</i> (Metastrongyloidea – Filaroididae)	Regional to local
	Eucestoda	
	<i>Moniezia</i> (Anoplocephalidae)	Holarctic?
	Nematoda	
	<i>Nematodirus</i> (Trichostrongylina – Nematodirinae)	Holarctic to regional
	<i>Nematodirella</i> (Trichostrongylina – Nematodirinae)	Holarctic to regional
	<i>Parelaphostrongylus</i> (Metastrongyloidea – Protostrongylidae)†	Nearctic to regional
	<i>Protostrongylus</i> (Metastrongyloidea – Protostrongylidae)†	Nearctic
	<i>Umingmakstrongylus</i> (Metastrongyloidea – Protostrongylidae)	Nearctic
	<i>Ostertagia</i> (Trichostrongylina – Ostertagiinae)†	Holarctic to regional
Canidae (Carnivora)	<i>Marshallagia</i> (Trichostrongylina – Ostertagiinae)†	Holarctic to regional
	<i>Teladorsagia</i> (Trichostrongylina – Ostertagiinae)†	Holarctic to local
	<i>Dictyocaulus</i> (Trichostrongylina)	Holarctic to regional
	<i>Skrjabinema</i> (Oxyurida)†	Holarctic to regional
	Eucestoda	
	<i>Taenia</i> (Taeniidae)†	Holarctic to regional
	<i>Echinococcus</i> (Taeniidae)	Holarctic to regional
	<i>Diphyllobothrium</i> (Pseudophyllidae)	Holarctic?
	<i>Mesocestoides</i> (Mesocestoidata)	Holarctic?
	Nematoda	
<i>Uncinaria</i> (Ancylostomatoidea)	Holarctic?	
<i>Trichinella</i> (Trichinelloidea)	Holarctic to regional	
Insectivora	Eucestoda	
	<i>Lineolepis</i> (Hymenolepididae)	?
	<i>Lockerrauschia</i> (Hymenolepididae)	?
	<i>Neoskrjabinolepis</i> (Hymenolepididae)	?
	<i>Spaskylepis</i> (Hymenolepididae)	?
Mustelidae (Carnivora)	Nematoda	
	<i>Soboliphyme</i> (Dioctophymatoidea)†	Holarctic
	Eucestoda	
	<i>Taenia</i> (Taeniidae)†	Holarctic to regional
	Nematoda	
Leporidae (Lagomorpha)	<i>Baylisascaris</i> (Ascaridoidea)	Holarctic to regional
	<i>Molineus</i> (Trichostrongylina – Molineoidea)	Holarctic to regional
	<i>Soboliphyme</i> (Dioctophymatoidea)†	Holarctic to regional
	<i>Trichinella</i> (Trichinelloidea)	Holarctic to regional
	Nematoda	
Ochotonidae (Lagomorpha)	<i>Obeliscoides</i> (Trichostrongylina – Lybiostrongylinae)	Holarctic
	<i>Rauschia</i> (Trichostrongylina – Nematodirinae)	Holarctic to regional
	<i>Protostrongylus</i> (Protostrongylidae)	Holarctic to local
Ochotonidae (Lagomorpha)	Eucestoda	
	<i>Schizorchis</i> (Anoplocephalidae)†	Holarctic to local
	Nematoda	
	<i>Graphidiella</i> (Trichostrongylina – Nematodirinae)	Holarctic to local, absent in Beringia
	<i>Murielus</i> (Trichostrongylina – Nematodirinae)	Holarctic to local, absent in Beringia

Table 4 continued

Hosts/host group	Generic groups of parasites	Distribution of species diversity*
	<i>Labiostrongylus</i> (Oxyurida)†	?
	<i>Eugenuris</i> (Oxyurida)†	?
	<i>Cephalurus</i> (Oxyurida)†	?

*Geographical distribution for diversity varies relative to parasite group, and different levels of spatial heterogeneity are apparent for species on a continuum linking intercontinental (Holarctic), continental (regional) and local scales. Based on current data some species and species groups appear to have broad distributions and are abundant across the Holarctic, whereas others appear to be partitioned at fine scales relative to hosts and geography and are patchy in space and time. This preliminary understanding of diversity defines the range of hypotheses to be explored for the history of the Holarctic and Beringian faunas.

