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Mammalian diversification across the Holarctic: spatiotemporal evolution in response to environmental change

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MAMMALIAN DIVERSIFICATION ACROSS THE HOLARCTIC: SPATIOTEMPORAL EVOLUTION IN RESPONSE TO ENVIRONMENTAL CHANGE

BY

ANDREW G. HOPE

B.Sc., Zoology, University of Glasgow, 1999
M.S., Biology, Eastern New Mexico University, 2002

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

Biology

The University of New Mexico
Albuquerque, New Mexico

July, 2011

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ABSTRACT

The primary focus in this dissertation is on the processes of environmental change that drive evolution. We are currently witnessing unparalleled changes in climate and associated changes in biotic communities. With a growing understanding that climate and habitat change, coupled with natural variability, will have an increased influence on biota into the future, it is our responsibility to learn how best to manage and conserve the Earth's natural resources. Among other things, this will require a firmer understanding of biodiversity, life histories, evolutionary relationships among species, and community dynamics over multiple species. One method of understanding how species will respond to future change is to interpret the legacy of genetic signatures borne through a given lineage or group of lineages over time by testing hypotheses of change in response to past environmental pressures. I have used a number of small mammal species distributed through the northern hemisphere to investigate genetic change in response to a changing environment. I associate the disciplines of population genetics, phylogeography, and

phylogenetics with knowledge of contemporary global change and paleoclimatology, landscape change through time, local geographic features within the study area and a variable ecology both within and among the study taxa.

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INTRODUCTION

Research presented in this dissertation is primarily focused on the processes of environmental change that drive evolution. We are currently witnessing changes in climate and associated changes in biotic communities that are unparalleled in the brief history of scientific investigation centered on diversification, speciation, and extinction (Oechel et al. 2000; Shuur et al. 2009). With a growing understanding that anthropogenically induced climate and habitat change, coupled with natural variability, will continue to have an increased influence on biota into the future, it is our responsibility to learn how best to manage and conserve the Earth's natural resources (McCarty 2001). Among other things, this will require a firmer understanding of biodiversity, life histories, and evolutionary relationships among species, and community dynamics in response to environmental change (Whittaker et al. 2005). One method of understanding how species will respond to future change is to interpret the legacy of genetic signatures borne through a given lineage or group of lineages over time by testing hypotheses of change in response to past environmental pressures (Hewitt 2004; Hickerson et al. 2010). In this dissertation, I use a number of small mammal species distributed through the northern hemisphere to investigate genetic change in response to a changing environment at various scales and incorporating a number of scientific disciplines. Groups of individuals within a recognized species are assessed using methods from the field of population genetics. Groups of populations comprising a given species are investigated using phylogeographic methods, and in a comparative sense among multiple co-distributed species (Avise 2000). And finally, closely related species are examined over a broad geographic range to study speciation within a phylogenetic context. Coupled with obtaining and analyzing genetic sequences (mostly from the mitochondrial cytochrome *b* gene), it was also necessary to achieve a firm understanding of the associated principles of contemporary global change and paleoclimatology, landscape geologic change through time, local geographic features within the study area and a variable ecology both within and among the study taxa.

Focal species utilized within all chapters of this dissertation comprise collectively the long-tailed (red-toothed) shrews. These shrews (Order: Soricomorpha; Family: Soricidae; Genus: *Sorex*) are among the smallest of all mammals, and yet among the most diverse of mammal genera with 77 described species (Hutterer 2005). They are widespread, occurring through most of Europe, Asia, and North America, and yet are rarely found in tropical latitudes and do not occur in the southern hemisphere. Within their range they occupy virtually every available habitat and niche, excepting the more arid desert ecosystems. The genus *Sorex* is split roughly in half according to previously published phylogenies (e.g. Ohdachi et al. 2006; Dubey et al. 2007) including the sub-genus *Sorex* with a generally Palearctic (Eurasian) distribution, and the sub-genus *Otisorex* with a generally Nearctic (North American) distribution. However, there are a number of exceptions to this clean-cut overview that make the group an especially interesting focus of study. Not all species have been unambiguously assigned to a sub-genus (e.g. George 1988). This highlights a general lack of rigorous systematic assessments within this group as well as ambiguity of results due to methodological constraints. Within each sub-genus, there are a number of species that are geographically incongruent (i.e. some species in the sub-genus *Otisorex* occur in the Palearctic; some species in the sub-genus *Sorex* occur in the Nearctic).   In addition, there are instances where a single species has a contemporary Holarctic distribution (Hope et al. 2010). This highlights both that transcontinental exchange has been an ongoing process within this group through time and also close biotic associations between the northern continents. Multiple invasions, or “introductions” between the continents present analogs to recent novel species associations through human mediated introductions. Finally, there is uncertainty within the current taxonomy, largely because these diminutive small mammals are inherently difficult to identify based on a very conserved and pleisiomorphic body plan (e.g. Nagorsen and Panter 2009). In this way, many species designations based on distinct geographic ranges and slight morphological character displacement are not concordant with levels of genetic differentiation.

The four chapters presented here represent independent studies prepared for publication in relevant peer-reviewed literature, but all are linked by a common goal of understanding differentiation in response to environmental change, and further by incorporating different components (species) of the northern mid- and high-latitude mammalian fauna as the study taxa. In each chapter evidence was gleaned from genetic DNA sequence data to test predictions with modern analytical methods. Each independent study progresses from previous work by incorporating additional methods and addressing more advanced hypotheses.

The first chapter introduces a Holarctic perspective to patterns of differentiation and addresses taxonomic uncertainty within a descriptive phylogeographic assessment of perhaps the smallest mammal species in the world: *Sorex minutissimus* (Hope et al. 2010). Based on historical locality records, predicted distributions through time are coupled with genetic population structure and demography throughout the geographic range to investigate how the species has responded to a recent (late-Pleistocene) glacial climate regime. The present limited distribution of this species in North America, and its known placement within the Palearctic sub-genus *Sorex* strongly suggests that transcontinental movement has recently occurred eastward as a consequence of population expansion in response to climate change. The area known as Beringia (Hultén 1937) formed an isthmus spanning the northern continents repeatedly through the Pleistocene acting as both a corridor for movement and/or a refugium in which populations could persist (Cook et al. 2005).

The second chapter consists of a phylogeographic assessment of the only other Holarctic shrew species: *Sorex tundrensis* (Hope et al. 2011). Again taxonomic considerations among geographic elements of this species are assessed considering a similar limited distribution in North America. Patterns of diversification are investigated by testing explicit hypotheses of coalescence times for designated groups. This chapter advances on the first by using methods of simulating datasets to test various model scenarios for divergence in response to climate change through space and time (e.g. DeChaine and Martin 2006). Also, the chapter represents a comparative study of potentially different evolutionary responses of multiple co-distributed shrew species to environmental perturbations.

In the first two chapters there is an emphasis not only on a Holarctic distribution but also on the poorly understood processes of diversification within Eurasia, particularly Siberia. The third chapter focuses instead on Beringia. As Pleistocene glacial episodes repeatedly and cyclically connected Eurasia and North America over the span of more than 2 million years, there was significant opportunity for populations within multiple species to diverge (and potentially reconnect) with the possibility of different genetic responses at multiple times. Here data from many of the small mammal species occurring through Beringia were analyzed concurrently using approximate Bayesian computation in the program msBayes, a novel technique for testing a hypothesis of simultaneous divergence of multiple taxon pairs across a common geographic barrier (Hickerson et al. 2007). Holarctic associations of not just shrews but also multiple vole species are investigated in a comparative framework to assess the role of Pleistocene glacial periodicity in speciation. In addition, Beringia is increasingly recognized not as a single large glacial refugium but as a heterogeneous landscape in terms of both climate and geography through the Pleistocene epoch (Elias et al. 1997; Guthrie 2001). Analyses of population demographics and coalescent divergence estimates consider taxon pairs individually to relate ecological differences to a variable evolutionary response.

The final chapter considers the *cinereus* complex (Demboski and Cook 2003) of 13 closely related species of shrew with a vast combined geographic distribution that extends the total study area of this dissertation to encompass most of North America. The distribution of this species complex is again Holarctic but compared to the two other Holarctic shrews (*S. minutissimus* and *S. tundrensis*), the *cinereus* complex has a limited distribution in Eurasia suggesting recent transcontinental movement westward through Beringia. In a comparative sense, diversification within the *cinereus* complex presents a scenario for diversification over multiple glacial cycles that can be considered for other co-distributed taxa and represents a rare example of such a vast and continuous distribution among so many closely related species. Parapatric distributions between species suggests that ecological associations concordant with phylogeny may help to reinforce rapid differentiation although hybridization through time may play a distinct role in the evolution of this group. A large dataset consisting of population-level sampling, multiple species, and several independent genetic loci contribute to a comprehensive phylogenetic assessment of the group using novel methods of species-tree estimation from multiple genealogies.

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CHAPTER 1

High latitude diversification within Eurasian least shrews and Alaska tiny shrews (Soricidae)

Running Title: HOPE ET AL.—PHYLOGEOGRAPHY OF HOLARCTIC *SOREX*

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ABSTRACT

A novel shrew was discovered recently in Alaska and described based on morphological characters as *Sorex yukonicus*. This species is closely allied to *Sorex minutissimus,* a widespread shrew ranging through Eurasia. Together their distribution spans Beringia, a large Pleistocene nonglaciated area that connected Asia and North America. Beringia was repeatedly divided due to raised sea levels during Pleistocene interglacials and subsequently reconnected during glacials. We tested predictions related to the influence of large-scale geologic events on genetic variability through a phylogeographic analysis of both species of shrew using evidence from 3 independent genetic loci. We found low genetic divergence between *S. minutissimus* and *S. yukonicus* across continents. However, major phylogeographic breaks were found for Eurasian and Maritime Northeast Asia populations. Neither species is reciprocally monophyletic for any of the loci examined. Coalescence times for all pairwise population comparisons within both species fall within the Wisconsinan/Weichselian glacial (< 130 kya), and significant population expansion estimates date to the Holocene suggesting that divergence between these taxa is minimal and may not warrant recognition of 2 distinct species. Phylogeographic relationships and sequence divergence estimates place populations of North American *S. yukonicus* and Siberian *S. minutissimus* as most closely related, and together they are sister to European *S. minutissimus*. We conclude that populations east and west of the Bering Strait represent a single Holarctic species, *S. minutissimus*. Temporal changes in range based on ecological niche predictions and a comparative assessment of other codistributed taxa provide a preliminary view of potential Last Glacial Maximum refugia in Northern Asia.

Key words: Bayesian skyline plot, Beringia, ecological niche model, multiple loci, phylogeography, Pleistocene refugia, *Sorex minutissimus*, *Sorex yukonicus*.

INTRODUCTION

Climatic variability during the Pleistocene had a major impact on the evolution and distribution of high latitude species (Hewitt 1996, 2004), with >20 significant glacial cycles recorded during this epoch (Williams et al. 1998). Northern species experienced major range shifts involving contractions into discrete refugia and subsequent expansions as they recolonized deglaciated areas (Schmitt 2007). The record of these demographic changes through repeated climatic cycles often are obscured by the actions of the most recent glacial cycle, effectively wiping the historical slate clean (Avise 2000); however, sometimes the signature of past glaciations persists through multiple glacial events (Lu et al. 2001; Runck et al. 2009). Fossil remains are independent evidence of previous occupation but provide only a minimum time estimate of geographic occupation. For many small mammals fossils often are not available or are difficult to identify (Near and Sanderson 2004; Smith and Peterson 2002). Geographic distributions coupled with knowledge of geologic and climate change through time can be compared with morphologic or genetic information from extant populations to infer the history of diversification and spatiotemporal change within and among species (Lister 2004).

In Europe, species occupied putative southern refugia during glacial maxima, and many recolonized northward following retreat of the Fennoscandian ice sheet in response to a warming climate (Hewitt 2001; Schmitt 2007). In addition, genetic signatures of other newly recognized refugia situated further east in Europe (e.g., Carpathians—Provan and Bennett 2008) also have been identified and implicated as sources for westward recolonization (Fedorov et al. 2008; Hewitt 2004). Likewise, most of northern North America was covered by the Cordilleran and Laurentide ice sheets. Following deglaciation, species that were pushed south subsequently expanded north to occupy newly exposed land (Runck and Cook 2005). In contrast, much of eastern Europe, Siberia, and northwestern North America remained virtually ice-free from the Taimyr Peninsula eastward across Beringia to the Mackenzie Mountains in the Yukon Territory (Hopkins 1967; Svendsen et al. 2004), and yet phylogeographic patterns for high-latitude species occupying North America and East Asia remain poorly understood. Heterogeneous topography including mountain ranges, large rivers, and lakes, coupled with variable climatic cycles, fragmented this immense region into discrete xeric or mesic refugia (Ehrich et al. 2008; Fedorov et al. 2008; Mangerud et al. 2004).

Beringia is perhaps the most recognized ice-free refuge at high latitudes (Abbott and Brochmann 2003; Hultén 1937). During glacial maxima lowered sea levels exposed a land bridge between Asia and North America effectively extending Asia eastward to the western limits of the North American ice sheets and allowing for continental exchange of terrestrial biota (DeChaine 2008; Elias and Crocker 2008; Sher 1999). During glacial episodes species from Asia could pass into eastern Beringia (central Alaska and northwestern Yukon Territory) whereas North American species were restricted to lower latitudes south of continental ice sheets. Consequently, most known intercontinental movements of species across Beringia are eastward, although notable exceptions include some shrews (Waltari et al. 2007b).

Species and complexes that span the nexus between Asia and North America provide a window into the historical biogeography of faunal exchanges. The Alaska tiny shrew, *Sorex yukonicus* (Dokuchaev 1997), was described from previously misidentified museum specimens. Originally thought to be the Eurasian least shrew, *S. minutissimus* (Dokuchaev 1994), these specimens were later elevated to a new species based on morphological differences (Dokuchaev 1997). Dokuchaev (1997) suggested that *S. minutissimus* invaded Alaska prior to the Illinoian glacial and then diverged within Beringia as *S. yukonicus* during the Illinoian (0.21-0.13 Ma). Although morphological differences were detected with principal component analysis, the study by Dokuchaev (1997) was based on a limited number of samples (6 individuals). Since that study an additional 27 specimens have been archived, all within the confines of Alaska. The geographic range of *S. minutissimus* is broad, extending from Scandinavia eastward across Asia to the Bering Strait and as far south as Mongolia and southeast to Primorsky Krai and Japan (Ohdachi et al. 2001; Sheftel 2005). The least shrew inhabits forest-tundra, taiga, forest-steppe, and dry steppe habitats (Yudin 1971).

Other taxa (e.g., arthropods, birds, fish, parasites, and plants) also exhibit broad Holarctic distributions (Fedorov et al. 2008; Haukisalmi et al. 2004, 2009; Hewitt 2004; Waltari et al. 2007b). Distinctive phylogeographic breaks are common among high-latitude mammals including an east-west split in the vicinity of the Ural Mountains of western Russia (Brunhoff et al. 2003; Deffontaine et al. 2005; Fedorov et al. 1999a, 1999b), splits between the major river basins of the Ob, Yenisei, Lena, and Kolyma (Fedorov et al. 2003; Galbreath and Cook 2004; Fedorov et al. 2008), the Beringian refugium (Eddingsaas et al. 2004; Galbreath and Cook 2004; Waltari et al. 2004), and parts of Maritime Northeast Asia including Primorsky Krai, Japan, and the Korean Peninsula (Ehrich et al. 2008; Fedorov et al. 2008; Lee et al. 2008; Ohdachi et al. 2001; Yasuda et al. 2005). Other species exhibit a distinct barrier at the Bering Strait (Elias and Crocker 2008; Fedorov and Goropashnaya 1999). Dokuchaev (1997) suggested that *S. yukonicus* is an autochthon of Beringia, although the distribution of this species is limited to Alaska (eastern Beringia only). At least 3 alternative hypotheses have been proposed for the distribution of *S. minutissimus* and *S. yukonicus*: 1) 2 distinct species divided at the Bering Strait (i.e., the current taxonomic arrangement); 2) a single Beringian autochthon, *S. yukonicus*, with a distribution that spans the Bering Strait; or 3) a single Holarctic species that subsumes the recently described *S. yukonicus* within *S. minutissimus*. Given the wide distribution (Europe through Siberia to Alaska) inherent in the "single species" hypothesis, good potential of significant phylogeographic structure exists.

We sequenced 3 independent genetic loci to investigate phylogeographic patterns within the *minutissimus-yukonicus* group and also develop distributional models based on ecological niche predictions to assess population-level demography and test spatial and temporal components of historical diversification. Finally, we place this study within the context of phylogeographic research on other Arctic species and discuss emerging evidence for the persistence of high-latitude species in multiple discrete refugia within largely ice-free areas of Eurasia during glacial periods.

MATERIALS AND METHODS

Sampling/lab techniques –Sorex yukonicus in North America and *S. minutissimus* in Eurasia are comparatively uncommon shrews through their present range (Fig. 1A). Few specimens of *S. minutissimus* from Eurasia exist, and most are preserved as study skins or formalin fluid samples. We obtained samples from 29 *S. yukonicus* (21 localities) and 66 *S. minutissimus* for this study (Appendix I). Samples were collected in conjunction with the Beringian Coevolution Project (*n* = 44—Cook et al. 2005), or received on loan from Europe and northern Asia (*n* = 41; Appendix I). We added 10 (mtDNA: cytochrome-*b*) partial sequences of *S. minutissimus* obtained from GenBank resulting in 61 total localities spanning northern Europe, through Asia to Alaska (Fig. 2).

Heart, liver, or skin were obtained from frozen (stored at -80°C), ethanol-preserved, or dried samples. Purified total genomic DNA was obtained through standard salt extraction, followed by PCR and cycle sequencing (Fleming and Cook 2002). We amplified 3 independent loci, the mtDNA cytochrome-*b* gene (*Cytb*: 561-1,140 bp), and two nuclear loci, the apolipoprotein B (ApoB: 514 bp—Dubey et al. 2007), and Breast Cancer Susceptibility 1 (BRCA1: 722 bp—Dubey et al. 2006) genes. Primers used for double-stranded amplifications and sequencing of *Cytb* were modified from Irwin et al. (1991—MSB14 5’-ccc atc tcy ggt tta caa gac-3’) and Anderson and Yates (2000—MSB05 5’-gac atg aaa aat cat tgt tgt aat tc-3’). For highly fragmented DNA the internal primers L15135 and H15392 (Ohdachi et al. 2001) were used. Primer pairs ApoBF/ApoBR and BRCA1F/BRCA1R (Dubey et al. 2006, 2007) were used to amplify and sequence ApoB and BRCA1 genes, respectively. For all targeted regions PCR reagents and conditions were: 1 µl DNA template (variable concentration), 1.5 µl each of dNTPs (10 mM), MgCl (25 mM), 10x PCR buffer, and BSA (1%), 0.5 µl of each primer (10 mM), 0.08 µl AmpiTaq® DNA polymerase (Applied Biosystems, Foster City, California), and 6.92 µl ddH$_2$O to total 15 µl reactions. PCR was performed in a PTC 200 thermocycler (MJ Research, Waltham, Massachusetts) with initial denaturation at 94°C for 5 min, followed by 40 cycles of denaturation at 94°C for 15 s, annealing at 50°C for 20 s, extension at 72°C for 1 min, and final extension at 72°C for 5 min, with cooling at 15°C for 10 min. PCR products were cleaned using polyethylene glycol 30% (PEG) precipitation (Bernstein and Abbot 1987) and cycle sequenced using the ABI BigDye® v3.1 Sequencing Kit (Applied Biosystems, Foster City, California). Reagents for each 12 µl cycle sequencing reaction included 1.25 µl H$_2$O, 2 µl BigDye buffer, 2 µl primer (10 mM), 0.75 µl ABI BigDye® v3.1 (Applied Biosystems, Foster City, California), and 5 µl DNA (variable concentration). Conditions for cycle sequencing followed Platt et al. (2007) and reactions were cleaned using a 125 mM EDTA/EtOH protocol. Automated sequencing of complimentary strands was conducted using the Applied Biosystems 3110 DNA sequencer of the molecular biological facility at the University of New Mexico. Complimentary strands of DNA were compared and contiguous sequences were then deposited in GenBank (Appendix I).

Phylogeny reconstruction – Degraded DNA from study skins (*n* = 37) coupled with availability of partial *Cytb* sequences from GenBank resulted in a mitochondrial phylogeny based on a range of gene length for *Cytb* (561-1,140 bp; *n* = 100). Phylogenies were estimated with and without a designated outgroup to explore the possibility of long-branch attraction. The purported sister species for the *minutissimus-yukonicus* group is *Sorex hosonoi*, an endemic to Honshu Island, Japan (Ohdachi et al.

1997; 2001), and 5 sequences were obtained from GenBank (AB028593-AB028597) for the *Cytb* genealogy. In addition, the *Cytb* data set was pruned to haplotypes excluding incomplete and repeat sequences and standardizing gene length (836 bp; 22 *S. minutissimus*; 8 *S. yukonicus*) to control for population bias. Nuclear data sets for ApoB (514 bp) and BRCA1 (722 bp) include 30 specimens from the *Cytb* pruned haplotype data set that are represented by all 3 genetic loci. Nuclear sequences for *S. hosonoi* were unavailable so 1 specimen each of *Sorex arcticus, Sorex caecutiens, Sorex daphaenodon, Sorex minutus,* and *Sorex roboratus* was included for subsequent nuclear analyses of multiple loci. These species were chosen based on their recognized taxonomic affiliations with *S. minutissimus* (all within the subgenus *Sorex*—Hutterer 2005).

Sequences were edited with SEQUENCHER 4.8 (Genecodes, Ann Arbor, Michigan), aligned in BioEdit 7.0.9 (Ibis Biosciences, Carlsbad, California) using ClustalW, and checked by eye. Sequences were translated to amino acids and examined for internal stop codons that might uncover pseudogenes. Alleles of nuclear heterozygotes were inferred using PHASE (Stephens et al. 2001; Stephens and Scheet 2005). The program PHASE implements a Bayesian statistical method for reconstructing haplotypes from population nuclear genotype data that includes multiple heterozygous base sites within individuals. PHASE was run 5 times, and results from the run with best goodness-of-fit to an approximate coalescent model were retained, resulting in 2 haplotype sequences per individual to obtain accurate estimates of allele frequencies. For Bayesian phylogenies a hierarchical likelihood ratio test was run on each sequence data set to determine the best model of DNA substitution using MrModeltest v2.3 (Nylander 2004). The Markov Chain Monte Carlo (MCMC) procedure was performed in MrBayes v3.1 (Ronquist and

Huelsenbeck 2003) to estimate posterior probabilities of phylogenetic trees for each sequence data set. Two separate runs were conducted for each data set, with sequences partitioned by codon position to allow for variable substitution rates among different codon positions. Each run computed 5,000,000 generations, sampling every 100 generations, with 4 independent chains, and the first 5000 trees discarded as burn-in. The resulting phylograms and posterior probabilities for each locus were visualized in FigTree v1.2.2 (Rambaut 2009).

Species tree estimation from multiple loci – Evidence from multiple independent genes is critical to inferring relationships within and among species (Edwards and Beerli 2000). Gene tree/species tree discord can result from gene duplication, introgression, sorting of ancestral polymorphism, or rapid fixation of linked loci through selective sweeps (Carstens and Knowles 2007). Multiple independent loci allow for the potential detection of these phenomena. For species tree estimation we used the minimizing deep coalescences method (MDC—Maddison and Knowles 2006) implemented in Mesquite v2.6 (Maddison and Maddison 2009). The MDC method is preferred over concatenation due to the independent (unlinked) nature of our 3 loci (Edwards et al. 2007; Kubatko and Degnan 2007). This topology-based method estimates species trees based on the minimum number of deep coalescences over all independent genealogies. Data were phased for all 3 loci (including the haploid mitochondrial gene for consistency) to estimate accurately alleles from nuclear gene sequences with multiple heterozygous sites and produce 2 haplotypes for each individual, including the 5 outgroup taxa ($n_{\text{tot}} = 70$). The same specimens were included in all 3 phylogeny reconstructions using independent loci. The MDC reconstruction was run with 100 iterations for a robust estimate.

Ecological niche modeling – For development of ecological niche models (ENMs) we used current and Last Glacial Maximum (LGM) monthly climate data at 2.5-minute (4 x 4 km) spatial resolution. Waltari et al. (2007a) and Peterson and Nyári (2008) discussed the process of layer development more fully. To summarize, LGM climate data were based on 2 general circulation model (GCM) simulations, the Community Climate System Model (CCSM—Collins et al. 2004) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2—Hasumi and Emori 2004; http://www.pmip2.cnrs-gif.fr). Each model was generated at a spatial resolution of 2.8º, or roughly 300 x 300 km, and model outputs were processed by interpolating differences between LGM and recent (preindustrial) conditions based on the WorldClim (http://www.worldclim.org/) data set to create monthly climate surfaces at 2.5-minute spatial resolution.

ENMs for both the present and LGM were based on the 19 bioclimatic variables in the WorldClim data set (Hijmans et al. 2005). These variables represent summaries of means and variation in temperature and precipitation and characterize dimensions of climate considered particularly relevant in determining species distributions. Present-day ENMs were developed within a mask consisting only of land north of 30º N.

From biodiversity information systems of natural history collection data (e.g., ARCTOS http://arctos.database.uaf.edu and MaNIS http://manisnet.org/—Stein and Wieczorek, 2004) we collated georeferenced occurrence points of both *S. minutissimus* and *S. yukonicus*. We refined these records by removing duplicate records, falsely georeferenced locations (e.g., locations over ocean), and records with low precision taken from atlas grid centroids, resulting in 78 occurrence points used for analysis.

We used Maxent version 3.3 (Phillips et al. 2006; Phillips and Dudik 2008) to construct ENMs. Maxent generates ENMs using only presence records, contrasting them with pseudo-absence or background data resampled from the remainder of the study area. In each case we developed present-day ENMs and then projected the ENM to LGM conditions. We used the default convergence threshold (10^{-5}; change in log loss per iteration) and maximum number of iterations (1,000) values. We allowed the program to select both suitable regularization values and functions of environmental variables automatically, which it achieves based on considerations of sample size. Maxent can run multiple analyses of a data set under a jackknife approach. We ran 5 replicates using the crossvalidate option, in which the localities are divided into 5 bins, with each bin used as a subset for model testing (equivalent to 20% testing).

Maxent outputs a logistic probability value as an indicator of relative suitability for the species, based on the principle of maximum entropy, as constrained by the input occurrence data. We chose a low and high threshold for consideration of ‘suitable’ habitat based upon the Maxent outputs using present-day climate data. The low threshold was the median value over the 5 replicates of the lowest presence threshold (LPT—Pearson et al. 2007), which is the threshold at which all occurrences in a training data set fall into suitable habitat, or a 0% omission rate. These values are more conservative than those used in recent studies (Pearson et al. 2007; Waltari et al. 2007a). The high threshold was the median value over the 5 replicates of the Maxent-generated value “Equal training sensitivity and specificity”, which we found to have the least variance of all standard thresholds generated by Maxent (E. Waltari, pers. obs.). This threshold identified smaller areas than a lowest presence threshold that yielded zero omission error, resulting in a more restricted picture of potential LGM distributions. We then generated summary maps in ArcGIS 9.3 that show Maxent predictions for present day and LGM.

Population genetic inference – Population parameters were calculated for the mtDNA *Cytb* data set to include the maximum number of specimens with a common gene length (549 bp; *n* = 84). Populations were grouped based on the reconstructed phylogenies for the 2 species, on our present knowledge of the geologic and phylogeographic history of the Holarctic, and on predicted potential distribution through ecological niche models. We grouped *S. yukonicus* as a single population (Alaska) based on a shallow phylogeny (Fig. 3) and a discrete distribution. We split *S. minutissimus* into 5 groups: a population consisting of individuals from Finland (Finland), a population consisting of individuals between Finland and the Yenisei River (Europe-to-Yenisei), a Siberia population (Siberia), a population consisting of individuals south of the Stanovoy Range and North of the Amur River (SE Siberia), and a Maritime Northeast Asia population (MNA) consisting of individuals from Primorsky Krai south of the Amur River, Northern Japan, and the Kurile Islands (Fig. 2). As an alternative we grouped all *S. yukonicus* and the 2 Siberia populations of *S. minutissimus* together to form a single population (Beringia) and similarly grouped the 2 European populations together (Europe). Summary statistics were calculated for each population to assess genetic diversity and patterns of population demographics: segregating sites (*S*), haplotype diversity (*Hd*), nucleotide diversity (π), and Watterson's theta (θ—Watterson 1975). For a potential signal of demographic expansion we used DnaSP (Librado and Rozas 2009) to calculate Tajima's *D* (Tajima 1989), Fu's *Fs* (Fu 1997), and *R2* (Ramos-Onsins and Rozas 2002) and assessed significance with 10,000 coalescent simulations.

Estimation of mutation rate and population size change – Estimations of mutation rate and effective population size are generally difficult. For example, estimates of mitochondrial *Cytb* mutation rates for mammals range from 0.7-60% per million years (Nabholz et al. 2008), although an established universal mammalian mitochondrial rate of 2.5% per million years often is used for phylogeographic investigations (Avise 2000). Statistical methods for analyzing population histories based on the coalescent rely on robust estimates of parameters for inferring historical demographics. We can calculate theta (θ) as a measure of effective population size proportional to the mutation rate ($\theta = 4N_e\mu$ for diploid loci; $\theta = 2N_f\mu$ for haploid loci). However, for a single locus such as *Cytb*, theta has broad confidence limits and so point estimates are potentially inaccurate (Edwards and Beerli 2000). Using the program BEAST (Drummond and Rambaut 2007), we included the entire set of mitochondrial sequences for the *minutissimus/yukonicus* group (*n* = 95) and 5 sequences of the sister species, *S. hosonoi*, retrieved from GenBank (AB028593-AB028597). We grouped individuals into populations as described above and designated monophyly for all *S. minutissimus* and *S. yukonicus* and all *S. hosonoi*. Under a strict molecular clock and HKY + G model of nucleotide substitution (obtained from Modeltest—Posada and Crandall 1998), 2 partitions into codon positions ((1+2) 3), and a Bayesian skyline tree prior, we ran independent MCMC analyses under a range of mutation rates (2%, 4%, and 6% per million years). All 3 estimates placed a most recent common ancestor (MRCA) in the region of 1 million years ago (Ma). *Sorex hosonoi* is endemic to Honshu Island (Ohdachi et al. 1997). The isolation history of Honshu Island includes a number of hypothesized isolation/reconnection events via land bridges through the Quaternary, with Hokkaido at the Tsugaru Strait, and with mainland Korea at the Tsushima Strait (Dobson and Kawamura 1998; Sota and Hayashi 2007; Van den Bergh et al. 2001; Yoshikawa et al. 2007; Fig. 2). However, late-Pliocene to early-Pleistocene events that coincide with a divergence estimate of ~1 Ma consist of only 2 possible bridges of ~2.5 Ma (Dobson and Kawamura 1998; vVan den Bergh et al. 2001) and ~ 1 Ma. The latter date is estimated by Yoshikawa et al. (2007) at 1.2 Ma, by Dobson and Kawamura (1998) at 1Ma, and by vVan den Bergh et al. (2001) at 1-0.8 Ma. All estimates are consistent with evidence from oxygen isotope ratios and records of historical sea-level change. Younger bridges are inferred at ~ 0.6 Ma, ~ 0.4 Ma, 130 ka, and finally the LGM at 20 thousand years ago (ka). All of these latter ages are outside the 95% bound of our 1 Ma divergence estimate, although other constituents of the mammalian fauna are considered to have used 1 or more of these recent potential bridges (Inoue et al. 2007; Kawamura 2007; Millien-Parra and Jaeger 1999; Sota and Hayashi 2007; Yasuda et al. 2005). We set a prior in BEAST of 1 Ma for the MRCA of *S. hosonoi* and the *S. minutissimus* clade with upper and lower bounds of 1.2 Ma and 0.8 Ma, respectively, unfixed the substitution rate, and set the molecular clock model to a relaxed clock: uncorrelated lognormal. We reran the MCMC algorithm with a length of chain of 30,000,000, logging trees every 3,000 to obtain an estimate for mutation rate of 5.5% per million years. Two further MCMC iterations were performed by fixing the substitution rate to 0.055 and applying a strict clock and then a relaxed clock to check for consistency among these 2 assumptions. These final iterations also provided divergence estimates for the time to MRCA (T_{MRCA}) of each designated population under our specified mutation rate.

Bayesian inference also can be used to assess change in population size through time. For Alaska, Siberia, and Europe clades individually we reran the Bayesian skyline estimation using our calculated mutation rate under similar model parameters but using all tree priors and constraining the tree root height to the T_{MRCA} for each group. Due to small sample sizes only these groups were analyzed. This provided us with Bayesian skyline plots (BSP) for population size change in each designated group. The x-axis of a BSP is reported as time in millions of years, and the y-axis is reported as $N_e\tau$ where N_e is the effective population size and τ is the generation time in the units ascribed to model parameters. Estimates of ancestral and contemporary N_e were calculated from BSP estimation for all specimens according to the equation $N_e=g/\tau$, where g is expressed as generation time in millions of years. Shrews (*Sorex*) are known to produce up to 3 litters per year with the potential of first litter females themselves reproducing in the same year (Dokuchaev 2005). However, survival rate is very low for shrews, and most newborn individuals that survive do not breed until the following spring (Churchfield 1990). We therefore maintained a generation time of 1 year.

RESULTS

Mitochondrial DNA – We sequenced 561-1,140 bp of *Cytb* from 29 individuals of *S. yukonicus* and 56 individuals of *S. minutissimus*, with an additional 10 sequences retrieved from GenBank. No sequences contained insertions, deletions, or internal stop codons. There were no second-position mutations. The Bayesian phylogeny illustrated well-supported and reciprocally monophyletic clades for *S. hosonoi* as the sister taxon and for the *minutissimus/yukonicus* group (Fig. 3) with uncorrected sequence divergence between sister taxa of 8.6%. Uncorrected sequence divergence within the *minutissimus/yukonicus* group varied from 0.6% to 2.2% (Table 1). We obtained high support for a monophyletic clade consisting of all *S. yukonicus* (post. probability = 0.93; Fig. 3), but *S. minutissimus* was paraphyletic with respect to *S. yukonicus*. Considering a potential Beringian autochthon, high support existed for a clade consisting of all *S. yukonicus* (eastern Beringia) and all *S. minutissimus* from Siberia (western Beringia; post. prob. = 0.97), although specimens within this clade include geographic localities west of the recognized limits of Beringia (e.g. Taimyr Peninsula; Fig. 3). A well-supported clade consisting of *S. minutissimus* from Europe and western Russia (including both Finland and Europe-to-Yenisei groups) represents the most divergent clade within the *minutissimus/yukonicus* group, followed by another well-supported clade from the Primorsky Krai area, south of the Amur River (Fig. 3; Table 1). Specimens from Finland form a distinct clade from other individuals occurring in Europe and Russia east to the Yenisei River. A reduced *Cytb* data set consisting of 30 haplotypes exhibits the same relationships as for the full data set, although relative support values for clades are weaker (Fig. 4C).

Species tree estimation and multiple loci – We reduced the data set to 30 individuals, including specimens from Finland, Europe-to-Yenisei, Siberia, MNA, and Alaska clades of the *minutissimus/yukonicus* group. All 3 genealogies exhibited similar major patterns of divergence within the *minutissimus/yukonicus* group. We found consistently low support or lack of reciprocal monophyly between *S. minutissimus* and *S. yukonicus* despite all 3 loci being phylogenetically informative (Fig. 4, A-C). Numbers of segregating sites (S) for the *minutissimus/yukonicus* group among the 3 loci are: ApoB =

26, BRCA1 = 7, *Cytb* = 57. European *S. minutissimus* were consistently separated from the remainder of the group, although they did not form a monophyletic clade in the BRCA1 phylogeny (Fig. 4B). Relationships among the outgroup taxa were largely unresolved over the 3 genealogies. A consistent sister relationship between *S. arcticus* and *S. daphaenodon* was observed in all genealogies, but the closest taxon to the *minutissimus/yukonicus* group was ambiguous. A species tree estimated using the MDC method based on all 3 genealogies (Fig. 4D) placed *S. yukonicus* and Siberian *S. minutissimus* as sister taxa, European *S. minutissimus* sister to these, and MNA *S. minutissimus* as basal to the rest of the group. Higher-level relationships among outgroup taxa were resolved with *S. minutus* closest to the *minutissimus/yukonicus* group, although elsewhere *S. roboratus* has been considered a closer relative (Ohdachi et al. 2006), and more often relationships are unresolved. Ancestral polymorphism between *S. yukonicus* and Siberian *S. minutissimus* is sorted only for the *Cytb* locus (not shown within the species tree) and clearly remains unsorted in the 2 nuclear genealogies (e. g. BRCA1; Fig. 4D). In contrast, European *S. minutissimus* specimens are sorted from the remainder of the *minutissimus/yukonicus* group in all 3 genealogies.

Ecological niche models – The predicted current distribution of *S. minutissimus* and *S. yukonicus* is generally consistent with the known range of these species (Fig. 1A). Notable exceptions to this are an absence of *S. yukonicus* in suitable habitat predicted for Canada. Likewise, *S. minutissimus* is not known to occur in central Europe. A projection of potential distribution back to conditions at 18 ka at the LGM indicates several potential refugia (Fig. 1B). Most notably, a large proportion of Alaska and the Bering Land Bridge are predicted as suitable at 18 ka, according to the ENM and much of MNA. More discrete refugia are predicted further west, including high suitability areas (dark shading) in the vicinity of the Carpathian Mountains, Black Sea, the Caucasus, and northwestern China. In Europe and Central Asia a shift of potential distribution southward occurs during the LGM, coupled with significant range contraction. However, MNA and discrete areas within Beringia are predicted as potential habitat during both glacial and interglacial maxima, providing the potential for species persistence in these areas. In addition, the vicinity of the Amga River basin between the Lena River and Verkhoyansk Range in central Siberia is strongly predicted during both time frames.

Population genetic statistics – European *S. minutissimus* are consistently most divergent from other populations at ~1.5%, followed by MNA *S. minutissimus* at ~ 1.0% uncorrected sequence divergence (Table 1). Siberian *S. minutissimus* are minimally divergent from Alaska *S. yukonicus* at 0.6%. Among populations, haplotype and nucleotide diversity are high for SE Siberia, MNA, and Europe-to-Yenisei (Table 2) and comparatively low for Alaska, Siberia, and Finland. In particular, Alaska *S. yukonicus,* and Siberia *S. minutissimus* exhibit minimal genetic diversity among all individuals, and all but 1 haplotype is unique to only 1 or 2 individuals. However, most Finland haplotypes are shared among multiple individuals. Specimens of *S. minutissimus* from Amga River collectively exhibit relatively high nucleotide and haplotype diversity (π = 0.004; *Hd* = 0.933). Population growth statistics (Table 2) are significant for Alaska and Siberia but not significant for SE Siberia, MNA, Finland, or Europe-to-Yenisei.

Temporal divergence and effective population size change - With an estimated mutation rate for *S. minutissimus* at 5.5%/million years (My), the time to coalescence of lineages within the *minutissimus/yukonicus* group for the *Cytb* locus was calculated using posterior probabilities. The T_{MRCA} can be considered a minimum estimate for divergence, considering times related to the glacial periodicity of the middle Pleistocene to present. The T_{MRCA} values for all lineages within the *minutissimus/yukonicus* group were dated from an earliest date in the previous (Sangamon) interglacial at 0.13 Ma to most recently near the close of the Wisconsinan/Weichselian glacial at 0.04 Ma (mean values; Table 3). The 95% *CI* includes times coincident with the Illinoian glacial (up to 0.22 Ma) for the T_{MRCA} of the entire *minutissimus/yukonicus* group and for T_{MRCA} of MNA and European populations, but T_{MRCA} for all Beringian populations and Finland fall strictly within the Wisconsinan glacial. Bayesian skyline plots (BSPs) give a visual interpretation of change in effective population size (N_e) through time. Alaska *S. yukonicus* (eastern Beringia), Siberia *S. minutissimus* (western Beringia excluding SE Siberia), and Europe all indicate an increase in N_e during the late stages of the Wisconsinan glacial followed by a leveling off towards the present (Fig. 5). Population growth was estimated earliest within Europe (from ~ 0.045 Ma) and latest in Alaska (~ 0.020 Ma). For the entire *minutissimus/yukonicus* group ancestral N_e was calculated to be 120,000 and contemporary N_e to be 2,000,000.

DISCUSSION

During Pleistocene glacial episodes the Nearctic and Palearctic were connected multiple times as a single continental landmass so genetic associations of the contemporary biota across the Holarctic are a result of this dynamic history. The *minutissimus/yukonicus* group has a current distribution that reflects the reach of Eurasia into North America across Beringia during glacial maxima. The close relationship of *S.*

minutissimus and *S. yukonicus* provides an opportunity to investigate the dynamics of northern intercontinental exchange and diversification. Although 2 species in this group are recognized (Hutterer 2005), the asymmetric distribution on either side of the Bering Strait and low divergence across loci suggests a relatively recent colonization of these shrews into North America.

This first investigation of genetic relationships within the *minutissimus/yukonicus* group reveals that although strong support exists for both an Alaska clade and a combined Beringia clade based on only the *Cytb* gene (Fig. 3), these relationships are supported only weakly across multiple loci (Fig. 4). Instead, the most distinct evolutionary lineages within the *minutissimus/yukonicus* group consist of European *S. minutissimus* and MNA *S. minutissimus* (Fig. 3; Fig. 4). European *S. minutissimus* are distinct in all genealogies, separately and combined. A lack of genetic distinction of *S. yukonicus* over multiple loci is consistent with recent isolation, and T_{MRCA} places divergence of the Alaska population from Asian populations in the late Wisconsinan glacial (Table 3).

Population genetics and demographics – Ohdachi et al. (2001) recognize a sister relationship between *S. minutissimus* and *S. hosonoi*. We found that these species were reciprocally monophyletic but closely related. Uncorrected sequence divergence between the *minutissimus/yukonicus* group and *S. hosonoi* of 8.6% (*Cytb*) is consistent with levels of differentiation observed in other sister species of shrews (Demboski and Cook 2001; Fumagalli et al. 1999). Levels of mtDNA sequence differentiation of ≤2.2% for all *S. minutissimus* and *S. yukonicus* comparisons are typical of intraspecific differentiation in shrews (e. g., *Sorex cinereus*—Demboski and Cook 2003). Sequence divergence between Siberian *S. minutissimus* and Alaskan *S. yukonicus* of 0.6% suggests that these populations have not been isolated for an extended period (Table 1). Haplotype and nucleotide diversity are low (Table 2), and we interpret these patterns as reflecting recent population expansion, a conclusion supported by significant values over multiple measures of expansion (Table 2). Significance over multiple expansion statistics suggests that expansion, and not selection, is the major influence producing this genetic signature (Lessa et al. 2003).

Biogeographic perspectives – European and MNA clades within the *minutissimus/yukonicus* group likely reflect distinct geographic partitioning and temporal divergence. Environmental associations in the form of ENMs provide a framework for generating hypotheses of spatiotemporal divergence within a species group. The limited distribution of *S. yukonicus* in North America to only Alaska, despite a predicted potential distribution that spans northern Canada (Fig. 1A), raises several possibilities: 1) this species is competitively excluded from some areas of potential habitat in North America, 2) it is physically constrained to Alaska by some geographic barrier, or 3) it has not had the time to disperse into available habitat across Canada. A competitive exclusion hypothesis has not been investigated, and little is known of interspecific ecological relationships for *S. yukonicus,* although it is sympatric with 5 other species of *Sorex* (MacDonald and Cook 2009). A physical barrier such as the north/south orientation of the Mackenzie Mountains at the border of Yukon and Northwest Territories delimits the eastern edge of Beringia (i.e., the western extent of the Laurentide Ice Sheet at the LGM) and could pose a significant barrier to dispersal of *S. yukonicus* eastward (Fig. 2). If the Mackenzie Mountains constituted a barrier to *S. yukonicus* over multiple glacial cycles, we would expect high genetic diversity within *S. yukonicus* combined with statistics reflecting population stability. Instead, the molecular signal suggests that *S. yukonicus* is a recent occupant of Alaska. Estimates of T_{MRCA} coincide with the most recent glacial period (Table 3), and BSPs indicate population expansion took place in the Holocene.

In Eurasia *Sorex minutissimus* exhibits 2 major phylogeographic breaks, 1 separating European individuals (east to the Yenisei R.) from Siberian (Ohdachi et al 2001) and 1 separating MNA individuals (Primorsky Krai and Insular) from all others. All 3 groups are consistent with diversification in ENM-predicted refugia (Fig. 1B). In addition, these breaks are shared across other taxonomic groups. Among mammals, a phylogeographic break at the Ural Mountains and again at the western edge of Beringia has been identified for lemmings, (*Dicrostonyx groenlandicus*—Fedorov and Goropashnaya 1999; Fedorov and Stenseth 2002) and the root/tundra vole (*Microtus oeconomus*—Brunhoff et al. 2003). A split between a clade centered on northern Eurasia and 1 centered on MNA (Primorsky Krai near the Amur River) has been suggested for *Myopus schisticolor* (Fedorov et al. 2008), *Micromys minutus* (Yasuda et al. 2005), and *Cervus elaphus* (Ludt et al. 2004). Although much of Siberia remained ice-free through Pleistocene glacial periods, much of northern Europe was covered by the Fennoscandian ice sheet. *Sorex minutissimus* likely persisted in 1 or more refugia south of the ice sheet such as the Carpathian, Black Sea, or Caucasian refugia, as predicted by our ENM (Fig. 1B; Fig. 2) and as has been predicted for other species (Flojgaard et al. 2009). The exact location of refugia for each clade within *S. minutissimus* is unknown, but evidence from fossils shows that *S. minutissimus* occurred from the Caucasus to north of the Black Sea during the late Pleistocene (Zaitsev and Osipova 2005). In addition, a fossil attributable to *S. minutissimus* was found in South Korea dating to the mid to late Pleistocene (Ohdachi et al. 1997). Structure within Europe uncovers 2 distinct clades, 1 consisting of Finland individuals and another of individuals distributed from Finland eastward to the Yenisei River. The most basal individuals from the Europe-to-Yenisei group are easternmost in distribution opening the possibility of an origin of this group in southcentral Russia (Fig. 2). Considering no individuals belonging to the Siberian clade occur west of the Yenisei River, the geographic area known as the Siberian Plain between the Ural Mountains east to the Yenisei River likely represents the geographic border between European and Siberian groups. The Siberian Plain constituted extensive pluvial lakes during glacial maxima (Mangerud et al. 2004) and currently constitutes extensive swamplands and formidable rivers, providing a potentially permanent barrier to dispersal of taxa. Il'yashenko and Onishchenko (2003) report a morphological break between west and east Siberian *S. minutissimus*, and a phylogeographic break in the vicinity of the Yenisei River also is shown for moose (Boyeskorov 1999; Grubb 2005; Hundertmark et al. 2002).

In Siberia and MNA, environmental predictions from ENMs suggest potential persistence of *S. minutissimus* in large refugial areas (Fig. 1), although LGM environments in Beringia were considered to have been harsh (DeChaine 2008; Elias and Crocker 2008). Within MNA population stability is reflected in expansion statistics (Table 3). Other populations (Alaska and Siberia) that might have persisted within Beringia all show significant expansion signals dated from the LGM (Table 2; Fig. 5). We suggest that ancestors of Alaskan and Siberian populations persisted in discrete areas within Beringia in low numbers through the Wisconsinan, followed by subsequent range expansion and population growth. Ancestral population size is greater than an order of magnitude lower than contemporary size estimates, suggesting emergence from a population bottleneck. Evidence for another refugium within Eurasia consists of a clade centered on SE Siberia that is bounded by the Dzhugdzhur Range and Stanovoy Range to the north and the Amur River to the south (Fig. 2). Additionally, high genetic diversity exists within the 6 individuals collected from the Amga Basin of Central Siberia that is indicative of persistence. The Amga Basin is geographically isolated in central Siberia and surrounded by the Verkhoyansk Range to the North, Dzhugdzhur Range to the East, Stanovoy Range to the South, and Lena River to the West (Fig. 2).

Taxonomy – We tested hypotheses pertaining to the taxonomic validity of *S. minutissimus and S. yukonicus*. Three distinct biogeographic regions for these shrews were identified: Europe, MNA, and Beringia. All are recently divergent at levels coincident with isolation through the Wisconsinan/Weichselian glacial period. Minimal sequence divergence across Beringia (0.6%; *Cytb*) is inconsistent with species-level molecular differentiation within *Sorex*. This pattern of minimal differentiation across the Bering Strait is comparable to levels of divergence among several nominal species within the *S. cinereus* group in Beringia (Demboski and Cook 2003) and suggests the need for careful reevaluation of a number of shrew complexes at these high latitudes. Low genetic divergence that reflects recent isolation in Alaska and lack of reciprocal monophyly between the two nominal species suggests that they represent a single species, *S. minutissimus*, as originally proposed (Dokuchaev 1994). We hypothesize that Alaskan populations were recently isolated from Siberian *S. minutissimus* by rising sea levels that inundated the Bering Land Bridge.

Evidence from multiple independent loci shows that European *S. minutissimus* is consistently diagnosable (e.g., genetic distance of 1.5%; *Cytb*). Recent coalescence of the *Cytb* gene within *S. minutissimus* is at odds with fossil evidence of this species occurring in Europe from the early Pleistocene (Rzebik-Kowalska 1995; 2005). However, Rzebik-Kowalska (1995) suggested marked movement of these shrews in response to climate change that would be consistent with ENM predictions within Europe (Fig. 1). Recognized karyotypic differences between European and Siberian *S. minutissimus* (2N = 38 versus 42, respectively—Hutterer 2005) further corroborate the genetic distinction between the shrews of these regions. The type specimen for *S. minutissimus* is described from the vicinity of the Yenisei River (Hutterer 2005) corresponding with our hypothesized phylogeographic break between European and Siberian clades; therefore, taxonomic revision should wait for additional sampling from this region.

Future directions – In light of our conclusions, *S. minutissimus* provides a contemporary snapshot into the evolutionary processes acting on mammals at the nexus between the northern continents. Alaskan populations of *S. minutissimus* are now on a unique evolutionary trajectory through physical isolation from Eurasia at the Bering Strait, although relatively short interglacial isolation could be followed by reconnection and population admixture before reproductive isolation is achieved. In addition, physical boundaries coupled with dynamic climate shifts in Eurasia have produced distinct genetic lineages within *S. minutissimus*, suggesting the presence of previously undiscovered refugial areas. We stress the relative paucity of information pertaining to spatiotemporal evolution of the biota within Siberia considering potential persistence in ice-free high-latitude areas through extended periods of glacial cycling. The 77 extant species of *Sorex* occur in either the Palearctic or Nearctic (Hutterer 2005), with the exception of *Sorex tundrensis* and now *S. minutissimus,* which are the only species recognized as Holarctic. Across its broad range *S. minutissimus* is sympatric or parapatric with up to 18 other species of *Sorex* (MacDonald and Cook 2009; Sheftel 2005). A comparative phylogeographic approach should be implemented that aims to explore the response of multiple related species as a precursor to understanding how members of this diverse genus will respond to future environmental scenarios (Carnaval et al. 2009). Understanding how the constituents of these high-latitude communities responded to past climatic cycling can provide insight into community change through time and pinpoint cold-adapted species that could be of future conservation concern (Lister 2004). Finally, further investigation of phylogenetic relationships within the genus *Sorex* throughout the Holarctic will help to clarify evolutionary processes within this widespread, diverse, and enigmatic genus of mammals.

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APPENDIX I

Specimens examined are listed by scientific name, specific locality number (corresponding to Fig. 2), specific locality, specimen number (museum catalog number or tissue number, corresponding to Fig. 3), and corresponding GenBank Accession numbers (mtDNA cytochrome-*b*, nDNA apolipoprotein B, nDNA breast cancer susceptibility 1). Acronyms for museum or tissue numbers are FN = Finland tissues (provided by H, Henttonen); MSB = Museum of Southwestern Biology; SZMN = Siberian Zoological Museum, Novosibirsk; UAM = University of Alaska Museum of the North, Fairbanks; ZMMU = Zoological Museum of Moscow University.

Sorex yukonicus – **(1)** USA, Alaska: Goodnews River: UAM45820 (GU223640, HM002722, HM002741); UAM45841 (GU223642, GU223686, GU223718); UAM45843 (GU223641, N/A, N/A); **(2)** USA, Alaska: Serpentine Hot Springs: UAM55806 (GU223647, GU223690, 223722); **(3)** USA, Alaska: Devil Mountain Lakes: UAM56130 (GU223644, GU223688, GU223720); UAM56133 (GU223645, GU223689, GU223721); UAM56157 (GU223646, N/A, N/A); **(4)** USA, Alaska: 12.5 km ENE of Kathul Mountain: UAM57059 (GU223656, N/A, N/A); UAM57104 (GU223654, GU223695, GU223727); UAM57111 (GU223655, HM002724, HM002743); UAM57142 (GU223652, GU223693, GU223725); UAM57395 (GU223653, GU223694, GU223726); UAM59401 (HM002706, N/A, N/A); **(5)** USA, Alaska: Carden Hills: UAM57531 (GU223657, GU223696, GU223728); **(6)** USA, Alaska: Glenn Creek Cabin: UAM58567 (GU223650, HM002723, HM002742); **(7)** USA, Alaska: Kandik Cabin: UAM60167 (GU223651, GU223692, GU223724); **(8)** USA, Alaska: across Yukon River from Glenn Creek Cabin: UAM60281 (GU223648, GU223691, GU223723); UAM60566

(GU223649, N/A, N/A); **(9)** USA, Alaska: Chilchukabena Lake: UAM64945 (GU223658, GU223697, GU223729); **(10)** USA, Alaska: 7 mi SW Red Devil: UAM72928 (GU223643, GU223687, GU223719); **(11)** USA, Alaska: Fortress Mountain: UAM78467 (GU223659, HM002725, HM002744); **(12)** USA, Alaska: Chulitna River and Turner Bay confluence: UAM91874 (GU223660, GU223682, GU223714); UAM91898 (GU223661, GU223683, GU223715); **(13)** USA, Alaska: Waring Mountains: UAM93385 (GU223685, GU223717); **(14)** USA, Alaska: Baird Mountains, Salmon River: UAM93397 (GU223663, N/A, N/A); **(15)** USA, Alaska: Baird Mountains, headwaters of Akillik River: UAM93432 (GU223664, N/A, N/A); **(16)** USA, Alaska: Kakagrak Hills: UAM94323 (HM002707, N/A, N/A); UAM94362 (GU223622, GU223648, GU223716); **(no specific locality recorded)** USA, Alaska: UAM29830 (GU223639, GU223681, GU223713).

Sorex minutissimus – **(17)** Finland: Haapavesi, Mieluskylä: FN 9834 (HM002675, N/A, N/A); **(18)** Finland: Utajärvi, Pälli: FN 14167 (HM002664, N/A, N/A); FN 16151 (HM002665, HM002708, HM002727); FN 16180 (HM002666, N/A, N/A); FN XX (HM002676, HM002711, HM002730); **(19)** Finland: Kuusamo: FN 17905 (HM002667, N/A, N/A); **(20)** Finland: Oulu, Kaukovainio: FN 21013 (HM002668, N/A, N/A); **(21)** Finland: Kiiminki: FN 28217 (HM002669, N/A, N/A); **(22)** Finland: Rovaniemi, Kaihua: FN 32194 (HM002670, HM002709, HM002728); **(23)** Finland: Kuivaniemi, Korkiakangas: FN 39930 (HM002671, N/A, N/A); Finland: Kuivaniemi, Näsiö: FN 39931 (HM002672, N/A, N/A); FN 39932 (HM002673, N/A, N/A); **(24)** Finland: Tervola, Karsikkokangas: FN 46979 (HM002674, N/A, N/A); **(25)** Finland: Enonkoski: FN EN13 (HM002676, HM002710, HM002729); **(26)** Finland: Salla: FN MSS

(GU223627, GU223678, GU223710); **(27)** Finland: Pallasjärvi: FN PJ11 (GU223628, GU223679, GU223711); FN PJ10809 (HM002696, N/A, N/A); FN PJ11009 (HM002697, HM002726, HM002745); FN 20809 (HM002698, N/A, N/A); **(28)** Finland: Kuhmo: UAM24767 (HM002693, HM002720, HM002739); **(no specific locality recorded)** Finland: FN 100 (HM002663, N/A, N/A); Finland: UAM53332 (HM002695, N/A, N/A); **(29)** Mongolia: Hangal Soum: MSB94040 (GU223629, N/A, N/A); **(30)** Russia, Magadanskaya Oblast: Stokovo Station: MSB144877 (HM002704, HM002712, HM002731); **(31)** Russia, Republic of Sakha: Delyankir River: MSB144903 (GU223631, GU223671, GU223703); **(32)** Russia, Khabarovskyi Krai: Okhotsk Village: MSB148033 (GU223632, GU223672 GU223704); MSB148072 (GU223633, GU223673, GU223705); **(33)** Russia, Republic of Sakha: Amga River Basin, 7 km N Sulgachi: MSB148416 (HM002705, HM002721, HM002740), ; MSB148592 (GU223634, GU223674, GU223706); MSB148593 (GU223635, N/A, N/A); **(34)** Russia, Republic of Sakha: Amga River. 10 km NE Sulgachi: MSB148567 (HM002694, HM002713, HM002732); **(35)** Russia, Republic of Sakha: Amga River, 8 km ENE Mikhaylovka: MSB148650 (GU223636, GU223675, GU223707); MSB148651 (GU223637, GU223676, GU223708); **(36)** Russia, Magadanskaya Oblast: Omolon: SZMN 2830 (HM002680, N/A, N/A); **(37)** Russia, Primorskyi Krai: Kedrovaya Pad Reserve: SZMN 2838 (HM002681, N/A, N/A); **(38)** Russia, Tomskaya Oblast: Kozhevnikovo Village: SZMN 6748 (HM002684, N/A, N/A); **(39)** Russia, Republic of Tuva: Totginskyi District, Lake Azas: SZMN 8327 (HM002686, N/A, N/A); **(40)** Russia, Republic of Altai: Cherga: SZMN11669 (HM002699, N/A, N/A); **(41)** Russia, Republic of Buryatia: Muhurshibir: FN B50 (GU223626, GU223677, GU223709); **(42)** Russia, Amurskaya Oblast: Zeya:

SZMN 12841 (HM002679, N/A, N/A); **(43)** Russia, Krasnoyarskyi Krai: Western Sayan, Abaza: SZMN 26895 (HM002700, HM002714, HM002733); **(44)** Russia, Irkutskaya Oblast: Zhigalovskyi District, Yakimovka: SZMN 32776 (HM002682, N/A, N/A; **(45)** Russia, Sakhalinskaya Oblast: Novoaleksandrovsk Village: SZMN 32783 (HM002701, HM002715, HM002734); **(46)** Russia, Krasnoyarskyi Krai: Taimyr, Pyasina River: SZMN 32801 (GU223638, HM002719, HM002738); **(47)** Russia, Republic of Tuva: Totginskyi District, Shurmak Village: SZMN 50322 (HM002683, HM002716, HM002735); **(48)** Russia, Zabaykalskyi Krai: Kyra, Sochondinskyi Reserve: SZMN 80119 (HM002685, HM002717, HM002736); **(49)** Russia, Novosibirskaya Oblast: Karasukskyi: SZMN M340 (GU223630, GU223680, GU223712); **(50)** Russia, Magadanskaya Oblast: near Magadan: UAM37987 (HM002702, N/A, N/A); **(51)** Russia, Kamchatskyi Krai: 22 km SW of Elizovo: UAM73463 (GU223625, N/A, N/A); **(52)** Russia, Republic of Buryatia: NE lakeside, Baikal: ZMMU S85347 (HM002689, N/A, N/A); **(53)** Russia, Republic of Karelia: Pudoch Region: ZMMU S95657 (HM002690, N/A, N/A); ZMMU S95658 (HM002691, N/A, N/A); ZMMU S95659 (HM002692, N/A, N/A); **(54)** Russia, Krasnoyarskyi Krai: Turukhanskyi District, Village Mirnoe: ZMMU S102719 (HM002687, HM002718, HM002737); **(55)** Russia, Kostroma Oblast: Manchurovskia: ZMMU S177601 (HM002688, N/A, N/A); **(no specific locality recorded)** Russia: SZMN 11770 (HM002678, N/A, N/A); **(56)** Russia, Magadanskaya Oblast: Chelomdzha River: (AB028584, N/A, N/A; AB028585, N/A, N/A; AB028587, N/A, N/A); **(57)** Russia, Kamchatskyi Krai: (AB028586, N/A, N/A); **(58)** Russia, Khabarovskyi Krai: (AB028588, N/A, N/A); **(59)** Russia Sakhalinskaya Oblast: Kuriles, Kunashir Island: (AB028589, N/A, N/A); **(60)** Russia, Primorskyi Krai: (AB175129,

N/A, N/A; AB175130, N/A, N/A); **(61)** Japan: Hokkaido Island: (AB028590, N/A, N/A; AB028591, N/A, N/A).