†Specimens appropriate for phylogeography available through collections from Beringian Co-evolution Project.

for protostrongyles in sheep, other ungulates and leporids (e.g. *Protostrongylus pulmonalis* in *Lepus* spp.) serve as the basis for powerful comparative frameworks to explore the role of episodic processes for geographical and host colonization in faunal diversification (Hoberg & Brooks, in press). Such integrative studies highlight the role of climate variation and cyclical ecological perturbation as determinants of complex host–parasite systems (e.g. Hoberg *et al.*, 2002; Kutz *et al.*, 2004, 2005; Jenkins *et al.*, 2006). A focus on Pleistocene systems additionally allows us to explore the equivalence of processes in evolutionary and ecological time with respect to the introduction, establishment and emergence of pathogens and parasites (Hoberg, 2005; Brooks & Hoberg, 2006).

The fossil record and ancient DNA

Extensive palaeontological and palynological research has led to a large body of knowledge on Beringian evolutionary history based on the fossil record (Elias, 1995; Guthrie, 2003; Brubaker *et al.*, 2005). However, a more complete fossil record, especially among smaller fauna, would much improve our understanding of Beringian biogeography. Similarly, molecular phylogeneticists have been increasingly successful at recovering ancient DNA (100–100,000 yr BP) from specimens (see Pääbo *et al.*, 2004; Willerslev & Cooper, 2005 for reviews). The Arctic provides one of the best environments for the study of ancient DNA because permafrost conditions substantially reduce degradation (Shapiro & Cooper, 2003). Recovery of ancient DNA adds a powerful temporal factor to molecular analyses (Willerslev & Cooper, 2005), and should significantly enhance our understanding of Beringian biogeography and evolutionary history (e.g. Barnes *et al.*, 2002; Shapiro *et al.*, 2004).

Inherent in high-latitude analyses is the assumed role of Pleistocene glaciations in the *in situ* diversification and extinction of many boreal and arctic taxa (Avisé & Walker, 1998; Avisé *et al.*, 1998; Weir & Schluter, 2004). Populations located outside the boundaries of Beringia were also important in recolonization of northern deglaciated areas (Fedorov *et al.*, 2003). Other Nearctic refugia have been hypothesized (e.g. the Canadian High Arctic: MacPherson, 1965), but palaeontological and palynological evidence is inconclusive. Several phylogeographical studies of boreal species implicate additional

refugia as important in the diversification of Arctic taxa and ultimately in structuring communities (e.g. Wilson & Hebert, 1998; Holder *et al.*, 1999; Waltari & Cook, 2005; Loehr *et al.*, 2006). All these investigations document a strong signal of historical climate change in the evolution of northern organisms (Cook *et al.*, 2006), and are consistent with the assertion that fluctuating Pleistocene environments had greater impact on the diversification of boreal organisms than on southern biota (Weir & Schluter, 2004). Recognition of the critical role of historical climate fluctuations on shaping high-latitude diversity provides a powerful framework to assess the impact of climate change on present-day environments. Current and predicted global trends indicate that the greatest warming is occurring and will continue to occur at high latitudes. In the near future, tundra habitat will likely be dramatically reduced and largely replaced by taiga (ACIA, 2004). Ecological perturbation associated with directional climate warming is further predicted to influence the distribution and dynamics of complex host–parasite systems at high latitudes (Hoberg *et al.*, 2002; Kutz *et al.*, 2004, 2005; Jenkins *et al.*, 2006). As current and future prospects in high-latitude phylogeography are developed, these relatively new approaches to interpreting environmental history should play a substantial role in understanding historical and present-day climate change.

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BIOSKETCHES

Eric Waltari developed this work as part of his PhD dissertation studying phylogeography and historical demography of arctic hares and shrews of the *Sorex cinereus* complex. Eric completed his dissertation in the laboratory of Joe Cook and is currently involved in research integrating genomic and GIS data.

Joe Cook primarily investigates phylogenetics, biogeography and conservation genetics of high-latitude mammals.

Eric Hoberg studies the systematics and co-evolution of helminth parasites and their hosts, with an emphasis on the Holarctic fauna.

Enrique Lessa focuses on speciation and diversification of vertebrates using phylogeographical and population genetic approaches, biogeography and refugial theory, and evolution at the molecular level.

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