Sorex hosonoi (all retrieved from Genbank; *Cytb* only) – Japan: Honshu Island: AB028593; AB028594; AB028595; AB028596; AB028597.

Sorex arcticus – Canada, British Columbia: Horn Lake: UAM77955 (GU223666, GU223698, GU223730).

Sorex caecutiens – Russia, Republic of Sakha: Lena River, 2 km NW Tochtur: MSB146478 (GU223668, GU223699, GU223731).

Sorex daphaenodon – Russia, Republic of Sakha: Amga River, 8 km ENE Mikhaylovka: MSB148704 (GU223669, GU223700, GU223732).

Sorex minutus – Hungary: Osli, Kiraly-to: MSB95476 (GU223667, GU223702, GU223733).

Sorex roboratus – Russia, Republic of Sakha: Kenkeme River, 40 km W Yakutsk: MSB148679 (GU223670, GU223701, GU223734

Table 1 -- Uncorrected sequence divergence between major clades within the *minutissimus/yukonicus* group using the cytochrome b gene. Beringia consists of 2, 3, and 4; Europe consists of both 7 and 8. Sorex hosonoi is the recognized sister taxon to the minutissimus/yukonicus group.

Group	1	2	3	4	5	6	7	8	9
1. Beringia	--	--	--	--	0.010	0.014	0.013	0.018	0.086
2. *S. yukonicus*- Alaska	--	--	0.006	0.009	0.010	0.014	0.013	0.018	0.086
3. *S. minutissimus*- Siberia	--	--	--	0.009	0.010	0.013	0.012	0.018	0.086
4. *S. minutissimus*- SE Siberia	--	--	--	--	0.014	0.017	0.016	0.022	0.086
5. *S. minutissimus*- MNA	--	--	--	--	--	0.011	0.010	0.016	0.082
6.Europe	--	--	--	--	--	--	--	--	0.086
7. *S. minutissimus* - Finland	--	--	--	--	--	--	--	0.006	0.086
8. *S. minutissimus* - Europe-to-Yenisei	--	--	--	--	--	--	--	--	0.086
9. *Sorex hosonoi*	--	--	--	--	--	--	--	--	--

Table 2 -- Population genetic statistics for all major clades within the *minutissimus/yukonicus* group. Summary statistics are *n* = sample sizes; *S* = segregating sites; *h* = number of haplotypes; *Hd* = haplotype diversity; ; π = nucleotide diversity. Population growth statistics are Tajima's *D*, Fu's *Fs*, and Ramos-Onsins and Rozas' *R2*. Significance of growth statistics are indicated by asterisks (* *P*<=0.05; ***P*<=0.01; ****P*<=0.001).

Group	*n*	*S*	*h*	*Hd*	π	*D*	*Fs*	*R2*
All	84	51	37	0.917	0.009	N/A	N/A	N/A
Beringia	56	26	22	0.843	0.005	-1.819*	-14.525***	0.043**
S. yukonicus- Alaska	29	8	8	0.571	0.001	-1.848**	-5.027***	0.054***
S. minutissimus- Siberia	20	9	8	0.647	0.002	-1.869**	-4.361***	0.069***
S. minutissimus - SE Siberia	5	7	4	0.900	0.005	-0.747	-0.332	0.172
S. minutissimus- MNA	6	11	6	1.000	0.007	-0.943	-2.587*	0.145
Europe	22	14	9	0.797	0.004	-1.552	-2.670	0.069***

S. minutissimus - Finland	14	2	3	0.582	0.001	0.036	-0.040	0.179
S. minutissimus - Europe-to-Yenisei	5	9	4	0.900	0.008	0.132	0.286	0.166

Table 3 -- Divergence estimates using BEAST showing the sample size (*n*), and the mean for time to most recent common ancestor (T_{MRCA}) for major groups with 95% C.I. within the *minutissimus/yukonicus*group and including the sister species *S. hosonoi.*

		Mean T_{MRCA}	
Group	*n*	My	*95% C.I.*
S. minutissimus/S. hosonoi	99	**0.98**	0.79-1.19
S. minutissimus/S. yukonicus	51	**0.13**	0.07-0.20
Beringia	57	**0.08**	0.04-0.13
S. yukonicus- Alaska	29	**0.04**	0.02-0.07
S. minutissimus- Siberia	21	**0.04**	0.02-0.07
S. minutissimus - SE Siberia	5	**0.05**	0.02-0.09
MNA	7	**0.12**	0.03-0.22
S. minutissimus - Primorski	3	**0.04**	0.01-0.08
Europe	30	**0.10**	0.05-0.16
S. minutissimus - Finland	20	**0.04**	0.02-0.08
S. minutissimus - Europe-to-Yenisei	8	**0.09**	0.04-0.14

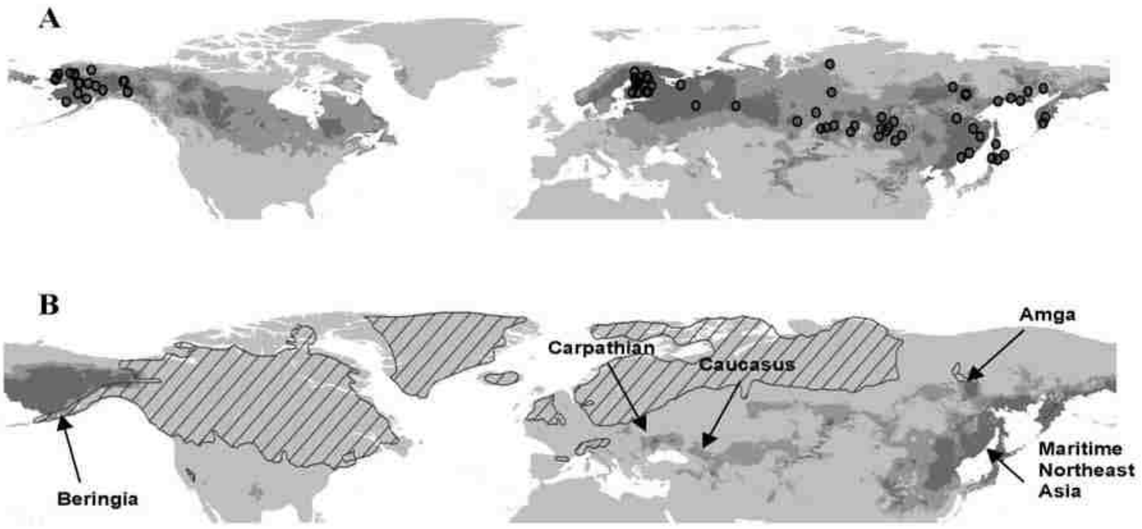

Fig. 1 – Ecological niche models depicting potential distribution for the *Sorex minutissimus/yukonicus* group during A), the present and B), the Last Glacial Maximum (LGM) dated to 18 ka. Circles indicate specimen locality records used to produce ecological niche models (ENMs). Dark shading indicates strong distributional prediction and light shading a weak prediction. Some potential refugia are labeled for the LGM. Slanted lines indicate extent of major ice sheets at the LGM.

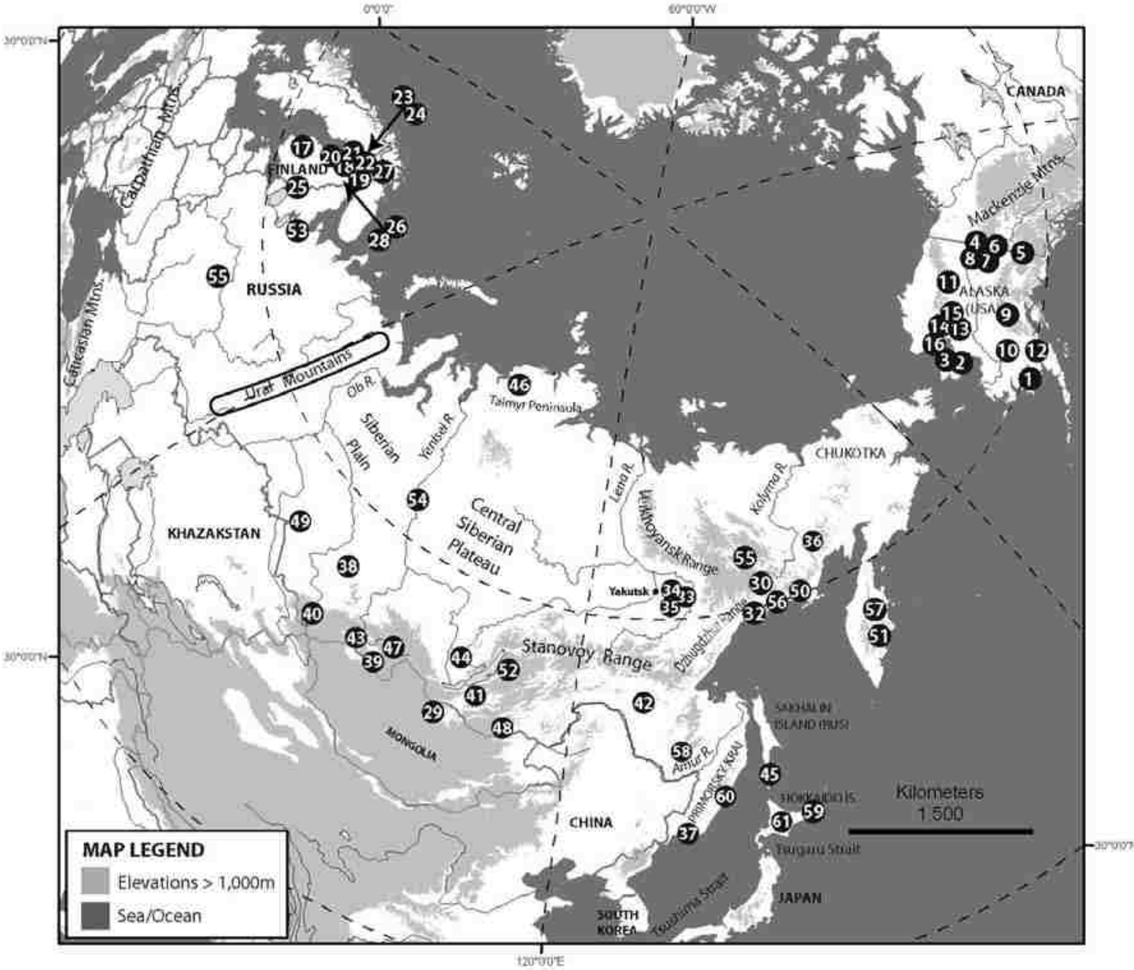

Fig. 2– Map of the study area illustrating major geographic features within the Holarctic that reflect potential phylogeographic breaks. Specimen localities are indicated by number corresponding with Appendix I and are associated with designated clades from Bayesian cytochrome-*b* phylogeny reconstruction (Alaska: 1-16; Siberia: 29, 30-36, 39, 44, 47, 50, 51, 54, 56-58; SE Siberia: 41, 42, 48, 52, 59; MNA: 37, 45, 60, 61; Europe-to-Yenisei: 25, 28, 38, 40, 43, 49, 53, 55; Finland: 17-24, 26, 27)

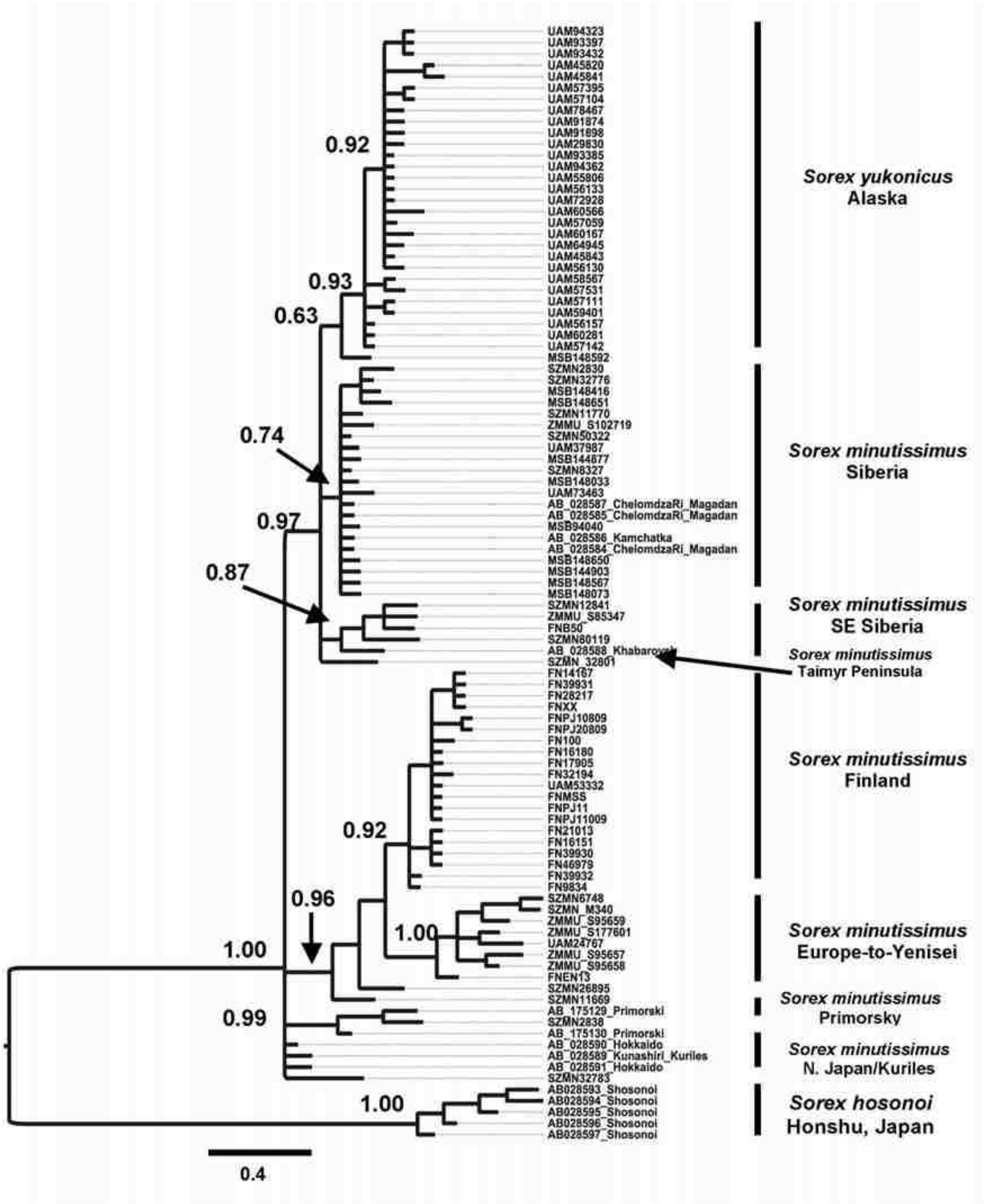

Fig. 3– Bayesian phylogeny representing a midpoint-rooted genealogy for the *Sorex minutissimus/yukonicus* group based on cytochrome-*b* gene sequences (561-1,140 bp). Posterior probabilities for major nodes are illustrated. *Sorex hosonoi*, a Honshu Island endemic, is included as the sister species.

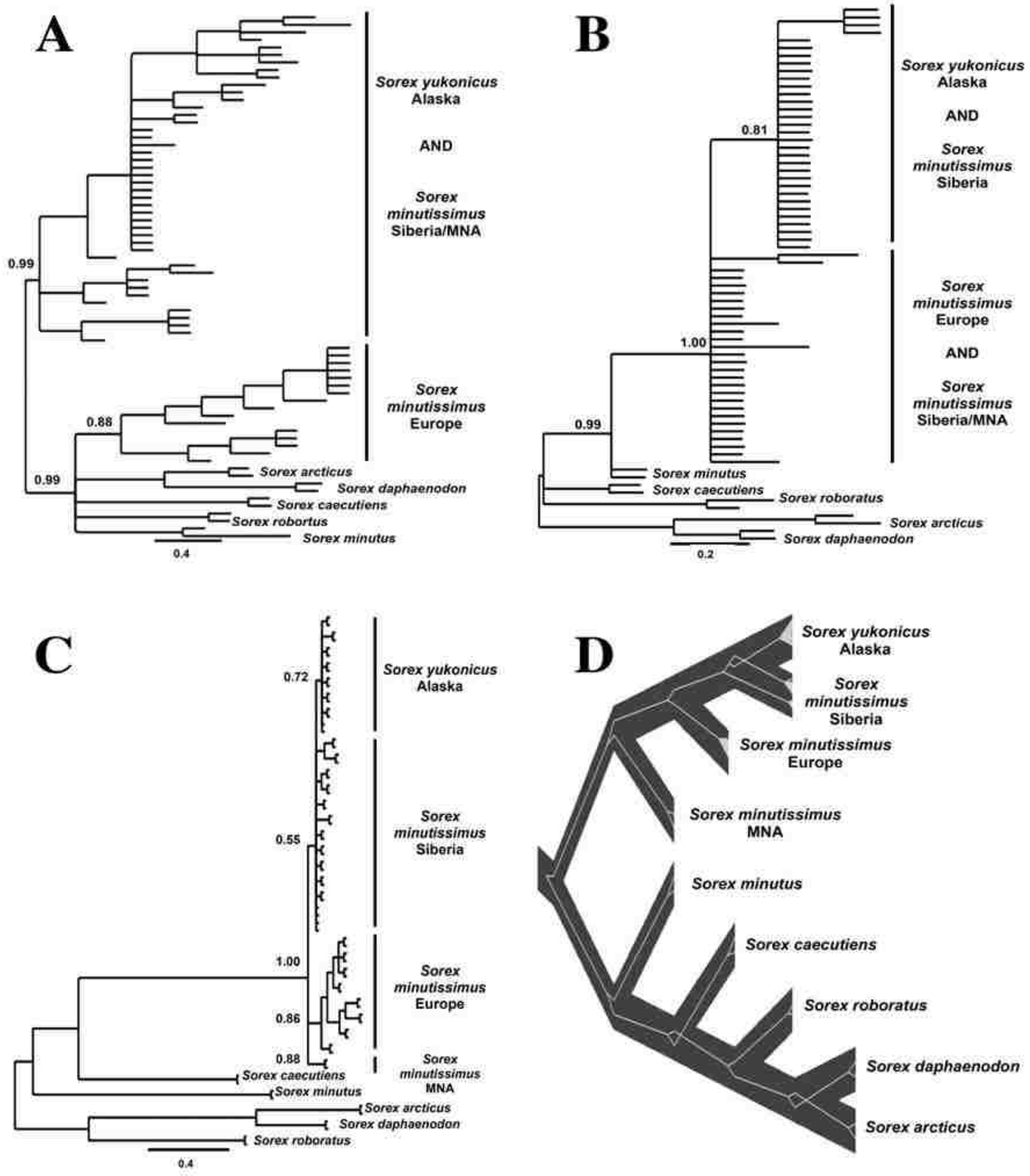

Fig. 4– Gene tree and species tree reconstructions for the *Sorex minutissimus/yukonicus* group using independent loci: A =ApoB; B = BRCA1; C = *Cytb*. Posterior probabilities for major nodes are illustrated (≥ 0.95 are considered significant) with major clade relationships. Species tree D was produced using the minimizing deep coalescences method and the line shows the BRCA1 genealogy.

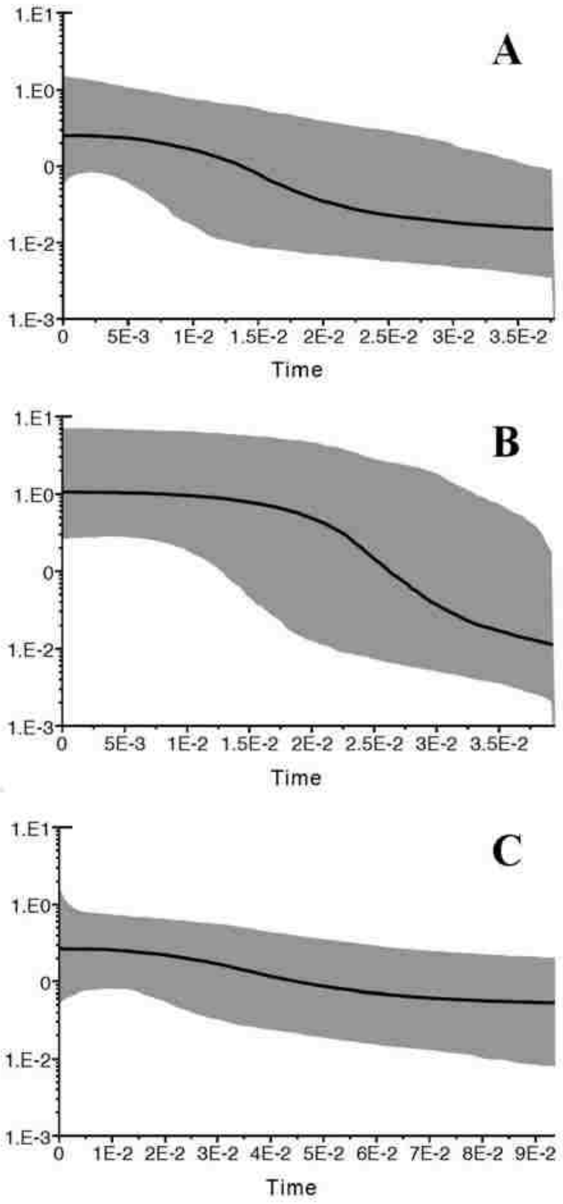

Fig. 5– Bayesian skyline plots for A), Alaska *S. yukonicus*; B), Siberia *S. minutissimus*; and C), Europe *S. minutissimus*, created in BEAST from the cytochrome-*b* data set. Central line indicates the BSP and change in effective population size through time. Shading defines the 95% *CI*. BSPs here extend right-to-left from past to present scaled in millions of years. Vertical axis represents τ as a function of generation time and effective population size.

CHAPTER 2

Persistence and diversification of the Holarctic shrew, *Sorex tundrensis* (Family Soricidae), in response to climate change.

Running Title: Phylogeography of a Holarctic shrew

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Key words: Beringia, ecological niche model, evolution, phylogeography, Pleistocene refugia, shrew.

Abstract

Environmental processes govern demography, species movements, community turnover, and diversification at high-latitudes and yet in many respects these dynamics are still poorly understood. We investigate the combined effects of climate change and geography through time for a widespread Holarctic shrew, *Sorex tundrensis*. We include a comprehensive suite of closely related outgroup taxa and three independent loci to explore phylogeographic structure and historical demography. We then explore the implications of these findings for other members of boreal communities. The tundra shrew and its sister species, the Tien Shan shrew (*S. asper*), exhibit strong geographic population structure across Siberia and into Beringia illustrating local centers of endemism that correspond to Late Pleistocene refugia. Ecological niche predictions for both current and historical distributions indicate a model of persistence through time despite dramatic climate change. Species tree estimation under a coalescent process suggests that isolation between populations has been maintained across timeframes deeper than the periodicity of Pleistocene glacial cycling. That some species such as the tundra shrew have a history of persistence largely independent of changing climate, whereas other boreal species shifted their ranges in response to climate change, highlights the dynamic processes of community assembly at high latitudes.

Introduction

The Holocene epoch represents an interglacial warming stage since the Last Glacial Maximum (LGM) of the Late Pleistocene (Brigham-Grette 2009; MacDonald 2010), with high potential for continued directional climate change in the immediate future, largely due to highly elevated atmospheric carbon dioxide (Oechel *et al.* 2000; Schuur *et al*. 2009). Understanding how species respond to such pronounced change could help guide management initiatives, including maintenance of the various components of biodiversity (Myers *et al*. 2000). To do this we can study the response of organisms to current (e.g.

McCarty 2001) or past (Hewitt 2000; Lister 2004; Hofreiter & Stewart 2009) ecological change. By identifying processes influencing patterns of diversification through space and time, for example, linkages between geography, climate, and diversity can be used to pinpoint vital biogeographic areas (Hewitt 2004). These may be common centers of endemism, significant geographic barriers, or corridors to dispersal. We can then focus management efforts by identifying and conserving populations, species, or communities that are most at risk due to environmental change (Carnaval *et al*. 2009).

High-latitude environments are heavily influenced by long-term climatic variability that is coupled with strong seasonality (Hewitt 2000). Resident species are, to varying degrees, specialized for a cold climate, as exemplified by the tundra community of the Arctic. Under current climate warming scenarios, tundra-associated species may be at significant risk of local extirpation or extinction (Lawler *et al*. 2009). The tundra shrew, *Sorex tundrensis*, is a cold-associated shrew found in mesic tundra and taiga habitats and particularly associated with low-lying floodplain areas from temperate to high Arctic latitudes (Nagorsen & Jones 1981; Churchfield *et al*. 1997). This shrew belongs within the *araneus-arcticus* group of 11 nominal species, which together span the Holarctic, from the United Kingdom and Spain eastward across Asia and into the Nearctic to the Canadian Maritime Provinces (Junge *et al*. 1983; Fumagalli *et al*. 1996; Stewart *et al*. 2002). This broad distribution provides an opportunity to investigate high latitude processes of diversification in response to climate change, and a stepping-stone for future research that can be extended across multiple tundra and taiga species to provide an integrated perspective on community dynamics.

Beringia is a recognized Pleistocene refugium, a center of endemism, and a corridor for transcontinental dispersal at the nexus of the Holarctic (Cook *et al*. 2005). Changing climate has led to multiple exchanges of species across Beringia, essentially mixing the biotas of Asia and North America. The direction, timing, and consequences of colonization through this corridor are now receiving greater attention, including a series of molecular studies of northern organisms (e.g. Dubey *et al*. 2007; Waltari *et al*. 2007b). Within Siberia however, phylogeographic patterns remain poorly understood. This region is key to understanding high latitude diversification because it remained largely ice-free during glacial episodes (Svendsen *et al*. 2004). In response to changing climate, Siberian species shifted their ranges to track preferred conditions, persisted in widespread or discrete refugia, or periodically became extirpated due to unfavorable conditions (Provan & Bennett 2008). Although currently widespread across the Palearctic, *S. tundrensis* has a limited Nearctic distribution (Alaska, nearby Yukon Territory and northernmost British Columbia; Nagorsen & Jones 1981; Junge *et al*. 1983). This asymmetric distribution suggests relatively recent eastward colonization from Eurasia, further indicating that Siberian populations are a critical component to understanding diversification of this species.

Recently, Bannikova *et al.* (2010) presented a phylogeographic assessment of *S. tundrensis* utilizing mitochondrial loci to describe genetic structure and demography, including an assessment of divergence times for described clades, and with strongest geographic representation from western Siberia. We present a complimentary study, providing comprehensive sampling of *S. tundrensis*, particularly from Beringia and Central Siberia, and including members of the closely related *araneus-arcticus* group.

We expand on Bannikova *et al.* (2010) by utilizing multiple loci to provide independent assessments and species tree estimation from multiple genealogies, all under a framework formed by predictions based on ecological niche modeling (ENM). We also provide the first assessment of species relationships that includes all recognized species within the *araneus-arcticus* group, and a demographic analysis of the sister species, the Tien Shan shrew, *S. asper* (Fumagalli *et al*. 1996). Little is known of *S. asper*, as few specimens previously were available for investigation.

In accordance with ENM predictions, we test a null prediction that *S. tundrensis* persisted in situ within Siberia and across Beringia through glacial cycling of the Late Pleistocene, experiencing periodic fragmentation and range reduction in response to unfavorable climate. In addition, we tie phylogeographic patterns within *S. tundrensis* and its sister *S. asper* to geography and climate. We investigate population demographic variability, placing our observations within the context of contemporary Arctic warming. Finally, we relate our analyses to other high-latitude species to begin to investigate generalized response of communities to environmental change.

Materials and Methods

Sample collection and lab techniques – We sampled a total of 216 *S. tundrensis* specimens from 65 specific localities (Fig. 1). Although *S. tundrensis* is widespread and considerable collections of fluid preserved and dried study skins exist in Russia, only 16 Palearctic specimens from the Siberian Zoological Museum, Novosibirsk, provided amplifiable molecular sequences. We therefore incorporated 94 further individuals from GenBank (mitochondrial cytochrome *b* [Cyt *b*] sequences; Bannikova *et al.* 2010). The remaining 101 specimens sequenced for this study were obtained from the Beringian Coevolution Project (Cook *et al.* 2005). We included 21 samples of *S. asper* collected from 10 proximate localities as well as two specimens from other species within the *araneus-arcticus* group (*S. antinorii, S. araneus, S. arcticus, S. coronatus, S. daphaenodon, S. granarius, S. maritimensis, S. samniticus, S. satunini*; Appendix I).

Heart, liver, or skin were obtained from frozen (stored at -80℃), ethanol preserved, or dried samples. Genomic DNA was obtained through standard salt extraction, PCR, and cycle sequencing methods outlined in detail elsewhere (Hope *et al.* 2010). We amplified variable lengths of the mtDNA Cyt *b* gene (624-1140bp). A single primer pair for the entire Cyt *b* gene was used for frozen samples (MSB05/MSB14; Hope *et al.* 2010). For degraded DNA samples, multiple species-specific internal primers were developed (Table S1). To improve DNA amplification from degraded DNA samples, we modified protocols of Hope et al. (2010) by substituting AmpliTaq Gold® DNA polymerase and 10x PCR buffer Gold. Automated sequencing of complimentary strands was conducted using an Applied Biosystems 3110 DNA sequencer (Molecular Biological Facility, UNM). Complimentary strands of DNA were compared and contiguous sequences were deposited in GenBank (Appendix I). We also sequenced 43 individuals with unique mtDNA haplotypes for 2 independent nuclear loci (501 bp of the apolipoprotein B gene [ApoB] and 776 bp of the breast cancer susceptibility 1 gene [BRCA1]) found to be phylogenetically informative for other *Sorex* species (Hope *et al.* 2010; Dubey *et al.* 2007). Primer pairs ApoBF/ApoBR and BRCA1F/BRCA1R (Dubey *et al*. 2006, 2007) were used to amplify and sequence ApoB and BRCA1 genes, respectively. We sequenced 1 specimen each of *S. araneus, S. arcticus, S. asper, S.*

caecutiens, S. daphaenodon, S. minutissimus, S. minutus, and *S. roboratus* for all three loci, and included additional samples from *S. antinorii*, *S. araneus*, *S. coronatus*, *S. granarius,* and *S. samniticus* represented by all three loci in GenBank (n_{tot}=63; Appendix I). These species were chosen based on their evolutionary affiliations with *S. tundrensis*. All are within the subgenus *Sorex* (Hutterer 2005) and several are members of the *araneus-arcticus* group (Volobouev & Dutrillaux 1991).

Sequences were edited in SEQUENCHER 4.8 (Genecodes, Ann Arbor, Michigan), aligned in BioEdit 7.0.9 (Ibis Biosciences, Carlsbad, California) using the ClustalW algorithm, and checked by eye. Sequences were translated to amino acids and examined for internal stop codons that might suggest a pseudogene. Alleles of nuclear heterozygotes were inferred using PHASE (Stephens *et al*. 2001; Stephens & Scheet 2005). PHASE implements a Bayesian method for reconstructing haplotypes from nuclear genotype data that include multiple heterozygous base sites within individuals. To estimate allele frequencies, PHASE was run 5 times with results of the best goodness-of-fit to an approximate coalescent model retained, resulting in 2 nuclear haplotypes (or alleles) per individual.

Phylogeny Reconstruction –We estimated phylogenies using Bayesian methods for two datasets consisting of mitochondrial sequences. The first included all samples of *S. tundrensis*, *S. asper*, 9 other species within the *araneus-arcticus* group, and rooted with *S. caecutiens* (n_{TOT} = 258) consisting of variable length sequences of the Cyt *b* gene (624-1140bp). We then pruned the dataset to standardize length (891bp; n = 243) by removing shorter sequences. From this refined dataset, 138 unique haplotypes were retrieved (107 *S. tundrensis*; 13 *S. asper*).

For Bayesian phylogenies, the best model of DNA substitution was determined using MrModeltest v2.3 (Nylander 2004) under the Akaike information criterion. Markov Chain Monte Carlo (MCMC) technique was performed in MrBayes v3.1 (Ronquist & Huelsenbeck 2003) to characterize the probability distribution of phylogenetic trees given the data. Two separate runs were conducted for each dataset with sequences partitioned by codon position. To avoid arriving at a false optimum long-tree topology, we utilized the short-branch method employed by Marshall (2010). Each run computed 10,000,000 generations, sampling every 100 generations, with 5 independent chains, and the first 10,000 trees discarded as burn-in. Convergence of MCMC runs was assessed in Tracer v1.4 (Rambaut & Drummond 2007) using likelihood scores from each separate run. Resulting phylograms and posterior probabilities were visualized in FigTree v1.2.2 (Rambaut 2009).

Species Tree Estimation From Multiple Loci – Evidence from multiple independent genes is critical to inferring species relationships (Edwards & Beerli 2000). Gene tree/species tree discord can result from gene duplication, introgression, sorting of ancestral polymorphism or rapid fixation of linked loci through selective sweeps (Carstens & Knowles 2007). Multiple independent loci can help detect these phenomena. To identify alleles from nuclear gene sequences with multiple heterozygous sites, data were phased for all 3 loci (including the haploid mitochondrial gene for consistent number of sequences), producing 2 haplotypes for each individual, including the 12 related species (n_{tot}=126). The same specimens were included for all 3 independent phylogeny reconstructions to produce genealogies for estimation of a combined species tree topology.   The method chosen for species tree estimation involved coalescent coestimation of multiple gene trees embedded within a corresponding species tree topology using *BEAST (Heled & Drummond 2010) and implemented in the program BEAST v1.6.1 (Drummond & Rambaut 2007). This method uses a Bayesian Markov chain Monte Carlo technique. Independent loci were partitioned according to substitution model, molecular clock model, and gene tree estimation. Taxa were assigned to species/populations as designated below. A strict molecular clock was employed and mutation rates for the two nuclear loci were estimated based on a Cyt *b* mutation rate of 5.5% per million years (Hope *et al.* 2010). A Species Tree: Yule Process tree prior was assigned for all three loci with a piecewise linear & constant root population size model. Initial tree root height was estimated and default settings were used for all priors and operators. The MCMC chain was run for 100,000,000 iterations. Resulting tree files were annotated in TreeAnnotator v1.6.1 (part of the BEAST software package), assessed for convergence using likelihood scores in Tracer v1.4, and visualized in Figtree v1.2.2 (Rambaut 2009).

Ecological Niche Modeling –For ENM development, we used current and LGM monthly climate data at 2.5’ (4 km) spatial resolution, with the LGM data based upon 2 general circulation model (GCM) simulations: the Community Climate System Model (CCSM; Collins *et al*. 2004) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; Hasumi & Emori 2004; http://www.pmip2.cnrs-gif.fr. Waltari *et al*. (2007a) and Peterson & Nyári (2008) discuss the process of layer development more fully.

ENMs for both the present and LGM were based on the 19 bioclimatic variables in the WorldClim data set (Hijmans *et al*. 2005). These variables represent summaries of means and variation in temperature and precipitation, and characterize dimensions of climate considered particularly relevant in determining species distributions. Present-day ENMs were developed within a mask consisting only of land north of 30º N.

From biodiversity information systems of natural history collection data (e.g., ARCTOS http://arctos.database.uaf.edu and MaNIS http://manisnet.org/; Stein & Wieczorek 2004) and localities reported in Bannikova *et al.* (2010), we collated georeferenced occurrence points for *S. tundrensis* (n_{tot}=203). We refined these records by removing duplicate records, falsely georeferenced locations (e.g., locations over ocean), and records with low precision taken from atlas grid centroids. In addition, to correct for biased sampling effort (Reddy & Davalos 2003), which can lead to model overfitting and subsequent bias, we spaced localities at least 100km apart by removing intervening records resulting in 87 occurrence points used for analysis.

We used Maxent, version 3.3.3e (Phillips *et al*. 2006; Phillips & Dudik 2008) to construct ENMs. Maxent generates ENMs using only presence records, contrasting them with pseudo-absence or background data resampled from the remainder of the study area. In each case, we developed present-day ENMs and then projected the ENM to LGM conditions. We followed the procedures as outlined in Hope *et al*. (2010), using 5 replicates under the "crossvalidate" option, and selecting both a low and high threshold for determining suitable habitat, with an additional model selection step. Because the default settings in Maxent have been shown to be inferior to tuned settings in simulations, particularly regarding the regularization multiplier beta (Warren & Seifert 2011), we used a model selection process recently incorporated into ENMTools (Warren *et al*. 2008; 2010). We initially examined 8 present-day models, using beta regulation values of 1, 3, 5, 7, 9, 11, 13, and 15. We then selected the best model based on corrected Akaike Information Criterion scores (Warren & Seifert 2011), and used this model for creating projected LGM predicted distributions. We then generated summary maps in ArcGIS 9.3 which show Maxent predictions for present day and LGM (Fig. 2).

Population Genetic Statistics – To investigate the genetic structure and diversity within and among distinct geographic areas, we calculated population parameters for the refined Cyt *b* dataset. We subdivided *S. tundrensis* into 7 populations within Siberia and the limited Nearctic distribution of this species. Populations included "Far West Siberia" from west of the Ural Mountains to east of the Ob River drainage, "West Siberia" generally encompassing the Yenisei River drainage, "Central Siberia" largely coincident with the Lena River drainage, "Amga Basin" within Central Siberia, "East Siberia" within Chukotka and encompassing the Kolyma and Anadyr River drainages, "Maritime Northeast Asia" (MNA; Hope *et al.* 2010) including the Amur River drainage, and "Nearctic" surrounding the Yukon River drainage. Populations differ in assignment from Bannikova *et al.* (2010) as we recognize a finer level of distinction between clades. Populations were based not only on the reconstructed Cyt *b* phylogenies including both *S. tundrensis* and *S. asper*, but also taking into account realized geographic distributions and predicted potential distributions through ENMs. Bannikova *et al.* (2010) designate an Eastern clade that encompasses Central Siberia, East Siberia, and MNA populations described herein. In addition, we constrained multiple groups into biogeographic regions based on recognized geographic associations including Beringia (East Siberia and Nearctic), and Sakha (Amga Basin and Central Siberia). We included a single population consisting of all *S. asper* specimens from the Tien Shan Mountain Region of Northwest

China. Summary statistics were calculated in DnaSP (Librado & Rozas 2009) for each population to assess genetic diversity: segregating sites (*S*); haplotype diversity (*Hd*); nucleotide diversity (π); and Watterson's theta (θ). Uncorrected pairwise sequence divergence between populations was calculated as percentage divergence per million years. Summary statistics and genetic diversity were also investigated for ApoB and BRCA nuclear loci for all *S. tundrensis* grouped together.

Estimation of Population Size Change – For tests of demographic expansion, we used DnaSP (Librado & Rozas 2009) to calculate Tajima's D (Tajima 1989), Fu's Fs (Fu 1997), and R2 (Ramos-Onsins & Rozas 2002) and assessed significance with 10,000 coalescent simulations. In addition, expansion statistics were calculated for ApoB and BRCA nuclear loci for all *S. tundrensis* grouped together. All groups and loci were assessed for potential selection using the McDonald-Kreitman test (McDonald & Kreitman 1991).

We used the program BEAST (Drummond & Rambaut 2007) to calculate population size change through time and divergence estimates based on time to most recent common ancestor (T_{MRCA}) per designated group. We used the refined mitochondrial dataset including all species within the *araneus-arcticus* group (n = 245) placing individuals into groups and designating monophyly for all *S. tundrensis* and for all *S. asper*. Under a HKY+I+G model of nucleotide substitution, 2 partitions into codon positions ((1+2) 3), and a Bayesian skyline tree prior, we ran 4 independent MCMC analyses (length of chain = 60 M logging trees every 6000) with a mutation rate of 5.5% per million years (Hope *et al.* 2010) testing both strict clock and relaxed clock uncorrelated log-normal to check for consistency among these assumptions. In addition to a mean point estimate of mutation rate (5.5%), we reran coalescence estimates using the associated upper and lower confidence limits of 2.8% and 8.9% per million years (Hope, unpublished data) to provide outside estimates for divergence times. Divergence estimates (T_{MRCA}) with confidence limits were visualized in Tracer v1.4 (Rambaut & Drummond 2007) to confirm that comparisons among different runs produced equivalent results. Bayesian skyline plots (BSP) were used to assess demographic changes for independent populations and for all *S. tundrensis* combined. The Bayesian skyline algorithm was rerun separately for each data subset representing individual populations under similar model parameters but using all tree priors and constraining the tree root height to the T_{MRCA} for each group.

Results

Phylogeny reconstruction – No sequences contained insertions, deletions, or internal stop codons. We sequenced 624-1140 bp of Cyt *b* from 122 *S. tundrensis* and 21 *S. asper* with 94 additional sequences of *S. tundrensis* retrieved from GenBank. However, we report a Bayesian phylogeny based on 891bp from a dataset of n = 138 unique haplotypes (107 *S. tundrensis*; 13 *S. asper*; 18 other species; Fig. 3). The full dataset was included in initial analyses to insure that samples with potential unique diversity were not excluded. Major groups were consistently revealed in Bayesian reconstructions across the full dataset, refined dataset, and haplotype datasets. The phylogeny defines 7 groups within *S. tundrensis* generally consistent with geographic distribution (Fig. 1, 3). Central Siberia, East Siberia, and MNA together form a well-supported clade. There is no support for a group representing Beringia (Alaska + Eastern Siberia) or a group representing Sakha (Central Siberia + Amga Basin), the latter combination with localities shared by both clades (localities 35, 38, 40; Fig. 1; Appendix I). Within the *araneus-arcticus* group, *S. samniticus* forms a basal split from the other species followed by the Nearctic species *S. arcticus* and *S. maritimensis* (Fig. 3). Lower support values illustrate weakly resolved relationships in the middle of the phylogeny. A clade containing *S. tundrensis* and *S. asper*, and a separate clade containing *S. granarius*, *S. araneus*, *S. antinorii*, and *S. satunini* each have a posterior probability of 1. However, *S. satunini* also occurs outside of this latter clade. The two independent nuclear loci yielded low variability over all *S. tundrensis* (Table 2; Fig. S1). Bayesian phylogenies based on each nuclear gene provided low support for designated groups. However, *S. asper* was consistently distinguishable from *S. tundrensis* over all three loci examined. A maximum likelihood topology based on the Cyt *b* gene (Bannikova *et al.* 2010) exhibited the same major clades as the Bayesian phylogeny (Fig. 3) although relationships among these groups were slightly different, illustrating lower support at deeper nodes within *S. tundrensis*.

Species tree estimation and multiple loci – The multi-locus dataset included sequences for three loci from 43 individuals of *S. tundrensis* including specimens from Nearctic, East Siberia, Central Siberia, Amga Basin, and West Siberia. Species tree estimations from *BEAST analysis (Fig. 4) indicate some agreement with the Cyt *b* genealogy (Fig. 3) in that West Siberia is basal to other clades although there is low support among the terminal clades within *S. tundrensis*. Higher-level relationships among the *araneus-arcticus* species are generally consistent over both Cyt *b* and species tree topologies. The position of *S. daphaenodon* with respect to other species is unresolved in both topologies although *S. arcticus* and *S. samniticus* are consistently more basal (respectively). Coalescence times for major clades based on three loci include all *S. tundrensis* at ~0.13 My, *S. asper* and *S. tundrensis* at ~0.29 My, the *araneus-arcticus* group including *S. samniticus* at 1.57 My and all included species at 2.29 My. Mutation rates were estimated at 0.48% and 0.24% per million years for ApoB and BRCA1 genes, respectively.

Ecological niche models – The predicted current potential niche of *S. tundrensis* encompasses its known distribution (Fig. 2), but also predicts large areas where *S. tundrensis* has not been collected despite extensive sampling efforts, including most of northwestern Russia, northern Europe, and Canada (Fig. 2A). High suitability predicted niche coincides geographically with lower elevation habitat interspersed between mountainous regions and including the Central Siberian Plateau (Fig. 1; 2). Predicted potential niche at the LGM under the CCSM model is more fragmented than current predicted distribution suggesting putative isolated refugia (Fig. 2B). However, results based on the MIROC model are more consistent with the current prediction (Fig. 2C). High suitability LGM areas are also nested within the current distribution and are not shifted latitudinally. In both LGM models, low suitability areas in central Beringia separate higher suitability areas to the east and west. Current localities of all major groups within *S. tundrensis* fall within high suitability areas both at present and at the LGM.

Population statistics – Uncorrected sequence divergence between *S. tundrensis* and *S. asper* is ~3.7% (Table S2). Within *S. tundrensis*, uncorrected sequence divergence between designated groups ranged from 0.6-1.6%. Closest genetic distances are between

Central Siberia, East Siberia, and MNA. West Siberia is least divergent from the Amga Basin group. Although Nearctic is least divergent from East Siberia, this relationship is not reciprocal, with East Siberia closer to Central Siberia (Table S2). Summary statistics indicate highest haplotype diversity and nucleotide diversity are in West Siberia followed by MNA and the Nearctic (Table 1). Corresponding values are lowest in East Siberia followed by Amga Basin. No groups tested positive for selection at any locus.

Temporal divergence and effective population size change –Using a mutation rate of 5.5%, the time to the most recent common ancestor (T_{MRCA}) for *S. tundrensis* and *S. asper* was estimated at ~416 ky , and ~192 ky for all *S. tundrensis* (Table 2). The oldest coalescence within *S. tundrensis* was the West Siberia group (90 ky) followed by Central Siberia (70 ky) and MNA (68 ky). However, coalescence estimates for each individual group within *S. tundrensis* overlapped at the 95% confidence interval, except for West Siberia (oldest) and East Siberia (most recent). Coalescence time for a combined Beringia is ~120 ky and for a combined Sakha region 140 ky, within the 95% confidence limits for T_{MRCA} of the entire species. The T_{MRCA} for the entire *araneus-arcticus* group was 2 My, without *S. samniticus* was 1.5 My, and without the Nearctic *S. arcticus* and *S. maritimensis* was ~1 My (Table 2). Coalescence estimates utilizing a lower (2.8%) or higher (8.9%) mutation rate uniformly increased or decreased the coalescence times respectively, although estimates within *S. tundrensis* remained within a late-Pleistocene timeframe from a maximum of 370 ky for all *S. tundrensis* to the most recent coalescence of the East Siberia clade at 26 ky. Even with a very high mutation rate, divergence within populations predates the LGM and between populations dates at least to the onset of the Wisconsinan glacial period (~75 ky). West Siberia, Central Siberia, and Nearctic populations show significant signals of expansion for three statistics (*D*, *Fs*, and *R2*). Far West Siberia exhibits no evidence of significant expansion, while a mixed set of significance values characterizes Amga Basin, East Siberia, and MNA (Table 1). West Siberia and Nearctic populations indicate a significant increase in population size from BSPs although increase in Western Siberia is coincident with the time period from 55-30 ky whereas increase in the Nearctic is from 30-5 ky (Fig. 5). Other populations indicate at most a gradual increase in population size, or relative stability (Fig. S2). BSPs for all groups followed a HKY substitution model variably utilizing a proportion of invariant sites and a gamma distribution (Table 2).

Discussion

Our primary objective is to investigate variability within Beringia. Apart from its importance for transcontinental migration of plants and animals, Beringia is traditionally considered a refuge for terrestrial species during glacial maxima that then became a source for subsequent colonizations of deglaciated regions in the Arctic (Hultén 1937) and areas further south in North America and Asia. Recent molecular evidence for Arctic mammals, however, has not tended to support the importance of Beringia as a source for extensive colonization of formerly glaciated regions. Instead, Beringia appears to represent an area of high intraspecific endemism for Arctic species (Fedorov *et al.* 2003). Separation of Eurasia and North America by the Bering Strait during interglacial periods generally is not reflected in phylogeographic analyses suggesting that this recurring barrier to terrestrial species dispersal has minimally influenced genetic structure or divergence within some mammals (Fedorov *et al.* 2003; Galbreath & Cook 2004).

However, in other Arctic species that are ecologically associated with dry environments, this barrier (most recently formed 11,000 years before present) delineates significant phylogeographic breaks (Fedorov *et al.* 1999; Wickström *et al.* 2003). These findings are consistent with paleoecological evidence suggesting that the Beringian Isthmus represented a moisture barrier to the dispersal of steppe-tundra biota indicative of regional dry environments (Elias & Crocker 2008). Here we discuss how genetic signatures may be used to infer Beringian environments through the Pleistocene.

Our secondary goal is to further explore the spatiotemporal dynamics of biotic diversification within Siberia, a high latitude area that remains poorly understood in terms of community assembly and demographic response through the Quaternary. Because vast areas of ice-free habitat were maintained in Siberia through Pleistocene glacial cycling, this region is essential to a complete understanding of high-latitude faunal diversification and intercontinental exchange. Ice-free areas in Siberia potentially were highly fragmented by local geographic barriers such as glaciated mountains and frozen rivers, or may have been periodically uninhabitable due to harsh environmental conditions. Below we discuss how diversification within *S. tundrensis* compares with other terrestrial high-latitude species to illustrate variable responses to local conditions.

Niche Predictions and Phylogeographic Relationships –Predictions pertaining to the history of *S. tundrensis* were formed by first relating the distribution of closely related species to potential niche through ENMs. All three loci support recognized relationships both within the *araneus-arcticus* group, and between other outgroup taxa (Fig. 5; Fumagalli *et al.* 1999; Ohdachi *et al.* 2006; Dubey *et al.* 2007). In particular, Nearctic *S. arcticus* is a basal member of the *araneus-arcticus* group. Species within the sub-genus

Sorex are recognized from fossil evidence to have a Palearctic origin (Hutterer 2005), so ancestral *S. arcticus* likely colonized the New World early in the history of the *araneus-arcticus* group (e.g. Stewart *et al.* 2002). Estimates for T_{MRCA} of *S. arcticus* (and *S. maritimensis*) with the remainder of the *araneus-arcticus* group indicate a time of 1.5 My (Table 2: Clade B), coincident with the middle Pleistocene. Lack of resolution within the middle of the *araneus-arcticus* group phylogenies, as exemplified by low nodal support, suggests a rapid radiation at ~ 1 My for Clade A (Table 2) that is largely coincident with the onset of 100 ky glacial periodicity. In addition, *S. satunini* is polyphyletic as has been shown elsewhere (Bannikova & Lebedev 2010) suggesting as yet unresolved diversity within this comparatively well-studied species group (Junge *et al*. 1983; Fumagalli *et al*. 1996; Stewart *et al*. 2002). Unfortunately, a multi-locus assessment of *S. satunini* within the group was not possible here, but polyphyletic individuals represented by the Cyt *b* gene were also markedly divergent from all other species within the *araneus-arcticus* group. Recently, further complications surrounding relationships within this group have been highlighted that suggest episodes of gene flow through time, for instance through incongruent nuclear and mitochondrial phylogenies (Bannikova & Lebedev 2010; Yannic *et al.* 2010) indicating that further multi-locus analyses are warranted to clarify relationships. *Sorex asper* and *S. tundrensis* are reciprocally monophyletic and jointly form a monophyletic group. Although divergence between these nominal species is low for species-level differentiation of mammals (3.7%; Baker & Bradley 2006), there is no evidence over multiple loci to suggest ongoing gene flow. When coupled with geographic isolation and distinctive body size differences (Sheftel 2005), the molecular data are consistent with their status as independent species.

The current potential niche for *S. tundrensis* predicted by ENM closely matches the combined geographic range of 6 species of this group found outside central Europe (e.g. Fig. 2). Current potential niche west of the range of *S. tundrensis* (western Russia and Europe) is occupied by *S. araneus* (although the two are broadly sympatric in westernmost Siberia) and east of *S. tundrensis* in North America by *S. arcticus* (Fig. 2). The smaller range of *S. asper* is restricted to the Tien Shan Mountains bridging northwestern China, Khazakstan, and Kyrgyzstan, while *S. daphaenodon* largely overlaps the range of *S. tundrensis* (Sheftel 2005). Concordance of niche predictions with distribution of northern members of the *araneus-arcticus* group suggests that ecology of these closely related species is similar and raises the possibility that competition plays a role in their distributions. Where *S. tundrensis* overlaps *S. araneus*, the latter generally is much more abundant (Churchfield *et al.* 1997). Similarly where *S. daphaenodon* is in high abundance, *S. tundrensis* is completely absent (Sheftel 2005). ENMs also suggest that *S. tundrensis* is a persistent constituent of northern high-latitude communities and has experienced simultaneous fragmentation in response to unfavorable climatic conditions. The haplotype phylogeny exhibits a central polytomy that may reflect simultaneous fragmentation (Fig. 3). Incomplete lineage sorting might explain why haplotypes from the Amga Basin and Central Siberia clades are found sympatrically (localities 35, 38, 40; Fig. 1; Appendix I), but appears unlikely considering: 1) comparable levels of genetic differentiation between other clades within the phylogeny (Table S2); 2) the Amga Basin clade is more divergent from the Central Siberia clade than any other except Western Siberia (Table S2); and 3) other shared geographic localities among clades are rare (locality 11; Fig. 1; Appendix I), with all these shared localities peripheral to the range of the corresponding clades. We suggest that shared localities reflect contact zones between geographic clades and further investigation should focus on potential areas of hybridization.

With regard to nuclear perspectives, ApoB is unsorted across all populations except Western Siberia. However, the BRCA1 genealogy indicates all but two alleles are distinct between Amga Basin and Central Siberia clades, and therefore consistent with the mtDNA genealogy (Fig. S1).

Demographic parameters, such as significant signals of population expansion for West Siberia, Central Siberia and Nearctic groups coupled with deep divergence estimates and ENM predictions, indicate extended persistence in isolation followed by periodic population size change in response to variable climate (Table 2). Most major clades coincide spatially with previously recognized subspecies (Junge *et al*. 1983). Finally, relatively low values of *Hd* and π (Table 1) for individual populations are consistent with small, persistent demes that experienced localized population expansion and contraction in response to climate change.

Timing of Diversification – Estimates of time to coalescence of the gene (minimal within-population divergence) do not necessarily reflect timing of geographic isolation between populations (Drummond & Rambaut 2007). For instance, West Siberia has a T_{MRCA} of 90 ky and Eastern Siberia a T_{MRCA} of 41 ky. To an extent, these estimates reflect higher genetic diversity in Western Siberia, indicating deeper coalescence within this population that is likely attributable to larger effective population size. All populations within *S. tundrensis* were estimated to coalesce at ~192 ky, potentially an overestimate of population divergence (Table 2). Coalescence of individuals within each population is conversely an underestimate of interpopulation divergence. Thus, we bracket vicariance within *S. tundrensis* to minimally ~90 ky (deepest intra-population coalescence time) and maximally ~192 ky (mean interpopulation coalescence considering simultaneous fragmentation; i.e., earlier than the LGM and possibly as early as the Illinoian glacial). Divergence estimates for all *S. tundrensis* using multiple loci are more recent (~126 ky) than estimates from the Cyt *b* gene alone, potentially due to the smaller sample used for multi-loci analysis. In addition, the combined coalescence of multiple loci narrows uncertainty around overestimation of coalescence. Divergence estimates suggest that the regional groups identified within *S. tundrensis* persisted in isolation for extended periods. Minimal and maximal coalescence times for *S. tundrensis* are close to those for polar bear and brown bear divergence from Beringia (Lindqvist *et al.* 2010) indicating similar histories of diversification within other cold-associated species.

Most *S. tundrensis* populations also show signals of demographic expansion (Table 1), with population growth initiated and sustained through the highly variable but cooler climate of the late Wisconsinan, generally leading up to the LGM (Fig. 5; Hofreiter & Stewart 2009). That *S. tundrensis* in West Siberia experienced population growth much earlier than the Nearctic population, indicates that parts of Siberia provided favorable conditions for *S. tundrensis* much earlier than within eastern Beringia. Regarding the potential geographic center of diversification for *S. tundrensis*, neither the easternmost Nearctic nor the Far West Siberia population of *S. tundrensis* were basal (Fig. 3). MNA and Central Siberia are the two populations least divergent from *S. asper* (uncorrected sequence divergence; Table S2) whereas West Siberia is the basal clade within *S. tundrensis*. Together these indicate a potential center of origin for *S. tundrensis* in west-central and south-central Siberia as postulated previously (Volobouev 1989; Fumagalli *et al*. 1996). Estimates of gene coalescence of *S. tundrensis* and *S. asper* are dated to the Kansan/Elsterian period of the mid-late Pleistocene (>380 ky) indicating that diversification spanned three major Pleistocene glacial cycles. These estimates are similar to Bannikova *et al.* (2010) using a divergence rate of 8.6% (4.3% mutation rate).

Regarding the Nearctic population, deep divergence estimates and high haplotype diversity coupled with the limited distribution of *S. tundrensis* in North America present a conundrum. Such a limited distribution suggests recent colonization from Eurasia through Beringia, yet estimated divergence times are much older. Extended isolation of North American *S. tundrensis* from Eastern Siberian populations is supported by a gap in predicted potential habitat on the Beringian Isthmus (Fig. 2B, C), well supported clades for each group (Fig. 3), and a divergence estimate (T_{MRCA}) for a constrained Beringia group that predates the onset of the Wisconsinan glaciation (119 ky; Table 2). We suggest that *S. tundrensis* occupied Nearctic Beringia for an extended period without dispersing eastward into Canada. Competitive exclusion between *S. tundrensis* and *S. arcticus*, a related shrew of comparable size, may have restricted the distribution of *S. tundrensis* to northwestern North America. However, Youngman (1975) considered *S. tundrensis* and *S. arcticus* to be entirely allopatric, with a zone through the Yukon Territory where neither occurs, suggesting a barrier to dispersal. Within Eurasia *S. tundrensis* is found sympatric with other relatives (e.g., *S. araneus* in western Siberia; Fig. 2). Both ENM predictions and realized distribution of *S. tundrensis* generally restrict this species to lower elevation habitat separated by intervening mountains. The Mackenzie Mountains in Yukon Territory may form a considerable barrier for colonization of North America outside of Alaska by *S. tundrensis* as suggested for other species of shrew (Hope *et al*. 2010) and passerine birds (e.g. Reeves *et al.* 2008).

Comparative Perspectives – The only other Holarctic shrew, *S. minutissimus*, also exhibits distinctive demographic patterns (Hope *et al*. 2010). While *S. minutissimus* shares overlapping phylogeographic structure with *S. tundrensis* (MNA, Amga Basin, similar limited distribution in North America), the Beringian clade encompassing both Alaska and East Siberia identified in *S. minutissimus* suggests that isolation across the Bering Strait was not a major factor driving diversification. Demographic analyses for *S. minutissimus* indicate rapid expansion within Beringia in response to climate warming since the LGM, whereas population growth within *S. tundrensis* was earlier, occurring prior to the LGM. These contrasting patterns imply that high-latitude shrews responded somewhat differentially to environmental change as would be predicted by differences in ecology. *Sorex minutissimus* generally feeds on small arthropods from surface litter in taiga forest and tundra habitats, whereas the larger *S. tundrensis* focuses on oligochaetes gleaned from the top layer of soil in mixed-brush mesic habitats, particularly associated with river floodplains (Churchfield *et al*. 1997). *Sorex minutissimus* evidently has shifted its distribution through time, following the extent of taiga and associated climate conditions, whereas *S. tundrensis* likely persisted in isolated refugia such as low-lying floodplains during glacial maxima (Hopkins *et al*. 1982). Significant population growth within *S. tundrensis* during the transitional climate leading up to the LGM, was followed by stable population size through the LGM (Fig. 6). The increase in effective population size is coincident with the latest Wisconsinan interstadials (MIS 3; Elias 2000) suggesting that this transitional climate (Hofreiter & Stewart 2009), albeit relatively colder than today, increased optimal habitat for *S. tundrensis*. This time period closely coincides with a sudden decrease in population size of steppe bison that were adapted to more xeric grassy steppe habitats (Shapiro *et al*. 2004), highlighting the temporal variability of Beringian environments (Elias *et al*. 1997; Elias & Crocker 2008). Mesic tundra-adapted species such as lemmings (*Lemmus*, Fedorov *et al*. 1999; 2003;), the tundra/root vole (*Microtus oeconomus*, Brunhoff *et al*. 2003; Galbreath & Cook 2004), multiple plant species (Abbott & Brochmann 2003; Ehrich *et al*. 2008; DeChaine 2008) and insects (Elias *et al*. 2000; Elias & Crocker 2008) all occupied Beringia during the LGM. Xeric-associated species occupying steppe-tundra and dry tundra habitat, such as collared lemmings (*Dicrostonyx*, Fedorov & Goropashnaya 1999; Fedorov & Stenseth 2002), megafaunal grazers (Hofreiter & Stewart 2009; Shapiro *et al*. 2004), and weevils (Elias & Crocker 2008) also prevailed during the LGM. Landscapes in western Beringia were apparently xeric, while northern and eastern Beringia were more mesic (Elias *et al*. 2000). Such a moisture gradient, including at times a mesic “buckle” in central Beringia (Guthrie 2001) may have maintained a significant ecological barrier to dispersal for many species exhibiting genetic signatures of persistence at high latitudes during glacial maxima (Fedorov *et al.* 1999; Wickström *et al.* 2003). As a consequence, populations may be highly structured into distinct clades despite an apparent lack of geographic barriers.

If climate changes rapidly, species that shift their ranges in response to change, such as *S. minutissimus* (Hope *et al*. 2010) and the red-backed vole (*Myodes rutilus*, Cook *et al*. 2004) may have an advantage over persistent cold-adapted species. *Sorex minutissimus* and *M. rutilus* are taiga-associated species that arrived in North America very recently and were subsequently isolated from Asia by the Bering Strait. Persistence of taiga within Beringia throughout the Wisconsinan glacial is controversial (Brubaker *et al*. 2005) but patchy forest, particularly scrub riparian woodland, may have occurred on the southernmost land bridge at the latest stages of the Wisconsinan just before inundation (e.g. Hopkins *et al.* 1982). Any recent transcontinental movement of taiga-associated species therefore may have led to rapid expansion into North America. Evidence from taiga associated passerines corroborates their persistence in isolated pockets within Beringia despite apparent lack of boreal forest, divergence due to barriers other than the Bering Strait, and recent expansion within Beringia coupled with a limited eastern distribution in North America (Reeves *et al.* 2008; Saitoh *et al.* 2010). Conversely, persistent species such as those forming the current high-Arctic tundra community may not be able to respond rapidly to directional climate change with northward movement limited by the Arctic Ocean. Close association of *S. tundrensis* with major riparian corridors through the Holarctic may have promoted persistence in basins isolated by surrounding glacial environments. Community structure at high latitudes is dynamic through time but an initial understanding of which species have been historically associated with xeric or mesic areas may be uncovered by comparing historical demographies among species. Wide ranging species such as *S. tundrensis* highlight the inherent heterogeneity within Siberia and across Beringia and illustrate that glacial periodicity can produce distinctive regional lineages.

Conclusions

Multiple phylogeographic studies within northern systems have demonstrated that climate cycling does not affect all species similarly. *Sorex tundrensis* and other tundra-dwelling or cold-associated species are seemingly able to persist in isolated areas at high latitudes through both glacial and interglacial periods, whereas other species shifted their ranges in response to climate change, providing a different suite of genetic signatures. However, *S. tundrensis*, unlike xeric tundra specialists is ecologically associated with river floodplain habitats. Discrete geographic regions support distinctive lineages of *S. tundrensis* and potentially other lowland/riparian associated taxa. Periodicity of Pleistocene glacial cycling is seemingly long enough to affect significant population differentiation within species, although the extended glacial periods and not the briefer interglacial periods likely drove diversification. Distinct phylogeographic structure, combined with variable demographics within Beringian *S. tundrensis*, reflects a highly dynamic region through each glacial cycle with local conditions and habitat frequently shifting. In addition to static geographic barriers such as the Kolyma uplands (Galbreath & Cook 2004; Reeves *et al.* 2008), shifting climate variably produced xeric or mesic conditions that may have isolated populations, even in the absence of a geographical barrier. Species that track shifting climates may be at an advantage relative to persistent xeric tundra specialists, particularly if habitats such as tundra periodically experience dramatic area reduction and isolation in response to climate change. Conversely, floodplain corridors may provide regional buffers wherein associated species, such as *S. tundrensis*, can persist.

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Data Accessibility:

DNA sequences: GenBank accession numbers are uploaded as online supplemental material in Appendix I, accompanied by specific locality information, map locality data, haplotype data, and museum catalog numbers.

Table 1 – Population genetic statistics for all major clades within *Sorex tundrensis* including the sister species *S. asper*. Values were calculated for cytochrome *b* gene except where indicated otherwise. Summary statistics are *n* = sample size; *S* = segregating sites; *h* = number of haplotypes; *Hd* = haplotype diversity; π = nucleotide diversity. Population growth statistics are Tajima's *D*, Fu's *Fs*, and Ramos-Onsins and Rozas' *R2*. Significance of growth statistics is indicated by asterisks (* P ≤ 0.05; **P ≤ 0.01***P ≤ 0.001).

Group	*n*	*S*	*h*	*Hd*	π	*D*	*Fs*	*R2*
S. tundrensis	203	122	102	0.985	0.0113	-1.714**	-86.107***	0.039*
Far West Siberia	34	14	10	0.818	0.0030	-0.711	-1.626	0.090
West Siberia	45	62	31	0.973	0.0064	-2.155**	-20.800***	0.037***
Sakha	51	36	22	0.940	0.0075	-0.639	-4.325	0.087
Central Siberia	31	20	14	0.912	0.0030	-1.719*	-6.058**	0.066*
Amga Basin	20	13	8	0.816	0.0024	-1.486	-1.924	0.078**
Beringia	59	39	28	0.939	0.0060	-1.215	-12.058***	0.063
East Siberia	23	6	7	0.802	0.0013	-0.843	-2.649*	0.096
Nearctic	36	30	21	0.914	0.0038	-1.877**	-13.491***	0.050***

MNA	14	19	11	0.967	0.0051	-0.978	-4.255*	0.093*
S. asper	21	23	13	0.948	0.0044	-1.491*	-4.779*	0.081*
ApoB gene (*S. tundrensis*)	86	6	8	0.682	0.0020	-0.251	-1.996	0.088
BRCA1 gene (*S. tundrensis*)	86	10	9	0.204	0.0004	-2.273***	-11.800***	0.0315

Table 2 – Coalescence times using BEAST based on mitochondrial cytochrome *b* gene. Coalescence times are given as the time to most recent common ancestor (T_{MRCA}) in millions of years with 95% confidence intervals in parentheses considering a point estimate mutation rate of 5.5% per million years, and upper and lower bounds of this point estimate (2.8% and 8.9% per million years). Models shown for each group were used for Bayesian skyline population size change reconstructions. Clade A includes outgroups *S. antinorii, S. araneus, S. coronatus, S. daphaenodon, S. granarius, S. satunini*. Clade B further includes *S. arcticus* and *S. maritimensis*. Clade C further includes *S. samniticus*.

Group	*n*	T_{MRCA} (95% C.I.) 5.5%	T_{MRCA} (95% C.I.) 2.8%	T_{MRCA} (95% C.I.) 8.9%	Model
S. tundrensis	203	0.192 (0.125-0.268)	0.376 (0.249-0.523)	0.118 (0.078-0.165)	HKY+I+G
Far West Siberia	34	0.056 (0.034-0.082)	0.110 (0.067-0.161)	0.035 (0.021-0.051)	HKY
West Siberia	45	0.090 (0.048-0.146)	0.178 (0.094-0.287)	0.056 (0.030-0.090)	HKY+G
Sakha	51	0.140 (0.088-0.200)	0.278 (0.176-0.393)	0.088 (0.055-0.124)	N/A
Central Siberia	31	0.070 (0.043-0.102)	0.137 (0.082-0.197)	0.043 (0.026-0.062)	HKY
Amga Basin	20	0.054 (0.030-0.084)	0.106 (0.058-0.164)	0.033 (0.019-0.052)	HKY+I

Beringia	59	0.119 (0.072-0.169)	0.231 (0.143-0.334)	0.073 (0.044-0.104)	N/A
East Siberia	23	0.041 (0.022-0.065)	0.081 (0.043-0.126)	0.026 (0.014-0.041)	HKY
Nearctic	36	0.061 (0.038-0.087)	0.119 (0.073-0.171)	0.038 (0.023-0.055)	HKY+I
MNA	14	0.068 (0.040-0.100)	0.133 (0.079-0.196)	0.042 (0.025-0.061)	HKY
S. asper	21	0.066 (0.036-0.103)	0.130 (0.073-0.204)	0.041 (0.023-0.064)	HKY+I
S. asper/S. tundrensis	224	0.416 (0.266-0.580)	0.817 (0.524-1.139)	0.257 (0.162-0.359)	N/A
Clade A	236	0.988 (0.733-1.259)	1.941 (1.451-2.448)	0.613 (0.460-0.780)	N/A
Clade B	240	1.500 (1.079-1.954)	2.937 (2.135-3.829)	0.928 (0.675-1.205)	N/A
Clade C	242	2.000 (1.348-2.749)	3.892 (2.660-5.233)	1.230 (0.857-1.666)	N/A

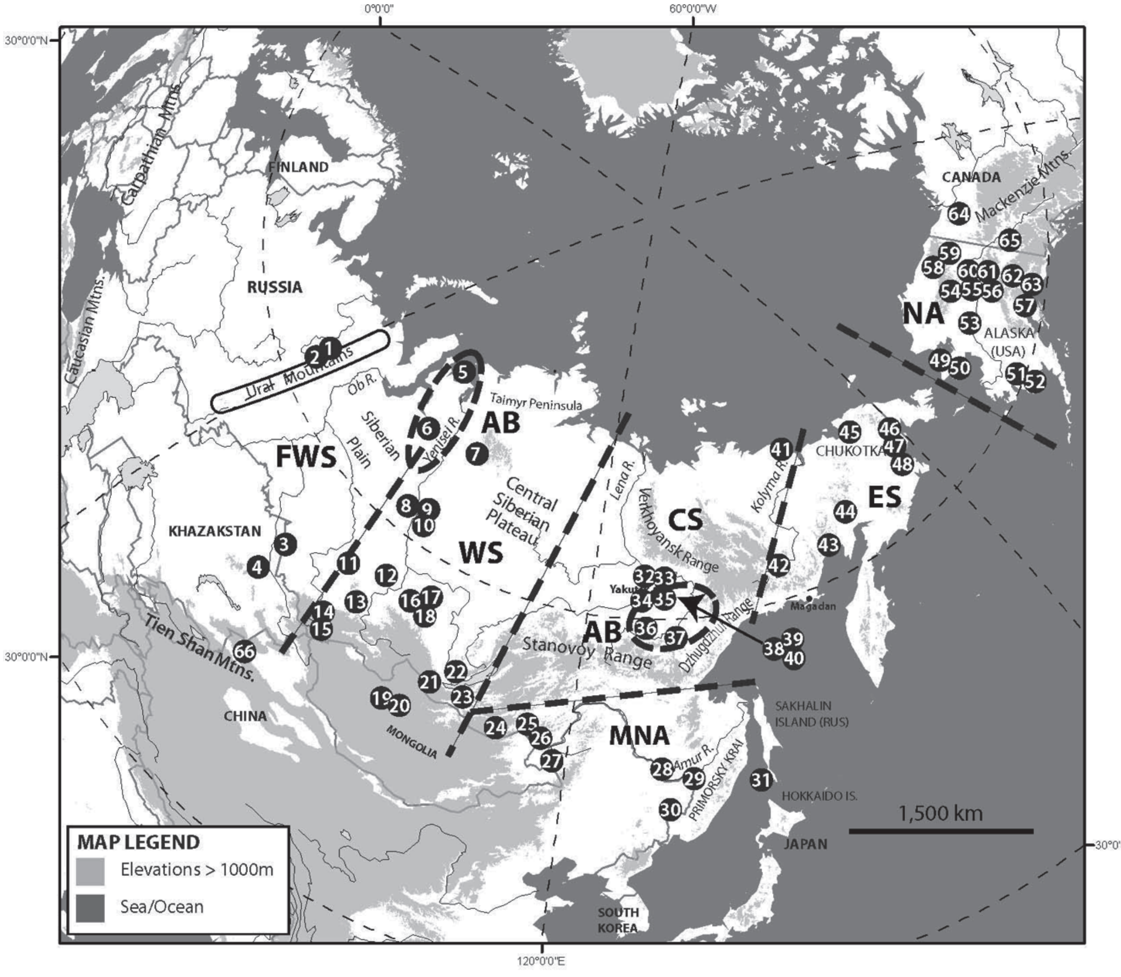

Fig. 1 – Map of the study area illustrating major geographic features within the Holarctic reflecting potential phylogeographic breaks. Specimen localities are indicated by number corresponding with Appendix I and are associated with designated groups from Bayesian cytochrome *b* phylogeny reconstruction. *Sorex tundrensis* – Far West Siberia (FWS); West Siberia (WS); Central Siberia (CS); Amga Basin (AB); East Siberia (ES); MNA; Nearctic (NA); *Sorex asper* – 66). Constrained groups for divergence estimates include Sakha (CS + AB) and Beringia (ES + AK).

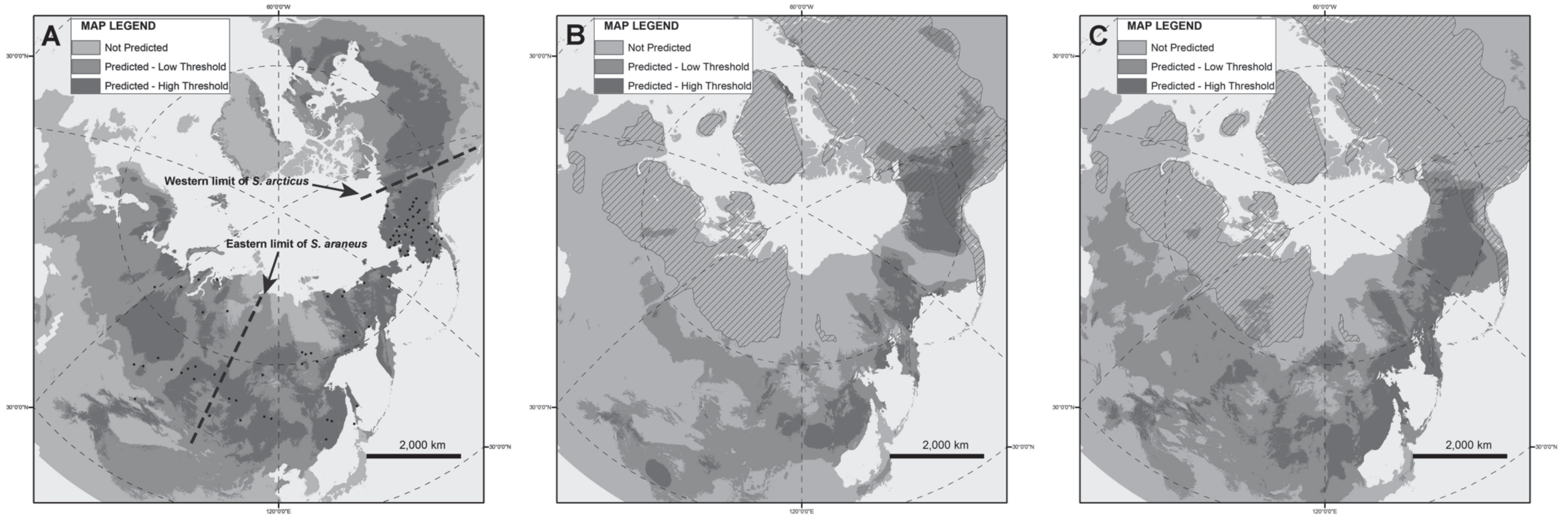

Fig. 2 – Ecological niche models depicting potential distribution for *Sorex tundrensis* during A, the present, and B (CCSM model) + C (MIROC model), the Last Glacial Maximum dated to 18 kya. Black dots indicate specimen locality records of *S. tundrensis* used to produce ENMs. Dark shading indicates strong distributional prediction and light shading a weak prediction. Dashed lines in A indicate the distributional limits for two other members of the *araneus-arcticus* group. Slanted lines in B and C indicate general extent of major ice sheets at the LGM.

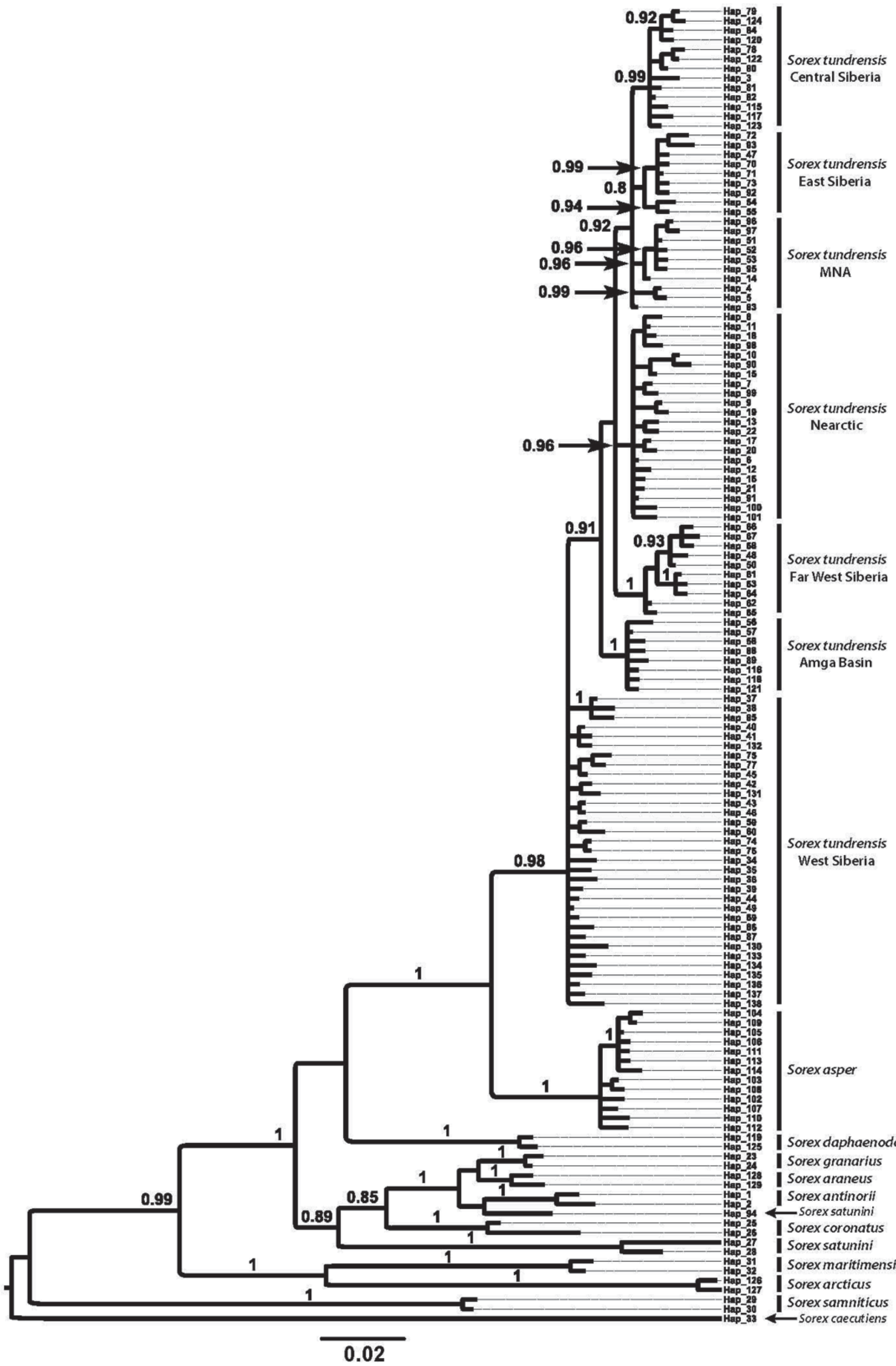

Fig. 3 – Bayesian phylogeny for *Sorex tundrensis* populations, *S. asper*, and all members of the *araneus-arcticus* group. The genealogy is based on cytochrome *b* gene haplotypes (891 bp) and rooted with *S. caecutiens*. Node labels represent posterior probabilities ≥0.8.

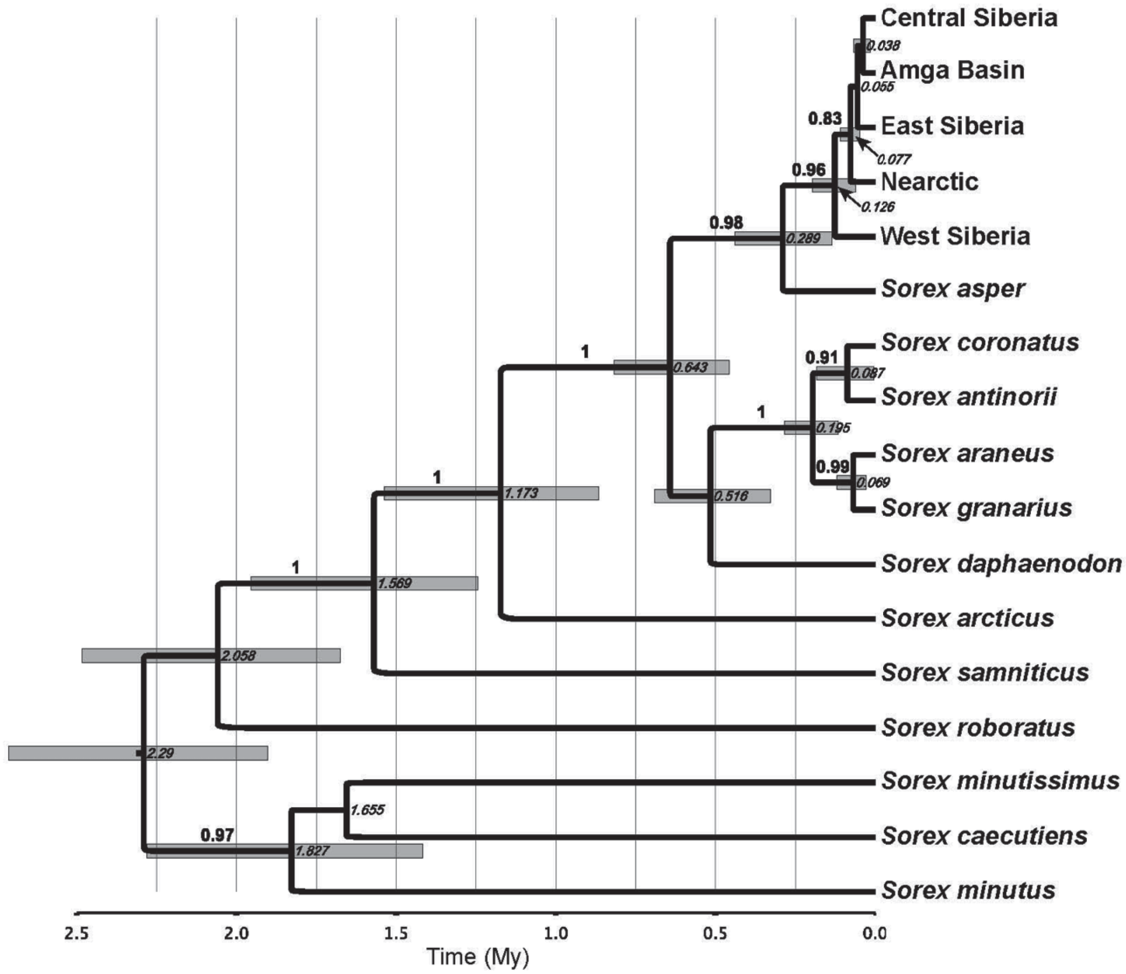

Fig. 4 – Species trees estimated from three unlinked loci (Cyt *b*, ApoB, BRCA1) using *BEAST reconstruction showing node ages (in italics) with associated error bars and posterior probabilities ≥0.8 (in bold). The phylogram exhibits branch lengths proportional to divergence time from each node as shown against the basal scale bar.

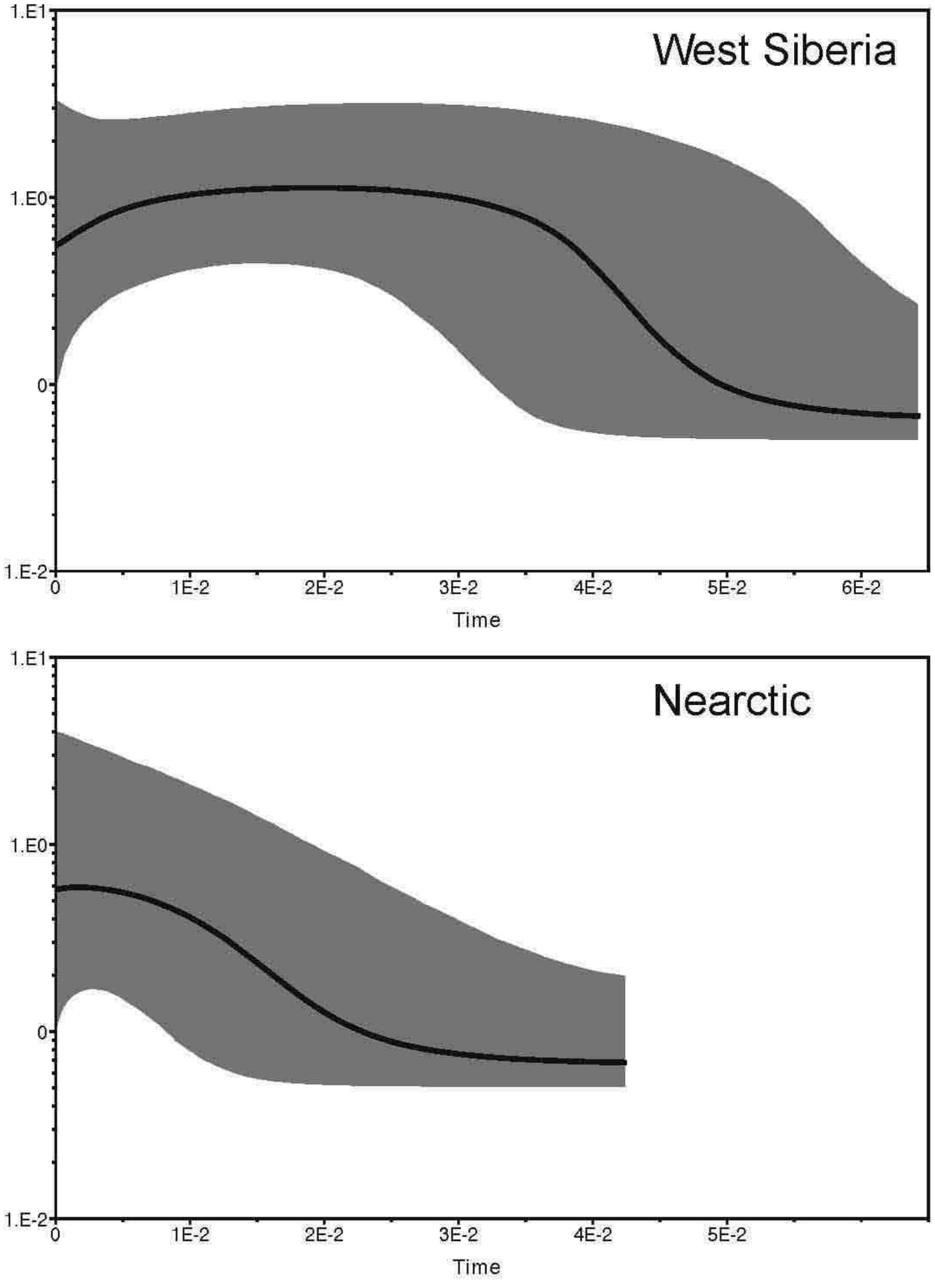

Fig. 5 – Bayesian skyline plots for West Siberia and Nearctic populations of *S. tundrensis*. Central line indicates change in effective population size through time; peripheral lines indicate the 95% C. I. The BSP here extends right-to-left from past to present scaled in millions of years. Vertical axis represents τ as a function of generation time and effective population size (logarithmic scale).

Appendix -- Specimens examined. Acronyms for museum or tissue numbers are IBPN = Institute of Biological Problems of the North; MSB = Museum of Southwestern Biology; PISR = Pechora-Ilych State Reserve; SZMN = Siberian Zoological Museum, Novosibirsk; UAM = University of Alaska Museum of the North, Fairbanks; ZISP = Zoological Institute RAS, St. Petersburg; ZMMU = Zoological Museum of Moscow State University. Numbers following specific localities correspond to Fig. 1. GenBank numbers correspond to Cyt b, ApoB, and BRCA1 genes respectively. Haplotypes correspond to Cyt b gene sequences used in phylogeny reconstruction. Sequences without associated haplotypes were short and did not represent unique diversity so were excluded from the represented phylogeny in Fig. 4. N/A = not applicable. GenBank acessions in bold were submitted in the current study.

Species	Specimen Number	Country	Specific Locality	Group	Cyt *b* Haplotype	GenBank Accession
Sorex tundrensis	ZMMU S-177788	Russia	Kemerovo Region, Middle Tom (11)	Far West Siberia	48	GU564758, N/A, N/A
Sorex tundrensis	ZMMU S-177789	Russia	Kemerovo Region, Middle Tom	Far West Siberia	50	GU564760, N/A, N/A
Sorex tundrensis	ZMMU S-177790	Russia	Kemerovo Region, Middle Tom	Far West Siberia	50	GU564761, N/A, N/A
Sorex tundrensis	ZMMU S-177791	Russia	Kemerovo Region, Middle Tom	Far West Siberia	50	GU564762, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I (1)	Far West Siberia	61	GU564782, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564783, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	64	GU564786, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564787, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	64	GU564790, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564791, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	65	GU564792, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564793, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	65	GU564795, N/A, N/A

Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	64	GU564796, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564797, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564798, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564799, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	64	GU564800, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	65	GU564801, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	64	GU564802, N/A, N/A
Sorex tundrensis	PISR	Russia	Komi Republic, Upper Pechora I	Far West Siberia	62	GU564803, N/A, N/A
Sorex tundrensis	ZMMU S-183259	Russia	Komi Republic, Upper Pechora II (2)	Far West Siberia	62	GU564784, N/A, N/A
Sorex tundrensis	ZMMU S-183258	Russia	Komi Republic, Upper Pechora II	Far West Siberia	63	GU564785, N/A, N/A
Sorex tundrensis	ZMMU S-183234	Russia	Komi Republic, Upper Pechora II	Far West Siberia	62	GU564788, N/A, N/A
Sorex tundrensis	ZMMU S-183256	Russia	Komi Republic, Upper Pechora II	Far West Siberia	62	GU564804, N/A, N/A
Sorex tundrensis		Russia	Novosibirsk Region, Baraba Steppe (3)	Far West Siberia	66	GU564805, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland (4)	Far West Siberia	50	GU564806, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	50	GU564808, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	50	GU564809, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	50	GU564810, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	67	GU564811, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	50	GU564812, N/A, N/A
Sorex tundrensis	SZMN	Kazakhstan	Pavlodar Region, Kazakh Upland	Far West Siberia	68	GU564813, N/A, N/A
Sorex tundrensis	ZMMU 48/09 78	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I (19)	West Siberia	43	GU564750, N/A, N/A
Sorex tundrensis	ZMMU 48/09 79	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	44	GU564751, N/A, N/A
Sorex tundrensis	ZMMU 48/09 80	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	45	GU564752, N/A, N/A
Sorex tundrensis	ZMMU 48/09 88	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	42	GU564753, N/A, N/A

Sorex tundrensis	ZMMU 48/09 89	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	42	GU564754, N/A, N/A
Sorex tundrensis	ZMMU 48/09 95	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	42	GU564755, N/A, N/A
Sorex tundrensis	ZMMU 48/09 96	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay I	West Siberia	46	GU564756, N/A, N/A
Sorex tundrensis	ZMMU S-181053	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay II (20)	West Siberia	40	GU564746, N/A, N/A
Sorex tundrensis	ZMMU S-181055	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay II	West Siberia	40	GU564747, N/A, N/A
Sorex tundrensis	ZMMU S-181056	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay II	West Siberia	41	GU564748, N/A, N/A
Sorex tundrensis	ZMMU S-181057	Mongolia	Arhangay Aymag, Tariat Somon, North Hangay II	West Siberia	42	GU564749, N/A, N/A
Sorex tundrensis	ZISP 83786	Russia	Buryatya, Middle Selenga (23)	West Siberia	69	GU564814, N/A, N/A
Sorex tundrensis	ZISP 98873	Russia	Gorno-Altai Republic, Tyutea River, South Altai II (14)	West Siberia	43	GU564781, N/A, N/A
Sorex tundrensis	SZMN	Russia	Gorno-Altai Republic, Ukok Plateau, South Altai I (15)	West Siberia	59	GU564779, N/A, N/A
Sorex tundrensis	SZMN	Russia	Gorno-Altai Republic, Ukok Plateau, South Altai I	West Siberia	60	GU564780, N/A, N/A
Sorex tundrensis	SZMN	Russia	Irkutsk Region, Biryusa River (17)	West Siberia	34	GU564736, N/A, N/A
Sorex tundrensis	ZMMU S-181339	Russia	Irkutsk Region, SW Baikal (22)	West Siberia	35	GU564737, N/A, N/A
Sorex tundrensis	ZMMU S-177787	Russia	Kemerovo Region, Middle Tom (11)	West Siberia	49	GU564759, N/A, N/A
Sorex tundrensis	ZMMU S-184034	Russia	Krasnoyarsk Region, Left bank, Middle Yenisei River (8)	West Siberia	74	GU564819, N/A, N/A
Sorex tundrensis	ZMMU S-186045	Russia	Krasnoyarsk Region, Left bank, Middle Yenisei River	West Siberia	49	GU564820, N/A, N/A
Sorex tundrensis	ZMMU S-186046	Russia	Krasnoyarsk Region, Left bank, Middle Yenisei River	West Siberia	75	GU564821, N/A, N/A
Sorex tundrensis	ZMMU S-186047	Russia	Krasnoyarsk Region, Left bank, Middle Yenisei River	West Siberia	76	GU564822, N/A, N/A
Sorex tundrensis	ZMMU S-186044	Russia	Krasnoyarsk Region, Left bank, Middle Yenisei River	West Siberia	77	GU564823, N/A, N/A
Sorex tundrensis	ZMMU 54/09 4	Russia	Krasnoyarsk Region, Podkamennay Tunguska Ri., SW Evenkia (10)	West Siberia	85	GU564838, N/A, N/A
Sorex tundrensis	ZMMU 54/09 9	Russia	Krasnoyarsk Region, Podkamennay Tunguska Ri., SW Evenkia	West Siberia	86	GU564839, N/A, N/A
Sorex tundrensis	ZMMU 54/09 1	Russia	Krasnoyarsk Region, Stolbovaya River, Southwest Evenkia I (9)	West Siberia	49	GU564837, N/A, N/A
Sorex tundrensis	ZMMU S-181835	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau (7)	West Siberia	36	GU564738, N/A, N/A
Sorex tundrensis	ZMMU S-181837	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	37	GU564739, N/A, N/A

Sorex tundrensis	ZMMU S-181838	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	38	GU564740, N/A, N/A
Sorex tundrensis	ZMMU S-181852	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	38	GU564741, N/A, N/A
Sorex tundrensis	ZMMU S-181856	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	38	GU564742, N/A, N/A
Sorex tundrensis	ZMMU S-181908	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	39	GU564743, N/A, N/A
Sorex tundrensis	ZMMU	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	38	GU564744, N/A, N/A
Sorex tundrensis	ZMMU	Russia	Krasnoyarsk Region, Taimyr district, Putorana Plateau	West Siberia	38	GU564745, N/A, N/A
Sorex tundrensis	ZMMU S-81674	Russia	Krasnoyarsk Region, Bolshoy Kemchug (12)	West Siberia	N/A	GU564851, N/A, N/A
Sorex tundrensis	ST94	Russia	Krasnoyarskiy District (18)	West Siberia	138	**HM992735, N/A, N/A**
Sorex tundrensis	ST95	Russia	Krasnoyarskiy District	West Siberia	N/A	**HM992736, N/A, N/A**
Sorex tundrensis	ST92	Russia	Krasnoyarskiy District	West Siberia	137	**HM992734, N/A, N/A**
Sorex tundrensis	ST82	Russia	Krasnoyarskiy District, village Maina (16)	West Siberia	N/A	**HM992730, N/A, N/A**
Sorex tundrensis	ST83	Russia	Krasnoyarskiy District, village Maina	West Siberia	134	**HM992731, HM992755, HM992678**
Sorex tundrensis	ST84	Russia	Krasnoyarskiy District, village Maina	West Siberia	135	**HM992732, N/A, N/A**
Sorex tundrensis	ST85	Russia	Krasnoyarskiy District, village Maina	West Siberia	136	**HM992733, N/A, N/A**
Sorex tundrensis	ST81	Russia	Krasnoyarskiy District, village Maina	West Siberia	133	**HM992729, N/A, N/A**
Sorex tundrensis	ST46	Russia	Kuznetskiy Alatau, village Priiskoviy (13)	West Siberia	N/A	**HM992722, N/A, N/A**
Sorex tundrensis	ST49	Russia	Kuznetskiy Alatau, village Priiskoviy	West Siberia	130	**HM992723, N/A, N/A**
Sorex tundrensis	ST45	Russia	Kuznetskiy Alatau, village Priiskoviy	West Siberia	N/A	**HM992721, N/A, N/A**
Sorex tundrensis	ST71	Russia	Tunki Mt Range (21)	West Siberia	46	**HM992725, N/A, N/A**
Sorex tundrensis	ST73	Russia	Tunki Mt Range	West Siberia	132	**HM992727, N/A, N/A**
Sorex tundrensis	ST74	Russia	Tunki Mt Range	West Siberia	N/A	**HM992728, N/A, N/A**
Sorex tundrensis	ST72	Russia	Tunki Mt Range	West Siberia	131	**HM992926, N/A, N/A**
Sorex tundrensis	ST70	Russia	Tunki Mt Range	West Siberia	N/A	**HM992724, N/A, N/A**
Sorex tundrensis	KZM 1453	Russia	Yamalo-Nenetsky Region, Middle Taz (6)	West Siberia	87	GU564840, N/A, N/A

Sorex tundrensis	MSB148635	Russia	Amga River Basin, 7 km N Sulgachi (38)	Amga Basin	116	**HM992603, HM992769, HM992692**
Sorex tundrensis	MSB148637	Russia	Amga River Basin, 7 km N Sulgachi	Amga Basin	116	**HM992604, N/A, N/A**
Sorex tundrensis	MSB148596	Russia	Amga River Basin, 7 km N Sulgachi	Amga Basin	57	**HM992657, N/A, N/A**
Sorex tundrensis	MSB148462	Russia	Amga River Basin, 7 km N Sulgachi	Amga Basin	116	**HM992740, N/A, N/A**
Sorex tundrensis	MSB148566	Russia	Amga River, 10 km NE Sulgachi (39)	Amga Basin	57	**HM992650, N/A, N/A**
Sorex tundrensis	MSB148565	Russia	Amga River, 10 km NE Sulgachi	Amga Basin	57	**HM992649, N/A, N/A**
Sorex tundrensis	MSB148552	Russia	Amga River, 8 km ENE Mikhaylovka (40)	Amga Basin	57	**HM992652, N/A, N/A**
Sorex tundrensis	MSB148628	Russia	Amga River, 8 km ENE Mikhaylovka	Amga Basin	118	**HM992742, HM992771, HM992694**
Sorex tundrensis	MSB148339	Russia	Lena River Basin, 6.5 km ESE Khocho (35)	Amga Basin	57	**HM992600, HM992765, HM992688**
Sorex tundrensis	MSB148709	Russia	Lena River Basin, 6.5 km ESE Khocho	Amga Basin	56	**HM992601, HM992766, HM992689**
Sorex tundrensis	MSB148324	Russia	Lena River Basin, 6.5 km ESE Khocho	Amga Basin	121	**HM992646, HM992764, HM992687**
Sorex tundrensis	MSB148325	Russia	Lena River Basin, 6.5 km ESE Khocho	Amga Basin	121	**HM992647, N/A, N/A**
Sorex tundrensis	ZMMU S-183445	Russia	Republic Sakha, Maya River, Central Yakutia (37)	Amga Basin	57	GU564775, N/A, N/A
Sorex tundrensis	ZMMU S-183448	Russia	Republic Sakha, Maya River, Central Yakutia	Amga Basin	57	GU564776, N/A, N/A
Sorex tundrensis	ZMMU S-183449	Russia	Republic Sakha, Maya River, Central Yakutia	Amga Basin	57	GU564777, N/A, N/A
Sorex tundrensis	ZMMU S-183447	Russia	Republic Sakha, Maya River, Central Yakutia	Amga Basin	58	GU564778, N/A, N/A
Sorex tundrensis	ZMMU S-181486	Russia	Republic Sakha, Middle Amga River (36)	Amga Basin	56	GU564774, N/A, N/A
Sorex tundrensis	ZMMU 05/10	Russia	Yamalo-Nenetsky Region, Gydan Peninsula (5)	Amga Basin	89	GU564842, N/A, N/A
Sorex tundrensis	KZM 1454	Russia	Yamalo-Nenetsky Region, Middle Taz (6)	Amga Basin	88	GU564841, N/A, N/A
Sorex tundrensis	SZMN	Russia	Chita Region, Ononskiy District, Torei Lakes (25)	MNA	71	GU564816, N/A, N/A
Sorex tundrensis	SZMN	Russia	Chita Region, Ononskiy District, Torei Lakes	MNA	72	GU564817, N/A, N/A
Sorex tundrensis	SZMN	Russia	Chita Region, Ononskiy District, Torei Lakes	MNA	73	GU564818, N/A, N/A
Sorex tundrensis	ZMMU S-182064	Russia	Chita Region, Zabaikalsky District, Upper Argun (26)	MNA	70	GU564815, N/A, N/A
Sorex tundrensis	NM4	China	Inner Mongolia, Eerguna National Nature Reserve (27)	MNA	70	GU570993, N/A, N/A

Sorex tundrensis	NM1	China	Inner Mongolia, Eerguna National Nature Reserve	MNA	92	GU570994, N/A, N/A
Sorex tundrensis	NM2	China	Inner Mongolia, Eerguna National Nature Reserve	MNA	93	GU570995, N/A, N/A
Sorex tundrensis		Russia	Jewish Autonomy Region, Middle Amur River (28)	MNA	54	GU564772, N/A, N/A
Sorex tundrensis	IBPN	Russia	Khabarovsk Region, 50 km S Khabarovsk (29)	MNA	55	GU564834, N/A, N/A
Sorex tundrensis	ZMMU S-145569	Russia	Primorsky Region, Gayvaron Village, Khanka Lake (30)	MNA	55	GU564773, N/A, N/A
Sorex tundrensis	N/A	Russia	Sakhalinskaya Oblast, Moneron Island (31)	MNA	5	AB244646, N/A, N/A
Sorex tundrensis	IBPN	Russia	Sakhalinskaya Oblast, Moneron Island	MNA	4	GU564771, N/A, N/A
Sorex tundrensis	N/A	Russia	Sakhalinskaya Oblast, Moneron Island	MNA	4	AB244645, N/A, N/A
Sorex tundrensis	ZMMU S-182209	Mongolia	Selenga Aymag, Upper Eroo River, West Hentey (24)	MNA	47	GU564757, N/A, N/A
Sorex tundrensis	MSB146729	Russia	4 km W Yakutsk (33)	Central Siberia	79	**HM992594, N/A, N/A**
Sorex tundrensis	MSB146730	Russia	4 km W Yakutsk	Central Siberia	115	**HM992595, N/A, N/A**
Sorex tundrensis	MSB146512	Russia	4 km W Yakutsk	Central Siberia	115	**HM992593, HM992759, HM992682**
Sorex tundrensis	MSB148636	Russia	Amga River Basin, 7 km N Sulgachi (38)	Central Siberia	81	**HM992602, HM992768, HM992691**
Sorex tundrensis	MSB148597	Russia	Amga River Basin, 7 km N Sulgachi	Central Siberia	117	**HM992648, HM992767, HM992690**
Sorex tundrensis	MSB148655	Russia	Amga River, 8 km ENE Mikhaylovka (40)	Central Siberia	84	**HM992741, HM992770, HM992693**
Sorex tundrensis	MSB148572	Russia	Amga River, 8 km ENE Mikhaylovka	Central Siberia	N/A	**HM992651, N/A, N/A**
Sorex tundrensis	MSB148479	Russia	Kenkeme River, 40 km W Yakutsk (32)	Central Siberia	80	**HM992584, N/A, N/A**
Sorex tundrensis	MSB148749	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	121	**HM992585, N/A, N/A**
Sorex tundrensis	MSB148750	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	82	**HM992586, N/A, N/A**
Sorex tundrensis	MSB148755	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	79	**HM992587, N/A, N/A**
Sorex tundrensis	MSB148763	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992588, N/A, N/A**
Sorex tundrensis	MSB148799	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	124	**HM992589, HM992757, HM992680**
Sorex tundrensis	MSB148825	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	122	**HM992590, HM992758, HM992681**
Sorex tundrensis	MSB148826	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	82	**HM992591, N/A, N/A**

Sorex tundrensis	MSB148831	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	82	**HM992592, N/A, N/A**
Sorex tundrensis	MSB148834	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992643, N/A, N/A**
Sorex tundrensis	MSB148842	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	81	**HM992644, N/A, N/A**
Sorex tundrensis	MSB148473	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	122	**HM992737, N/A, N/A**
Sorex tundrensis	MSB148476	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992738, N/A, N/A**
Sorex tundrensis	MSB148829	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	79	**HM992739, N/A, N/A**
Sorex tundrensis	MSB148481	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992751, N/A, N/A**
Sorex tundrensis	MSB148797	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992752, N/A, N/A**
Sorex tundrensis	MSB148832	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	82	**HM992753, N/A, N/A**
Sorex tundrensis	MSB148477	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	123	**HM992754, N/A, N/A**
Sorex tundrensis	MSB148470	Russia	Kenkeme River, 40 km W Yakutsk	Central Siberia	80	**HM992583, HM992756, HM992679**
Sorex tundrensis	MSB148708	Russia	Lena River Basin, 6.5 km ESE Khocho (35)	Central Siberia	120	**HM992599, HM992763, HM992686**
Sorex tundrensis	MSB146503	Russia	Lena River, 2 km NW Tochtur (34)	Central Siberia	78	**HM992597, HM992761, HM992684**
Sorex tundrensis	MSB146504	Russia	Lena River, 2 km NW Tochtur	Central Siberia	79	**HM992598, HM992762, HM992685**
Sorex tundrensis	MSB146505	Russia	Lena River, 2 km NW Tochtur	Central Siberia	78	**HM992645, N/A, N/A**
Sorex tundrensis	MSB146479	Russia	Lena River, 2 km NW Tochtur	Central Siberia	82	**HM992596, HM992760, HM992683**
Sorex tundrensis	IBPN	Russia	Magadan Region, Chukochya River, Lower Kolyma (41)	Central Siberia	3	AB175127, N/A, N/A
Sorex tundrensis	UAM84265	Russia	3 km SSE confluence Volchya River and Liman Sea (47)	East Siberia	51	**HM992607, N/A, N/A**
Sorex tundrensis	UAM84270	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	52	**HM992608, N/A, N/A**
Sorex tundrensis	UAM84310	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	14	**HM992609, HM992772, HM992695**
Sorex tundrensis	UAM84313	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992610, HM992773, HM992696**
Sorex tundrensis	UAM84315	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	52	**HM992611, HM992774, HM992697**
Sorex tundrensis	UAM84322	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	95	**HM992612, N/A, N/A**
Sorex tundrensis	UAM84362	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992613, N/A, N/A**

Sorex tundrensis	UAM84375	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	52	**HM992614, N/A, N/A**
Sorex tundrensis	UAM84378	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992615, N/A, N/A**
Sorex tundrensis	UAM84388	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992616, N/A, N/A**
Sorex tundrensis	UAM84395	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	N/A	**HM992617, N/A, N/A**
Sorex tundrensis	UAM84400	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	96	**HM992618, HM992775, HM992698**
Sorex tundrensis	UAM84407	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992619, N/A, N/A**
Sorex tundrensis	UAM84409	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	97	**HM992620, HM992776, HM992699**
Sorex tundrensis	UAM84269	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	51	**HM992654, N/A, N/A**
Sorex tundrensis	UAM84277	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	N/A	**HM992655, N/A, N/A**
Sorex tundrensis	UAM84260	Russia	3 km SSE confluence Volchya River and Liman Sea	East Siberia	52	**HM992606, N/A, N/A**
Sorex tundrensis	UAM84247	Russia	3.5 km ESE of Mt. Dionysus, S of Liman Sea (48)	East Siberia	53	**HM992622, HM992778, HM992701**
Sorex tundrensis	UAM84242	Russia	3.5 km ESE of Mt. Dionysus, S of Liman Sea	East Siberia	53	**HM992621, HM992777, HM992700**
Sorex tundrensis	IBPN	Russia	Chukotka Region, Ust'-Chaun, Chukotka (45)	East Siberia	83	GU564833, N/A, N/A
Sorex tundrensis	IBPN	Russia	Magadan Region, NE Okhotsk coast, Magadan (43)	East Siberia	14	GU564768, N/A, N/A
Sorex tundrensis	IBPN	Russia	Magadan Region, Upper Kolyma River (42)	East Siberia	51	GU564770, N/A, N/A
Sorex tundrensis	UAM80496	Russia	Omolon River, 10 km SSW Kegali River (44)	East Siberia	14	**HM992605, N/A, N/A**
Sorex tundrensis	UAM80449	Russia	Omolon River, 10 km SSW Kegali River	East Siberia	14	**HM992653, N/A, N/A**
Sorex tundrensis	ZMMU S-182096	Russia	Chukotka Region, Anadyr (46)	East Siberia	N/A	GU564763, N/A, N/A
Sorex tundrensis	MSB142945	USA	120 mi W Paxson on Denali Highway (62)	Nearctic	98	**HM992640, HM992795, HM992718**
Sorex tundrensis	MSB145646	Canada	2 mi N Rock River on Highway 5 (64)	Nearctic	100	**HM992642, HM992796, HM992719**
Sorex tundrensis	MSB145585	Canada	2 mi N Rock River on Highway 5	Nearctic	N/A	**HM992656, N/A, N/A**
Sorex tundrensis	UAM76157	USA	5 mi S of Bonanza Creek Experimental Forest (61)	Nearctic	15	**HM992744, HM992780, HM992703**
Sorex tundrensis	IBPN	USA	Alaska, Anchorage (63)	Nearctic	91	GU564847, N/A, N/A
Sorex tundrensis	UAM102213	USA	Alaska, Fairbanks (55)	Nearctic	90	GU564843, N/A, N/A

Sorex tundrensis	UAM102208	USA	Alaska, Fairbanks	Nearctic	90	GU564844, N/A, N/A
Sorex tundrensis	UAM22042	USA	Creamer's Field, Fairbanks (56)	Nearctic	6	**HM992624, HM992781, HM992704**
Sorex tundrensis	MSB144200	Canada	Dawson City, West Bank Yukon River (65)	Nearctic	99	**HM992641, N/A, N/A**
Sorex tundrensis	UAM31687	USA	Fort Richardson (57)	Nearctic	6	**HM992637, N/A, N/A**
Sorex tundrensis	UAM31395	USA	Fort Richardson	Nearctic	6	**HM992636, N/A, N/A**
Sorex tundrensis	UAM47527	USA	Goodnews River (52)	Nearctic	9	**HM992638, HM992793, HM992716**
Sorex tundrensis	UAM36758	USA	Grayling Creek Shelter (49)	Nearctic	6	**HM992748, N/A, N/A**
Sorex tundrensis	MSB143124	USA	Galbraith Lake Campground (59)	Nearctic	101	**HM992639, HM992794, HM992717**
Sorex tundrensis	UAM45203	USA	Lost Creek vicinity (60)	Nearctic	10	**HM992623, HM992779, HM992702**
Sorex tundrensis	UAM46825	USA	Mouse Lake (54)	Nearctic	11	**HM992626, N/A, N/A**
Sorex tundrensis	UAM36746	USA	Mouse Lake	Nearctic	22	**HM992625, HM992782, HM992705**
Sorex tundrensis	UAM77955	USA	Nearctic, Horn Lake	Nearctic	16	GU223666, GU223698, GU223730
Sorex tundrensis	UAM34065	USA	Nulato Quad (53)	Nearctic	12	**HM992628, HM992784, HM992707**
Sorex tundrensis	UAM34142	USA	Nulato Quad	Nearctic	13	**HM992629, HM992785, HM992708**
Sorex tundrensis	UAM37961	USA	Nulato Quad	Nearctic	7	**HM992630, HM992786, HM992709**
Sorex tundrensis	UAM34067	USA	Nulato Quad	Nearctic	11	**HM992745, N/A, N/A**
Sorex tundrensis	UAM34068	USA	Nulato Quad	Nearctic	11	**HM992746, N/A, N/A**
Sorex tundrensis	UAM34064	USA	Nulato Quad	Nearctic	11	**HM992627, HM992783, HM992706**
Sorex tundrensis	UAM32959	USA	Pilgrim Springs (50)	Nearctic	19	**HM992631, HM992787, HM992710**
Sorex tundrensis	UAM32960	USA	Pilgrim Springs	Nearctic	20	**HM992632, HM992788, HM992711**
Sorex tundrensis	UAM32961	USA	Pilgrim Springs	Nearctic	21	**HM992633, HM992789, HM992712**
Sorex tundrensis	UAM32963	USA	Pilgrim Springs	Nearctic	18	**HM992634, HM992790, HM992713**
Sorex tundrensis	UAM46991	USA	Pilgrim Springs	Nearctic	17	**HM992635, HM992791, HM992714**
Sorex tundrensis	UAM32957	USA	Pilgrim Springs	Nearctic	18	**HM992747, N/A, N/A**

Sorex tundrensis	UAM47526	USA	Togiak National Wildlife Refuge (51)	Nearctic	9	**HM992750, N/A, N/A**
Sorex tundrensis	UAM47524	USA	Togiak National Wildlife Refuge	Nearctic	8	**HM992749, HM992792, HM992715**
Sorex tundrensis	UAM75505	USA	Toolik Lake Research Station (58)	Nearctic	6	**HM992743, N/A, N/A**
Sorex asper	MSB158585	China	23.5 km E, 6.2 km S Narati (66)	N/A	102	**HM992668, N/A, N/A**
Sorex asper	MSB158589	China	23.5 km E, 6.2 km S Narati	N/A	104	**HM992670, N/A, N/A**
Sorex asper	MSB158405	China	23.5 km E, 6.2 km S Narati	N/A	106	**HM992658, N/A, N/A**
Sorex asper	MSB158588	China	23.5 km E, 6.3 km S Narati (66)	N/A	103	**HM992669, HM992797, HM992720**
Sorex asper	MSB158507	China	24.2 km E, 8 km S Narati (66)	N/A	106	**HM992664, N/A, N/A**
Sorex asper	MSB158539	China	24.2 km E, 8 km S Narati	N/A	105	**HM992665, N/A, N/A**
Sorex asper	MSB158609	China	24.2 km E, 8 km S Narati	N/A	111	**HM992672, N/A, N/A**
Sorex asper	MSB158613	China	24.2 km E, 8 km S Narati	N/A	105	**HM992673, N/A, N/A**
Sorex asper	MSB158614	China	24.2 km E, 8 km S Narati	N/A	108	**HM992674, N/A, N/A**
Sorex asper	MSB158503	China	24.2 km E, 8 km S Narati	N/A	109	**HM992663, N/A, N/A**
Sorex asper	MSB158608	China	24.2 km E, 8.1 km S Narati (66)	N/A	111	**HM992671, N/A, N/A**
Sorex asper	MSB158567	China	24.2 km E, 8.1 km S Narati	N/A	112	**HM992667, N/A, N/A**
Sorex asper	MSB158540	China	24.4 km E, 7.9 km S Narati (66)	N/A	103	**HM992666, N/A, N/A**
Sorex asper	MSB158496	China	24.4 km E, 7.9 km S Narati	N/A	107	**HM992662, N/A, N/A**
Sorex asper	MSB158453	China	24.5 km E, 7.8 km S Narati (66)	N/A	108	**HM992661, N/A, N/A**
Sorex asper	MSB158450	China	24.5 km E, 7.8 km S Narati	N/A	107	**HM992660, N/A, N/A**
Sorex asper	MSB158781	China	24.6 km E, 7.8 km N. Narati (66)	N/A	113	**HM992677, N/A, N/A**
Sorex asper	MSB158416	China	24.6 km E, 7.8 km S Narati (66)	N/A	110	**HM992659, N/A, N/A**
Sorex asper	MSB158768	China	29.3 km E, 7.1 km N. Narati (66)	N/A	105	**HM992676, N/A, N/A**
Sorex asper	MSB158666	China	29.4 km E, 7.1 km N. Narati (66)	N/A	114	**HM992675, N/A, N/A**
Sorex antinorii	IZEA1394	Italy	Grand Sasso	N/A	1	AB175124, N/A, N/A

Sorex antinorii	IZEA7514	Italy	Piacenca	N/A	2	AB175125, N/A, N/A
Sorex antinorii	IZEA5325	Italy	Grand Sasso	N/A	N/A	N/A, GU473817, GU473751
Sorex antinorii	IZEA7515	Italy	Piacenca	N/A	N/A	N/A, GU473825, GU473758
Sorex araneus	MSB95461	Hungary	Gyor-Sopron-Moson	N/A	128	GQ374416, N/A, N/A
Sorex araneus	MSB94609	Hungary	Zala, 1.5 km S. from Bazakerettye	N/A	129	**HQ008361, HQ008362, HQ008363**
Sorex araneus	IZEA4355	France	Etang de Balcère, Pyr. Or	N/A	N/A	EF636502, GU473807, GU473741
Sorex araneus	IZEA4356	France	Etang de Balcère, Pyr. Or	N/A	N/A	EF636502, GU473809, GU473743
Sorex araneus	IZEA2980	Switzerland	Champ-Pittet Vaud	N/A	N/A	EF636503, GU473809, GU473743
Sorex arcticus	MSB156205	Canada	Alberta, Kananaskis	N/A	126	**JF439297, N/A, N/A**
Sorex arcticus	MSB156215	Canada	Alberta, Kananaskis	N/A	127	**JF439298, JF439300, JF439301**
Sorex caecutiens	MSB146478	Russia	Lena River; 2 km NW Tochtur	N/A	33	GU223668, GU223699, GU223731
Sorex coronatus	IZEA4163	France	Pyrenees Orientales	N/A	26	AJ000420, N/A, N/A
Sorex coronatus	IZEA3374	France	Vercors, Isere	N/A	25	AJ000419, N/A, N/A
Sorex coronatus	IZEA2984	Switzerland	Champ-Pittet Vaud	N/A	N/A	EF636516, GU473832, GU473769
Sorex coronatus	IZEA3018	Switzerland	Champ-Pittet Vaud	N/A	N/A	EF636516, GU473833, GU473770
Sorex coronatus	IZEA3242	Switzerland	Jorat, Vaud	N/A	N/A	EF636516, GU473835, GU473773
Sorex daphaenodon	MSB148704	Russia	Amga River, 8 km ENE Mikhaylovka	N/A	119	GU223669, GU223700, GU223732
Sorex daphaenodon	MSB149784	Russia	Magadan Region, Buyunda	N/A	125	**JF439299, N/A, N/A**
Sorex granarius	IZEA E62	Spain	Piedrahita, Avila	N/A	23	AJ000417, N/A, N/A
Sorex granarius	IZEA E69	Spain	Rascafria, Salamanca	N/A	24	AJ000418, N/A, N/A
Sorex granarius	IZEA632	Spain	Rascafria	N/A	N/A	EF636513, GU473788, GU473723
Sorex granarius	IZEA637	Spain	Rascafria	N/A	N/A	EF636515, GU473793, GU473729
Sorex maritimensis	KD430	Canada	New Brunswick, Cape Jourimain	N/A	32	EU035327, N/A, N/A
Sorex maritimensis	KD346	Canada	Nova Scotia, Oxford	N/A	31	EU035326, N/A, N/A

Sorex minutissimus	MSB148592	Russia	Amga River Basin, 7 km N Sulgachi	N/A	N/A	GU223634, GU223674, GU223706
Sorex minutus	MSB95476	Hungary	Gyor-Sopron-Moson, Osli, Kiraly-to	N/A	N/A	GU223667, GU223702, GU223733
Sorex roboratus	MSB148679	Siberia	Kenkeme River, 40 km W Yakutsk	N/A	N/A	GU223670, GU223701, GU223734
Sorex samniticus	IZEA507	Italy	Opi, Abruzzi	N/A	29	AJ000429, N/A, N/A
Sorex samniticus	IZEA509	Italy	Opi, Abruzzi	N/A	30	AJ000430, N/A, N/A
Sorex samniticus	IZEA5332	Italy	Pescasseroli, Abruzzo	N/A	N/A	EF636522, GU473842, GU473782
Sorex samniticus	IZEA4739	Italy	Pescasseroli, Abruzzo	N/A	N/A	EF636523, GU473841, GU473781
Sorex satunini	IAPG MM789	Turkey	Bagdasan	N/A	27	AJ000421, N/A, N/A
Sorex satunini	IAPG MM840	Turkey	Guzyurdu	N/A	28	AJ000422, N/A, N/A
Sorex satunini	S42R	Russia	Krasnodar Region, Pervomayskoe	N/A	94	GU827398, N/A, N/A
Sorex satunini	S69R	Russia	Krasnodar Region, Pervomayskoe	N/A	94	GU827402, N/A, N/A

Table S1 - Primers developed for amplification of the cytochrome *b* gene. Degraded quality DNA was amplified using multiple primer pairs; complete sequences were obtained from high quality DNA using only MSB05/MSB14, developed previously (Hope *et al.* 2010).

	Forward			Reverse			
Pair	Name	Sequence	Start	Name	Sequence	Start	Product Size (bp)
1	MSB05	GACATGAAAAATCATTGTTGTAATTC	-43	MVZ06S	TGTGTCTGATGTGTAGTGTA	177	220
2	St1	CTCATCATGGTGAAACTTCG	81	MSB12S	AGAACATTGATGCTCCGTTT	271	191
3	MSB03S	AACGGAGCATCAATGTTCTT	253	St2	CCGATATAAGGGATTGCTGA	470	220
4	St3	ATCCCTTATATCGGCTCAGA	457	H15392S	GTAAGGGTGAAAGGGGATTT	669	213
5	St4	ATCCCTTATATCGGCTCAGA	611	MSB41S	GTTAGGGATGGATCGTAGG	858	248
6	St5	CCACCCCATATTAAACCAGA	793	St6	TGCGACTAGGATTCAGAAGA	990	198
7	St7	TAATATTCCGCCCATTTAGCC	944	MSB14	CCCATCTCTGGTTTACAAGAC	1186	243

Table S2 – Uncorrected sequence divergence within the cytochrome *b* gene between major clades within *Sorex tundrensis* and including the sister species *S. asper*.

Group	3	4	5	6	7	8	9	10	11
1. *S. tundrensis*	--	--	--	--	--	--	--	--	0.0365
2. Far West	0.0161	0.0121	0.0125	0.0116	0.0110	0.0115	0.0107	0.0118	0.0380
3. West	--	0.0153	0.0164	0.0134	0.0154	0.0159	0.0151	0.0155	0.0363
4. Sakha	--	--	--	--	0.0097	0.0084	0.0105	0.0092	0.0356
5. Central	--	--	--	0.0124	0.0088	0.0064	0.0103	0.0073	0.0344
6. Amga Basin	--	--	--	--	0.0111	0.0114	0.0108	0.0121	0.0375
7. Beringia	--	--	--	--	--	--	--	0.0088	0.0364
8. East	--	--	--	--	--	--	0.0091	0.0064	0.0356
9. Nearctic	--	--	--	--	--	--	--	0.0103	0.0368
10. MNA	--	--	--	--	--	--	--	--	0.0340
11. *S. asper*	--	--	--	--	--	--	--	--	--

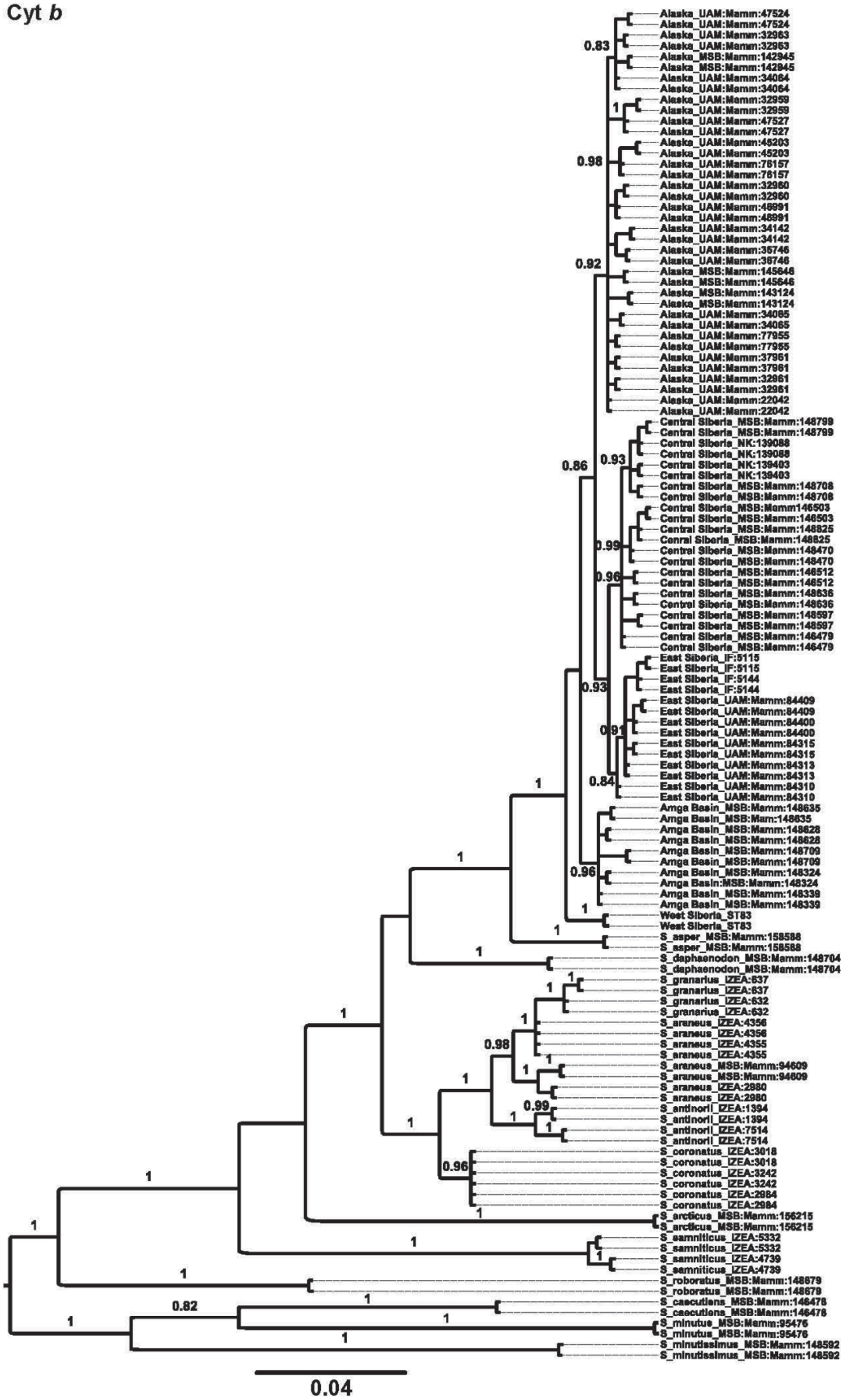

Fig. S1A – Bayesian phylogeny for the Cyt *b* gene using a reduced dataset of all specimens from species tree estimation. Posterior probabilities ≥0.8 are shown.

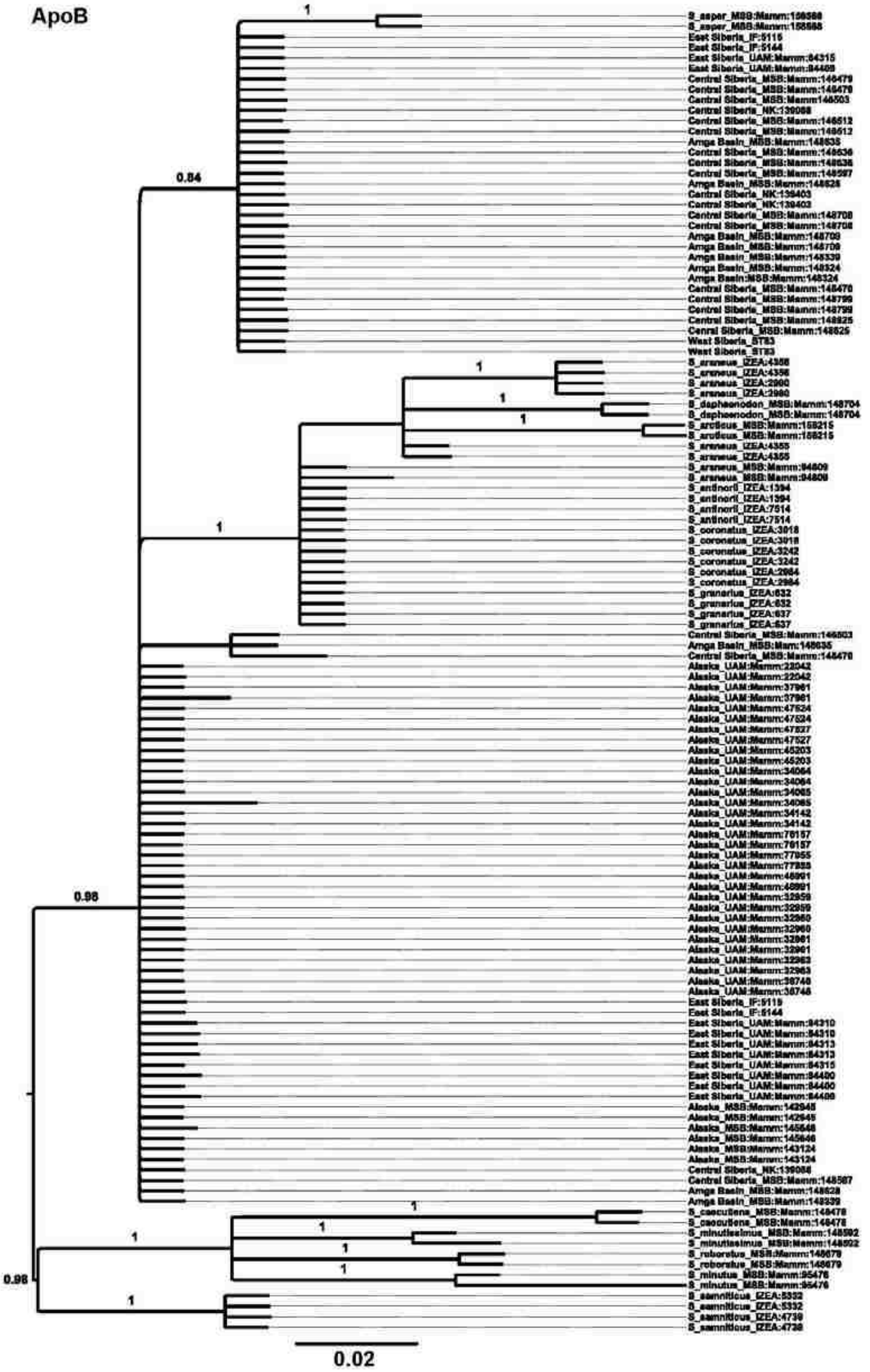

Fig. S1B – Bayesian phylogeny for the ApoB gene using a reduced dataset of all specimens from species tree estimation. Posterior probabilities ≥0.8 are shown.

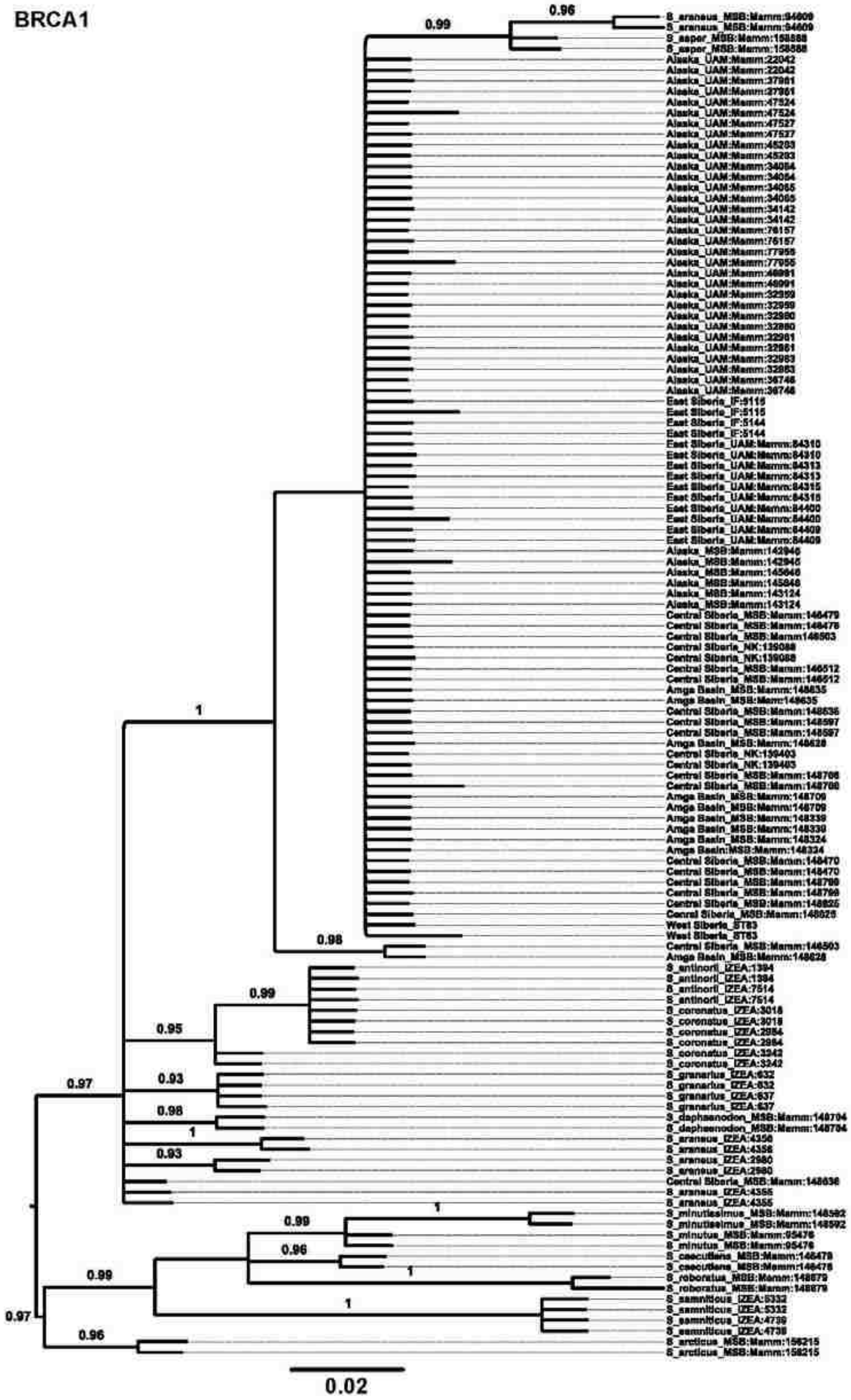

Fig. S1C – Bayesian phylogeny for the BRCA1 gene using a reduced dataset of all specimens from species tree estimation. Posterior probabilities ≥0.8 are shown.

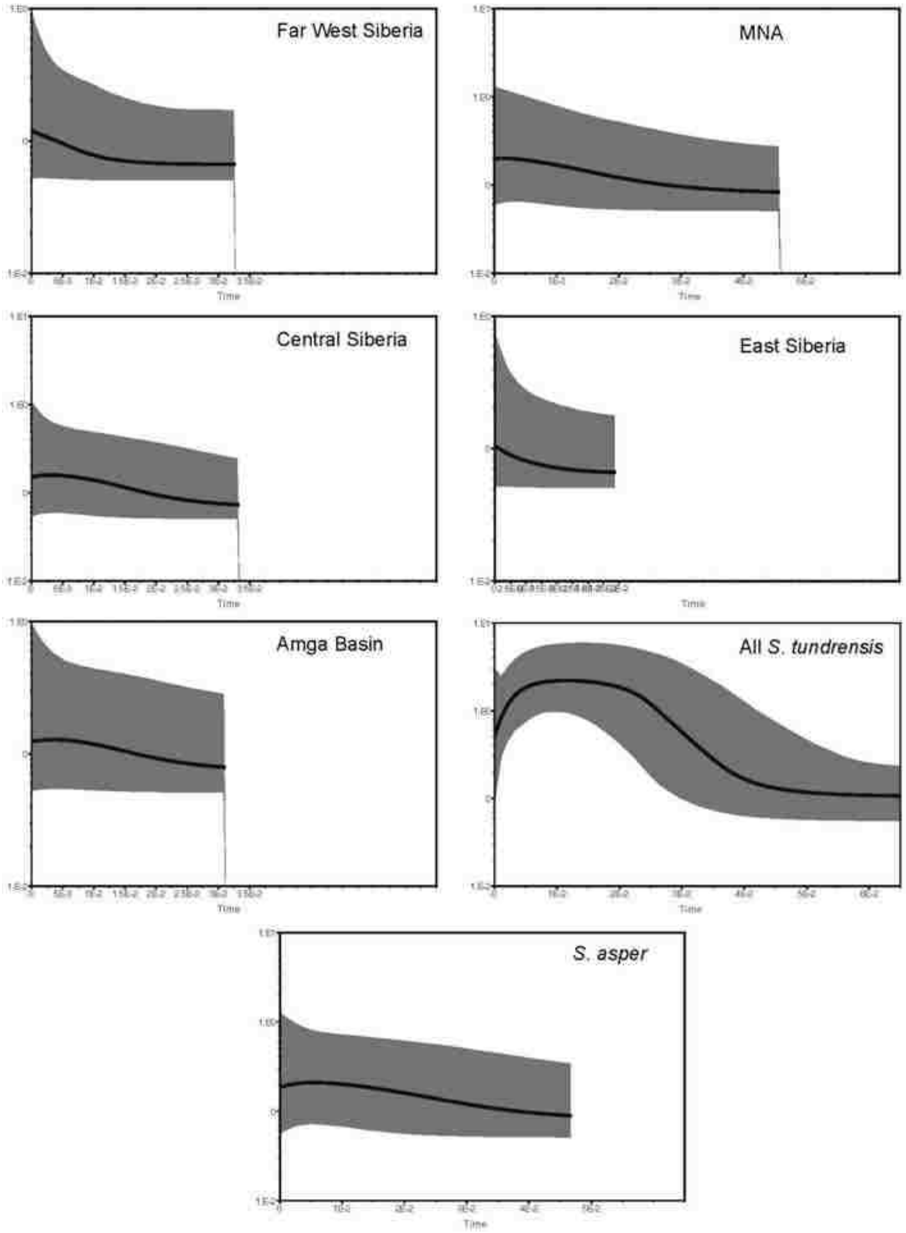

Fig. S2 – Bayesian skyline plots for independent populations (not provided in Fig. 5) of *S. tundrensis*, and including *S. asper*, and all combined populations of *S. tundrensis*. Central line indicates change in effective population size through time; peripheral lines indicate the 95% C. I. The BSP's here extend right-to-left from past to present scaled in millions of years (maximum X = 0.065 My). Vertical axis represents τ as a function of generation time and effective population size (logarithmic scale).

CHAPTER 3

TEMPORAL DYNAMICS OF SPECIATION AMONG AMPHI-BERINGIAN SMALL MAMMALS

Running Title: Amphi-Beringian comparative phylogeography

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KEY WORDS: Bayesian skyline plot, comparative phylogeography, msBayes, Pleistocene refugium, simultaneous divergence

Abstract

Phylogeographic studies have shown that Pleistocene climate cycles played an important role in driving intraspecific diversification and speciation at northern high-latitudes. In a comparative phylogeographic context, we investigate timing and frequency of divergence events across Beringia, the nexus of the northern continents, for a suite of small mammal species with Holarctic distributions. Using a coalescent approach to control for genealogical stochasticity, we test a hypothesis of simultaneous divergence of twelve taxon pairs of rodents and shrews, investigating time to coalescence as well as population demographics for each pair. Among all taxon pairs there is a clear signal that divergences were coincident with Pleistocene glacial cycling, and levels of divergence vary from shallow structure to species-level differentiation. Further, demographic responses to environmental change through time differed among species, reflecting variable histories of both persistence and movement. Factors including a heterogeneous landscape within Beringia and variable ecological affinities among species have resulted in dynamic community assembly and turnover. Methodological constraints associated with resolving recent (Late Pleistocene) isolation events and drawing inferences from a single locus are discussed.

Introduction

Considerable controversy regarding the role of Pleistocene glacial cycles in driving speciation has led to debate over the relative tempo of speciation and extinction across latitudinal gradients (e.g. Weir and Schluter 2004; Zink et al. 2004). At high latitudes, a general view that Pleistocene periodicity was too brief or the climate too harsh to promote speciation (Klicka and Zink 1997) has been replaced by recognition that Pleistocene cycles both initiated allopatric genetic divergence among populations and reinforced divergences that were initiated pre-Pleistocene (Avise and Walker 1998; Avise et al. 1998; although see Marshall 2007). Despite instances where repeated introgression through admixture overwhelms novel divergence following isolation in refugia (Petit et al. 2003), multiple phylogenetic assessments have revealed speciation events within a Pleistocene timeframe (Weir and Schluter 2007; Moyle et al. 2009). Pleistocene cycles have been implicated in population structure among numerous species ranging from arthropod populations in sky-island systems (Knowles 2001) to plant taxa at high latitudes (Brochmann and Brysting 2008). Among mammals, multiple phylogeographic investigations of individual species demonstrate that Pleistocene climate variability caused demographic fluctuations and divergence of isolated populations within discrete refugia, though the temporal resolution of these historical events is coarse (Hewitt 2004; Waltari et al. 2007). In the current study, we examine multiple mammalian taxa within Beringia, the northern high-latitude refugium that spans eastern Siberia and northwestern North America, to test hypotheses related to the temporal diversification of this fauna.

The Pleistocene epoch spanned 2.5 million years (My) leading up to the Holocene (11 thousand years ago [ky] to present) and consisted of over twenty recognized glacial-interglacial cycles due in large part to insolation changes brought about by Croll-Milankovitch processes (Muller and MacDonald 1997; Jannson and Dynesius 2002). Climatic oscillations during the Pleistocene caused major geophysical and ecological change, the timing and extent of which are reflected in genetic signatures of populations (Hewitt 1996; 2000; 2004). Pleistocene refugia are areas where species or populations persisted in isolation during times of inclement climate (Haffer 1969; Bennett and Provan 2008). The traditional concept of Pleistocene refugia focused on isolation during glacial stages, but this perspective has broadened with the recognition that species respond to climate change in various ways depending on their ecological characteristics (Stewart et al. 2010). Refugial concepts are conditional on the species in question, and therefore a given refugium could have existed during either cold or warm periods (Hoffreiter and Stewart 2009; Stewart et al. 2010). Divergence within cold-associated species may have occurred due to isolation during warm climate phases, temporally staggered from divergence in more temperate species due to isolation during cold glacials (Stewart and Dalen 2008).

Recognized high-latitude refugia during cold phases ranged in size from tiny mountaintop nunataks and small exposed areas of the coastal shelf, to much larger continental ice-free zones (e.g. Bennett et al. 1991; Fedorov and Stenseth 2002; Carrara et al. 2007; Holderegger and Thiel-Egenter 2009). Beringia was first described by Hultén (1937) as a biotic refugium and distinct biogeographic region. Beringia was not only a high-latitude ice-free refugium for species during glacial periods, but also a corridor for transcontinental movement between Asia and North America, a potential center of endemism, a source for post-glacial recolonization, and a region of phylogeographic suture zones that delineate distinct clades within and among species (Abbott and Brockmann 2003; Cook et al. 2005; Waltari et al. 2007; DeChaine 2008). The Beringian Isthmus has enabled taxa to move and subsequently diverge across the Holarctic, and yet the spatial and temporal components of these dynamics in Beringia remain poorly understood.

From early recognition and consideration of Beringia as a large and relatively homogeneous single refugium (Hopkins 1967; Hopkins et al. 1982), a more refined view is emerging that Beringia was a shifting mosaic of regional paleoenvironments through time (Elias et al. 1997; Edwards et al. 2000; Guthrie 2001). Large refugia tend to be heterogeneous and dynamic (e.g. Hoffmann 1981; Elias 1992), potentially encompassing multiple cryptic (Stewart and Lister 2001; Provan and Bennett 2008) or micro-refugia (Rull 2009) that lead to fine scale population structure and complex community dynamics (Hofreiter and Stewart 2009). Instead of absolute ice-bound isolation through a glacial phase, populations within refugia may have experienced intermittent local habitat fragmentation and reconnection accompanied by periodic instances of gene flow in response to shifting local climate conditions (DeChaine 2008; Elias and Crocker 2008). In addition to these somewhat ephemeral determinants of population structure, the heterogeneous geography in and surrounding Beringia included more persistent barriers to dispersal during both glacial maxima and minima (Cook et al. 2005). Cordilleran and Laurentide ice sheets delineated the eastern boundary during maxima and extensive mountain ranges and river systems dissected the area. Non-volant terrestrial species were intermittently isolated across Beringia by the Bering Sea during interglacial phases (Sher 1999). Multiple cycles of isolation and reconnection across these major barriers provided repeated opportunities for diversification.

Here, we test temporal hypotheses of genetic divergence to investigate the extent and timing of Pleistocene differentiation among multiple Holarctic taxon pairs. Individual range-wide phylogeographic assessments exist for most study taxa included herein, enabling a multi-species comparative assessment of processes within Beringia. Distributions among taxon pairs are not always concordant and pairs may be isolated across the Bering Strait with varying levels of genetic differentiation, or pairs may have a genetic discontinuity elsewhere in Beringia (e.g. Siberia in the vicinity of the Kolyma and Omolon Rivers), where one taxon of the pair actually spans the Bering Strait. This presents an ideal opportunity to investigate the genetic consequences of multiple possible isolation events through time within the same taxa, including deeper (= older) divergences, followed by latest Pleistocene (= more recent) allopatry across the Bering Strait. This study system allows us to investigate not only the number and timing of isolation events over multiple paired taxa, but also population demography through time. Genetic diversity indices and estimates for population size fluctuations are used to test predictions of demographic change associated with the ecology of individual species and to relate our findings to community assembly and turnover.

Methods

STUDY SYSTEM, SAMPLING, AND TAXA

We follow Hultén (1937) in delimiting Pleistocene Beringia as the geographic area between 125ºE and 130ºW and 45°50' N latitude north to the Arctic Ocean. This area lies roughly between the Lena River in Siberia and the Mackenzie River in western

Canada and extends southward to the Kurile Islands, Aleutian Islands, northernmost Southeast Alaska and northwestern British Columbia. We recognize that the extent of Beringia has been defined in various ways (Harington 2005), but we follow Hultén's (1937) concept, in part due to striking congruence among "Beringian" clades from phylogeographic studies that identified phylogeographic breaks along the periphery of Beringia as delimited here (Hewitt 2004).

We investigated amphi-Beringian rodents (6 species) and shrews (5 species) that present opportunities to compare eastern and western populations isolated across the Bering Strait and/or genetically divergent across a specific phylogeographic boundary in western Beringia (Table 1). These populations may represent intra- or interspecific taxon pairs according to current taxonomy (Wilson and Reeder 2005), and they encompass a wide range of genetic divergence. From these species we identified three categories of taxon pairs:

Group 1. Rodents (deep divergence) – These taxon pairs (two interspecific and two intraspecific) exhibit high levels of genetic differentiation across Beringia and a phylogeographic break in the region of the Kolyma and Omolon Rivers separating a western geographic clade that stretches into central Siberia and an eastern geographic clade that spans the Bering Strait into North America. For the eastern clade only individuals from east of the Strait are included in final analyses so that an assumption of panmixia is not unduly violated by isolation across the Bering Sea (see approximate Bayesian computation [ABC] methods below). To confirm that limiting the dataset in this way did not bias results, relative divergence within these taxon pairs was assessed both with and without western Beringian individuals and no significant difference was found.

Group 2. Rodents (recent allopatry) – All of these pairs are intra-specific and fall within the geographic bounds of the eastern clades of the first four “deep divergence” taxon pairs. Individuals are grouped into either west or east populations depending on their occurrence relative to the Bering Strait, allowing tests of divergence due to isolation at this important ocean barrier.

Group 3. Shrews – Four taxon pairs represent both intra- and interspecific relationships, all delineated by the Bering Strait.

Individuals used for analyses were collected within the limits of Beringia and did not belong to peripheral phylogeographic clades that probably evolved elsewhere. By focusing on clades that are presumed to have originated in Beringia and that do not contain significant substructure, we avoided combining potentially independent evolutionary units. Individuals were also excluded if they occurred in documented hybrid zones (e.g. *Myodes rutilus* from southeast Alaska; Runck et al. 2009) as hybrid individuals may carry introgressed genetic signatures from other independent lineages. Populations occurring on land-bridge islands were excluded from analyses except for *Dicrostonyx groenlandicus* from Wrangel Island. This population represents the only known western Beringia population for the *D. groenlandicus* intraspecific taxon pair (Table 1: Group 2). Other insular specimens were excluded to comply with the assumption of panmixia within current west or east clades respectively, to control for potential effects of isolated small populations and because, in the case of shrews, there is no clear affiliation of insular populations with either west or east clades. These criteria identified twelve taxon pairs that have a Holarctic distribution (Fig. 1; Table 1).

Mitochondrial cytochrome *b* (Cyt *b*) sequences from previously published phylogeographic datasets were retrieved from GenBank (Appendix S1). Datasets for *M. rutilus*, *Sorex camtschatica*, *S. ugyunak*, and *S. portenkoi* were supplemented by sequencing additional specimens. These data were obtained through salt extraction of frozen tissues, PCR, and cycle sequencing methods outlined elsewhere (Hope et al. 2010) using a single primer pair for the entire Cyt *b* gene (MSB05/MSB14). Automated sequencing of complimentary strands was conducted using an Applied Biosystems 3110 DNA sequencer (Molecular Biological Facility, UNM). Sequences were edited in SEQUENCHER 4.8 (Genecodes, Ann Arbor, Michigan) and translated to amino acids to check for internal stop codons that might suggest a pseudogene. Complimentary strands of DNA were compared and sequences were deposited in GenBank (Appendix S1). For sequences retrieved from previous studies, all base positions with ambiguities were discarded, as well as individuals with short sequences that would reduce the entire dataset by ≥ 200 bp. All datasets were aligned in BioEdit 7.0.9 (Ibis Biosciences, Carlsbad, California) using the ClustalW algorithm and checked by eye. Datasets were pruned to a common length for all individuals although this varied by taxon pair depending on sequence length availability (Table 1). Tests of neutral evolution (McDonald and Kreitman 1991) and likelihood ratio tests (LRT) for adherence to a molecular clock (Felsenstein 1981) were performed for each dataset.

PHYLOGENY ESTIMATION

Phylogenies have generally been reported for individual phylogeographic investigations of our focal taxa, but we performed additional Bayesian tree searches, rooted by sister taxa, to provide a visual interpretation of relative divergence within each taxon pair. The best model of DNA substitution was first determined using MrModeltest v2.3 (Nylander 2004). Markov Chain Monte Carlo (MCMC) searches of tree space were performed in MrBayes v3.1 (Ronquist and Huelsenbeck 2003). Three separate runs were conducted for each dataset. Each run computed 10,000,000 generations, sampling every 100 generations, with 5 independent chains, and the first 10,000 trees discarded as burn-in. Convergence of individual runs was assessed using AWTY (Nylander et al. 2008). Phylograms and posterior probabilities were visualized in FigTree v1.2.2 (Rambaut 2009).

GENETIC DISTANCE AND TIMING OF DIVERGENCE

We calculated uncorrected sequence divergence for each taxon pair in DnaSP v5.9 (Librado and Rozas 2009) as a baseline indicator of relative genetic distance and then used the program BEAST v.1.6 (Drummond and Rambaut 2007) to estimate timing of divergence based on coalescence time to most recent common ancestor (T_{MRCA}) per designated group, applying an appropriate mutation rate for each gene. Rodents in general are considered to have an elevated mutation rate for the Cyt *b* gene relative to the standard rate of $1\% \cdot My^{-1}$ (2% divergence rate) suggested by Avise (2000) for mammals, and estimates have ranged from 2.5% to > $6.5\% \cdot My^{-1}$ for arvicoline genera including *Dicrostonyx* (Fedorov and Stenseth 2002), *Lemmus* (Fedorov et al. 2003; 2008), and *Microtus* (Conroy and Cook 2000; Brunhoff et al. 2003; Galbreath and Cook 2004). Here we use an average mutation rate for rodents of $4\% \cdot My^{-1}$ based on other studies (discussed in Brunhoff et al. 2003). It has been suggested that shrews may have elevated mutation rates due to their relatively high metabolism and short generation time (Stewart and Baker 1994). We previously estimated a mutation rate for *Sorex minutissimus* of 5.5%·My^{-1}, which is higher than that generally found in rodents (Hope et al. 2010). Here we apply this rate for all shrew taxon pairs.

We excluded outgroup taxa for the BEAST analyses and grouped individuals into "west" or "east" populations for each taxon pair, constraining each combined taxon pair to be monophyletic. We set substitution models as determined by MrModeltest, a Bayesian skyline tree prior, and ran 3 independent MCMC analyses (50,000,000 generations; sampling every 1000) applying the appropriate mutation rate for each group. We used a relaxed uncorrelated log-normal clock model for all taxon pairs that did not adhere to a strict molecular clock, and fixed the clock for all other pairs. We calculated T_{MRCA} with 95% posterior probability distributions using Tracer v1.5 (Rambaut and Drummond 2007) after discarding 5000 samples as burn-in. Convergence of independent MCMC runs was assessed by comparing results across independent runs, which were then combined using LogCombiner v1.6.1(Drummond and Rambaut 2007) prior to calculating final parameter values.

DEMOGRAPHY

To assess change in population size for each taxon pair, we generated Bayesian skyline plots (BSP) based on combined tree files and implemented in additional BEAST analyses using the Bayesian skyline model (Drummond et al. 2005) and then visualized in Tracer v.1.5. BSPs also were inferred for separate datasets representing western and eastern groups of each taxon pair, except for small samples (n < 10). For tests of demographic expansion, we used DnaSP to calculate Tajima's *D* (Tajima 1989) and tested for significance with 10,000 coalescent simulations. Nucleotide and haplotype diversity were calculated for each group using DnaSP to assess genetic variability. Datasets from previous phylogeographic studies on *Lemmus* and *Dicrostonyx* (Table 1) represent unique haplotypes and not individuals; therefore geographic expansion statistics and haplotype diversity indices for these taxon pairs were not calculated.

TESTS OF SIMULTANEOUS DIVERGENCE

For each group of taxon pairs, we tested a simple null hypothesis of simultaneous divergence using msBayes v20081106 (Hickerson et al. 2007) under an ABC analytical framework (Beaumont et al. 2002) developed to compare divergence across multiple taxon pairs concurrently using summary statistics. We initially analyzed each group of taxon pairs separately to optimize summary statistics because accuracy of simultaneous divergence estimates vary when investigating relatively recent versus older divergences respectively (Hickerson et al. 2006a). Each combined Group 2 taxon pair (west + east rodent populations divided by the Bering Strait) is equivalent to Group 1 (deep rodent divergence across western Beringia) east populations (Fig. 1), and as such these two groups represent isolation over different time scales and possibly different barriers within the Beringian region.

Variance in T_{MRCA} among taxa distributed across a common geographic barrier is often attributed to multiple divergence events, but this variance may instead be due to geneaological stochasticity and demographic history (Hickerson et al. 2006a; 2006b). Factors such as effective population size, mutation rate, gene flow, and population structure may all contribute to differences in divergence estimates among taxa. Thus, although the depth of genetic divergence varies between Group 1 and Group 2, we still tested for simultaneous divergence among all vole taxon pairs combined (Groups 1 + 2). The coalescent-based approach implemented in msBayes accounts for demographic variation among taxa and genealogical stochasticity when estimating the mean, variance, and number of divergence events across multiple taxon pairs (Hickerson et al. 2007).

Closely related taxa generally have similar rates of mutation (Kumar and Subramanian 2002) so we assumed a common rate for taxa within each group, although we recognize that actual rates for individual species may vary. To control for differences in mutation rate between voles and shrews in tests of simultaneous divergence among all taxon pairs combined (Groups 1 + 2 + 3) and among the recently diverged voles and shrews (Groups 2 + 3), we used the ratio of mutation rates for voles and shrews as a relative standard rate (1.0:1.375). Finally, we acknowledge that gene flow (particularly between intraspecific populations) may be ongoing during glacial phases when the Bering Isthmus is present with the potential for underestimates of initial divergence times. However, assuming that these non-volant species cannot migrate across the Bering Strait during interglacial phases, gene flow has not been a factor since most recent isolation and any subsequent divergence.

Methods for tests of simultaneous divergence are explained elsewhere in detail (Hickerson et al. 2007; Hickerson and Myer 2008; Carnaval et al. 2009). Briefly, the process involves calculating summary statistics that take into account the empirical DNA sequence data and sample sizes, simulating multiple datasets under a coalescent model and utilizing parameters drawn from the hyper-prior $P(\varphi)$ and prior $P(\Phi)$ pool of summary statistics, and finally comparing the empirical results to distributions of summary statistics generated from the simulated data. Simulated sequence data is produced using the joint prior $P(\varphi,\Phi)$ from which a joint posterior distribution $P((\varphi,\Phi)|\text{Data})$ is approximated. A sample of simulated datasets that have summary statistics consistent with the empirical data are retained from which the posterior distributions are created. In this way, distributions can be inferred over multiple taxon pairs while allowing for demographic uncertainty and genealogical stochasticity within each individual taxon pair.

We summarized posterior distributions using estimates of Psi (Ψ; number of divergence events) and Omega ($\Omega = [\mathrm{var}(\tau)/E(\tau)]$; Bayesian posterior credible interval) across taxon pairs. For all analyses including Group 1 taxon pairs, we set maximum τ (average divergence) = 2 coalescent units (number of 2Ne generations) due to relatively higher genetic diversity, otherwise maximum $\tau = 1$ coalescent unit. Individual analyses for Groups 1 and 3 taxon pairs utilized π (nucleotide diversity), θ_w (Watterson's theta), π_{net} (Nei and Li's net nucleotide divergence), and Tajima's D as summary statistics. All analyses including Group 2 substituted π_b (between populations nucleotide diversity) for π_{net} because one population from Group 2 was represented by a single individual (Table 1). We ran 8,000,000 simulations for individual group analyses and 16,000,000 simulations for combined analyses, retaining in each analysis 500 simulations with best fit to the empirical data. We assessed significance of estimates for number of divergences where $\Omega = 0$ corresponds to simultaneous (=1) divergence and we could not reject this scenario if the 95% CI of Ω encompassed 0. In addition, we calculated the Bayes factor (BF) for Ψ_{mode} (the value of Ψ observed most frequently) against $\Psi \neq \Psi_{mode}$, where BF ≥ 3 (Jeffreys scale of interpretation) indicates substantial support for Ψ_{mode}.

Results

STUDY SYSTEM, SAMPLING, AND TAXA

We investigated local phylogeographic patterns among 12 taxon pairs, with individual populations ranging in size from 1 to 149 individuals, and using 626-1143bp of the mitochondrial Cyt *b* gene (Table 1). We could not reject the assumption of neutral evolution for any dataset based on the McDonald-Kreitman tests. An assumption of clock-like evolution was rejected for half of the datasets (Table 2).

PHYLOGENY ESTIMATION

Relationships based on Bayesian phylogenies for each taxon pair were in general agreement with expectations based on previous studies (Table 1; Fig S1). Western and eastern populations for Group 1 all exhibit deep divergence, though they are not reciprocally monophyletic in all cases. None of the Group 2 taxon pairs is reciprocally monophyletic. In Group 3, most taxon pairs show a pattern in which one population is paraphyletic with respect to the other.

GENETIC DISTANCE AND TIMING OF DIVERGENCE

Uncorrected sequence divergences between west and east populations for taxon pairs range from 2.8-11.3% in Group 1, 0.7-1.7% in Group 2, and 0.3-0.9% in Group 3 (Table 2). Divergence estimates from BEAST analyses were plotted for each taxon pair along a Pleistocene timeline of the global oxygen isotope ratio record (Fig. 2) to illustrate relative coalescence times (T_{MRCA}) for each taxon pair (both combined and as separate populations) in relation to glacial periodicity. Coalescence times for combined taxon pairs in Group 1 are significantly greater than for individual west and east populations whereas T_{MRCA} for combined and separate populations are similar among Group 2 taxon pairs and among most of Group 3 taxon pairs. Mean T_{MRCA} for Group 1 taxon pairs are coincident with the mid- to early-Pleistocene, ranging from 0.38-2.59 My (Table 2; Fig. 2) although confidence limits are broad. Individual west and east population T_{MRCA} for Group 1 are coincident with a late-Pleistocene timeframe and range from 0.09-0.29 My. T_{MRCA} for all combined Group 2 and Group 3 taxon pairs range from 0.05-0.23 My, which spans the two most recent glacial phases (Illinoian to Wisconsinan).

POPULATION DEMOGRAPHICS

Population size change through time inferred through BSPs (Fig. S2) showed a general increase in effective population size from 50-10 ky for most taxon pairs although *Dicrostonyx* and *Lemmus* (lemmings) pairs indicate population growth from > 100 ky. Population increase generally slows or levels off towards the present. In *Microtus oeconomus*, a population decline is evident most recently in the demographic history. Tajima's *D* statistic was generally significantly negative for eastern populations (indicating population expansion) but not for western populations, although both west and east populations for *M. rutilus* and *S. minutissimus* were significant. Lowest values for both nucleotide and haplotype diversity were found among the shrew taxon pairs (Group 3; Table 2).

TESTS OF SIMULTANEOUS DIVERGENCE

For analyses combining all groups, combining Groups 1 and 2, (Table 3; Fig. 3), significantly high values of Ω clearly indicate multiple divergences. The 95% C.I. of Ω encompassed 0 for all other analyses meaning we could not reject simultaneous divergence. Joint posterior probability density plots should exhibit either a peak posterior probability situated centrally in relation to the x and y axes ($E(\tau)$ and Ω) to illustrate a high degree of discordance between divergence times among taxon pairs (= multiple divergences) or a peak posterior probability flat along 0 of the y-axis (Ω) to illustrate zero discordance and therefore simultaneous divergence (Hickerson et al. 2006b; Fig. 3). Our plots generally exhibit intermediate peak posterior probabilities that are not easily assigned to either outcome (Fig. S3) apart from the two combined group analyses mentioned above (Fig. 3. That prior and posterior curves for Ω were often closely overlapping further suggests weak statistical power (Fig. S3). The number of divergences (Ψ) could not be determined with confidence (Table 3; Fig. S3). A value of Ψ_{mean} = 5.47 for the combined vole taxon pairs (Groups 1 + 2) suggests 5 divergence events and there is substantial support from Bayes factor for 5 divergence events. However, often Ψ_{mode} and Ψ_{mean} were markedly different, suggesting that Ψ is unresolved. For analyses where a hypothesis of simultaneous divergence could not be rejected, there was little statistical support either for or against simultaneous divergence except for the combined analysis for Groups 2 and 3 (Fig. 3) where the Bayes factor was significant (Table 3; BF = 3.409). Of the remainder, the best resolved result was in the Group 3 analysis where a Bayes factor of 2.94 leant limited support (<3) for Ψ_{mode} = 1 (Table 3; Fig. S3).

Discussion

A growing body of scientific evidence supports the important role of Pleistocene glacial cycles in driving evolutionary diversification of high-latitude biota over the last 2.5 My (Hewitt 2004; Waltari et al. 2007). Yet, despite all taxa experiencing the same processes associated with cyclic climate change through the Pleistocene, the responses of different taxa to this common driver of diversification may be highly variable leading to marked community turnover through time (Faunmap working group 1996; DeChaine 2008; Lawler et al. 2009; Stewart 2009). Similarly, within any widely distributed species, independent populations may experience a range of environmental conditions related to both climate and geography that could result in variable demographies among populations (Hewitt 2011). For instance, winter conditions in some areas of interior Beringia during the last glacial maximum may have been warmer than those of interior Alaska during the present (Elias et al. 1997), while other areas experienced polar desert conditions. Substantial variability could also be explained by inherent genetic stochasticity and the attendant effects of highly variable demographic histories (Carstens et al. 2005; Hickerson et al. 2006b). By controlling for stochasticity, this comparative analysis provides evidence for multiple divergence events among the taxon pairs (at least 5 separate divergence events) within a Pleistocene timeframe, and for multiple different demographic responses. Some limited evidence also suggests that many isolation events among taxon pairs are recent, and statistically indistinguishable from simultaneous. These results stress first that diversification across Beringia has been ongoing, probably due to a cyclical climate with the significantly divergent taxon pairs (Group 1) coalescing to multiple different glacial cycles. Also, as half of the divergence events detected by our analysis appear to have occurred within the most recent glacial cycle, it is possible that every cyclical climate extreme results in multiple instances of allopatry, only some of which eventually lead to speciation.

By plotting divergence time estimates for combined taxon pairs and for each separate west and east Beringia population against a glacial timeframe (Fig. 2), we report high temporal variability in coalescence estimates, particularly within Group 1 taxon pairs (Fig. 2A). Though broad confidence intervals preclude a high degree of precision, divergence estimates for Arctic tundra specialists (*Dicrostonyx* and *Lemmus*) conservatively date to the early-Pleistocene, indicating a relatively deep history of diversification. Similarly, coalescence times for Beringian *M. oeconomus* and *M. rutilus* date to the mid- to late-Pleistocene representing divergence that persisted through at least four glacial episodes. Conversely, individual west and east populations of Group 1 taxon pairs all coalesce more recently. Intra-population coalescence times date to the Illinoian/Kansan glacials (200-300 ky) for the tundra adapted lemmings (*Dicrostonyx* and *Lemmus*) and the Sangamon interglacial (~130 ky) and Wisconsinan glacial (~100 ky) for the more generalist voles (*M. oeconomus* and *M. rutilus*). A similar recent history is exhibited by all taxon pairs within Groups 2 and 3, most within the timeframe of the most recent Wisconsinan glacial (Fig. 2B). These results are consistent with reduction in genetic diversity as a consequence of climate change through a given glacial episode (Hewitt 2011). We suggest that similarities between coalescence estimates for individual populations and combined taxon pairs reflect very recent isolation and divergence, where genetic diversity of each population is comparable to the combined diversity. This is also apparent in individual taxon pair phylogenies that exhibit either paraphyly or polyphyly (Groups 2 and 3; Fig. S1) and may reflect periodic panmixia within the Beringia refugium that was sundered only recently by rising sea levels. Alternatively, shallow coalescence times could reflect a recent and rapid expansion into and through Beringia followed by isolation across the Bering Strait. These scenarios should be distinguishable by comparing patterns of genetic diversity. Persistent panmictic species in Beringia should exhibit higher genetic diversity and larger effective population size than rapidly expanding species, as appears to be the case here.

At least three apparently distinct life histories within Beringia can be detected. Tundra specialists such as *Lemmus* and *Dicrostonyx* (e.g. Fedorov and Stenseth 2002; Fedorov et al. 2003) show high values for nucleotide diversity and non-significant signals of demographic expansion indicating persistence, while species such as *M. rutilus* (generalist), and *S. minutissimus* (taiga habitat) exhibit lower genetic diversity and significant expansion in both west and east populations (Table 2) coupled with recent population growth occurring since the last glacial maximum (LGM; <20 ky) for *S. minutissimus* (Fig. S2) and leading up to the LGM for *M. rutilus*, both indicating rapid movement. *Microtus oeconomus* (wet meadow habitats), also reflects a history of rapid expansion within Beringia up to the LGM but in addition exhibits a population decline most recently, coincident with the Holocene (Fig. S2), and reflecting possible ecological affinities with cool wet habitats. Finally, there is some evidence for both persistence and significant diversification within Beringia during the latest glacial period. *Sorex tundrensis* has a combined (west + east) coalescence time that is markedly older than respective individual populations (Fig 2B), the phylogeny exhibits distinct structure between west and east populations (Fig S1), and population growth pre-dates the LGM (Fig. S2). To summarize, different scenarios for responding to climate fluctuations include: 1) persistent tundra associated species occupying a single area within Beringia (although there is no evidence to suggest that this was the only common area to all tundra endemics; e.g. *Dicrostonyx, Lemmus*), 2) species moving rapidly into and through Beringia in response to favorable climate (e.g. *M. rutilus*, *M. oeconomus*, *S. minutissimus*; Hope et al. 2010), or 3) other persistent species occupying multiple isolated areas within Beringia, such as separate river systems (e.g. *S. tundrensis*; Hope et al. 2011). It is possible that species conforming to the latter scenario, with extended isolation and divergence through glacial cold phases, are those that most readily result in speciation events.

We are ~11 ky into the Holocene interglacial period, a timeframe consistent with the total duration of other interglacial warm phases. Although we do not know when the current interglacial will end, abundant genetic evidence from multiple taxon pairs across Beringia (isolated for ~11 ky) suggests that genetic differentiation is minimally associated with the Bering Strait and that there is only a limited influence of interglacial periods driving population divergence. This is not to suggest that interglacial periods have no effect on genetic structure within populations. Dry- and cold-adapted species (Fedorov and Goropashnaya 1999) or isolated insular populations may be vulnerable to severe population decline in response to a warming climate and a transition to more mesic conditions within Beringia over relatively short periods (Elias et al. 1997). In the absence of significant levels of novel mutations, this could lead to loss of genetic diversity and even local extirpation.

METHODOLOGICAL CONSIDERATIONS

The coalescent-based approach to testing for simultaneous divergence that we implemented relies on a number of important assumptions that warrant further consideration (Carstens et al. 2005; DeChaine and Martin 2006; Hickerson et al. 2006b). Although variance around coalescent parameter estimates based on a single mitochondrial locus are broad and increasing the number of loci can improve divergence estimates (Hickerson et al. 2006a; Huang et al. 2011), inferences from msBayes have been shown to be robust to both single-locus datasets and small sample sizes (Hickerson et al. 2006b). However, our dataset illustrates that too few taxon pairs and/or too little genetic information from a single locus and recent isolation may limit resolution of numbers of divergences. For instance, separate analyses for Group 1, 2, and 3 taxon pairs resulted in estimates of Ψ_{mode} = 4, 1, and 1 divergences respectively (Table 3). These results are reasonable considering coalescent divergence estimates from BEAST analyses (Table 2; Fig. 2), but they lack statistical support (consider Bayes factors and values for Ω; Table 3). In general, values of Ψ were not well resolved, and although Ω is a more rigorous estimator of simultaneous vs. non-simultaneous divergence (Hickerson et al. 2006b), our data were often not sufficient to resolve clear estimates of either statistic.

Probably the most important factor limiting our ability to resolve the relative timing of divergence for Beringian mammals is the fact that we used only a single mitochondrial locus. This was a necessary constraint when compiling data from independent studies where data from multiple loci are not available for all taxa, but we recognize that the benefits of using multiple loci in coalescent analyses are increasingly evident (Edwards and Beerli 2000). Data from multiple loci have potential to narrow the confidence limits around coalescent estimates of population parameters, and new methods incorporate multi-locus datasets within msBayes for multiple species comparisons (Huang et al. 2011). However, the Beringian mammalian system is dominated by recent divergences and population structure that is still largely unresolved. Incorporating data from a feasible number of nuclear loci may not provide clearer resolution, considering that neutral nuclear substitution rates may be an order of magnitude lower than for Cyt *b* (Lynch et al. 2006). Slow rates alone may not in future be insurmountable given emerging methods for dealing with more variable nuclear markers such as microsatellites or genome sequencing methods.

CONCLUSIONS

This investigation of multiple Holarctic mammals assesses the processes that drive evolution across Beringia. We have tested a suite of 12 small mammal taxon pairs for simultaneous divergence across Beringia and rejected that hypothesis in favor of several distinct divergence events through time among these taxon pairs. This explicit analysis of taxon pairs concurrently extends the implications of multiple independent studies while controlling for genealogical stochasticity inherent in coalescent processes. The Pleistocene epoch has resulted in repeated diversification events among small mammals in response to a changing climate. Further, a variable evolutionary response to climate change within Beringia is likely reflected in ecological differences between species. Tundra-associated species persisted in Beringia within continuous habitat during glacial maxima, but failed to diverge across the Bering Strait during interglacials. Other species more generally associated with taiga habitat show significant signals of demographic expansion, suggesting range change and population growth in response to a warming climate. Finally, some species show evidence of multiple isolated populations within Beringia and significant divergence during only a single extended glacial phase. Though the statistical rigor of our comparative phylogeographic analysis is limited by recent and/or recurring allopatry across Beringia with only minimal genetic divergence, a small number of taxon pairs within each group, and single locus datasets, we have shown that repeated episodes of allopatry over multiple glacial cycles is probably a major driver of speciation in Beringia. Future studies should assess whether multiple additional independent loci provide more accurate resolution of divergence estimates and narrower confidence limits around coalescent estimates.

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Table 1. Summary of taxon pairs including west and east populations, sample sizes (*N*), length of gene sequences for the mitochondrial cytochrome *b* gene, and previous literature.

Taxon Pairs				
West	East	*N* (west/east)	Length (bp)	Systematic/Phylogeographic Assessments
Group 1				
Dicrostonyx torquatus	*D. groenlandicus*	10/10	838	Fredga et al. 1999; Fedorov and Goropashnaya 1999; Ehrich et al. 2000; Wickström et al. 2001; Fedorov and Stenseth 2002; Fedorov et al. 2003; Smirnov and Fedorov 2003
Lemmus sibiricus	*L. trimucronatus*	6/12	789	Chernyavsky et al. 1993; Fredga et al. 1999; Chernyavsky and Kartavtseva 1999; Fedorov et al. 2003
Microtus oeconomus	*M. oeconomus*	69/80	1143	Lance and Cook 1998; Brunhoff et al. 2003; Frisman et al. 2003; Galbreath and Cook 2004; Iwasa et al. 2009
Myodes rutilus	*M. rutilus*	22/26	1140	Iwasa et al. 2002; Cook et al. 2004; Iwasa et al. 2009
Group 2				
D. groenlandicus	*D. groenlandicus*	1/10	838	See Group 1 references

L. trimucronatus	*L. trimucronatus*	2/11	626	“
M. oeconomus	*M. oeconomus*	21/80	1143	“
M. rutilus	*M. rutilus*	3/26	1140	“
Group 3				
Sorex camtschaticus	*S. ugyunak*	7/18	1014	Demboski and Cook 2003
Sorex minutissimus	*S. minutissimus*	13/27	1056	Dokuchaev 2004; Hope et al. 2010
Sorex portenkoi	*S. ugyunak*	10/18	933	Demboski and Cook 2003
Sorex tundrensis	*S. tundrensis*	21/27	1050	Bannikova et al. 2010; Hope et al. (In Revision)

Table 2. Genetic diversity indices and divergence estimates for all small mammal taxon pairs and individual populations within each group. *N* = sample size; *S* = number of segregating sites; *h* = number of haplotypes; *Hd* = haplotype diversity; π = nucleotide diversity; *D* = Tajima's *D* (with associated *P*-value); Diverg. = uncorrected sequence divergence between population pairs; T_{MRCA} = time to most recent common ancestor (coalescence time with associated confidence interval); adherence to a molecular clock was based on results of likelihood ratio tests and used for divergence estimates.

Taxon Pairs	*N*	*S*	*h*	*Hd*	π	*D*	*P*	Diverg. (%)	T_{MRCA} (My)	95% C.I. (My)	Molecular Clock
Group 1											
Dicrostonyx torquatus/D. groenlandicus	20	86	N/A	N/A	0.0402	N/A	N/A	6.7	1.413	0.552-2.412	Relaxed
D. torquatus	10	31	N/A	N/A	0.0122	N/A	N/A	--	0.292	0.129-0.513	Relaxed
D. groenlandicus	10	24	N/A	N/A	0.0092	N/A	N/A	--	0.210	0.097-0.360	Relaxed
Lemmus sibiricus/L. trimucronatus	18	117	N/A	N/A	0.0588	N/A	N/A	11.3	2.593	1.166-4.129	Relaxed
L. sibiricus	6	27	N/A	N/A	0.0123	N/A	N/A	--	0.227	0.112-0.364	Relaxed
L. trimucronatus	12	34	N/A	N/A	0.0100	N/A	N/A	--	0.256	0.124-0.421	Relaxed
Microtus oeconomus	149	104	63	0.978	0.0170	0.006	0.577	2.9	0.501	0.285-0.727	Relaxed

M. oeconomus (west)	69	47	31	0.945	0.0052	-1.327	0.070	--	0.131	0.074-0.191	Relaxed
M. oeconomus (east)	80	53	32	0.963	0.0092	-1.416	0.050	--	0.109	0.066-0.159	Relaxed
Myodes rutilus	48	101	46	0.998	0.0166	-0.627	0.311	2.8	0.377	0.248-0.517	Relaxed
M. rutilus (west)	2	43	21	0.996	0.0051	-1.999	0.013	--	0.096	0.060-0.136	Relaxed
M. rutilus (east)	26	52	25	0.997	0.0051	-2.186	0.006	--	0.089	0.058-0.126	Relaxed
Group 2											
Dicrostonyx groenlandicus	11	28	N/A	N/A	0.0099	N/A	N/A	1.3	0.228	0.117-0.368	Relaxed
D. groenlandicus (west)	1	N/A	N/A	N/A	N/A	N/A	N/A	--	--	--	--
D. groenlandicus (east)	10	24	N/A	N/A	0.0092	N/A	N/A	--	0.214	0.106-0.348	Relaxed
Lemmus trimucronatus	13	32	N/A	N/A	0.0113	N/A	N/A	1.7	0.227	0.128-0.347	Relaxed
L. trimucronatus (west)	2	8	N/A	N/A	0.0128	N/A	N/A	--	0.131	0.037-0.279	Relaxed
L. trimucronatus (east)	11	23	N/A	N/A	0.0092	N/A	N/A	--	0.209	0.112-0.317	Relaxed
Microtus oeconomus	101	70	40	0.970	0.0067	-1.416	0.058	0.9	0.137	0.091-0.189	Strict
M. oeconomus (west)	21	26	8	0.824	0.0062	-0.050	0.527	--	0.134	0.087-0.188	Strict

M. oeconomus (east)	80	53	32	0.963	0.0053	-1.416	0.054	--	0.115	0.071-0.163	Strict
Myodes rutilus	29	57	28	0.998	0.0054	-2.197	0.001	0.7	0.105	0.071-0.145	Strict
M. rutilus (west)	3	7	3	1.000	0.0041	N/A	N/A	--	0.065	0.028-0.120	Strict
M. rutilus (east)	26	52	25	0.997	0.0051	-2.186	0.006	--	0.102	0.068-0.140	Strict
Group 3											
Sorex camtschatica/S. ugyunak	25	22	16	0.917	0.0029	-1.828	0.022	0.4	0.059	0.031-0.088	Strict
S. camtschatica	7	7	3	0.524	0.0022	-1.208	0.148	--	0.053	0.022-0.086	Strict
S. ugyunak	18	15	13	0.902	0.0020	-2.002	0.005	--	0.049	0.023-0.074	Strict
Sorex portenkoi/S. ugyunak	28	16	14	0.881	0.0021	-1.820	0.014	0.3	0.054	0.026-0.079	Strict
S. portenkoi	10	1	2	0.467	0.0005	0.820	0.869	--	0.019	0.003-0.031	Strict
S. ugyunak	18	15	12	0.863	0.0021	-1.962	0.005	--	0.052	0.024-0.077	Strict
Sorex minutissimus	40	38	28	0.956	0.0335	-2.047	0.005	0.5	0.070	0.040-0.100	Strict
S. minutissimus (west)	13	19	12	0.987	0.0032	-1.888	0.010	--	0.065	0.029-0.099	Strict
S. minutissimus (east)	27	20	16	0.906	0.0019	-2.171	0.002	--	0.043	0.021-0.068	Strict

Sorex tundrensis	48	50	30	0.969	0.0058	-1.601	0.033	0.9	0.100	0.059-0.144	Strict
S. tundrensis (west)	21	11	10	0.900	0.0020	-1.146	0.140	--	0.043	0.021-0.065	Strict
S. tundrensis (east)	27	36	20	0.960	0.0037	-2.171	0.001	--	0.061	0.033-0.089	Strict

Table 3. Results of msBayes analyses. S. S. = summary statistic set where set 1 includes π, θ_w, π_{net}, and Tajima's *D* and set 2 includes π, θ_w, π_b, and Tajima's *D*; Max. τ = maximum average divergence in coalescent units depending on relative genetic diversity; Ω = (var(τ)/E(τ)); Ψ = number of divergence events; B. F. = Bayes factor. Values in bold suggest substantial support for multiple divergence events.

Analysis	Taxon pairs	S. S.	Max. τ	Ω_{mean}	Ω 95% C.I.	Ψ_{mode}	Ψ_{mean}	Post. Prob. Ψ_{mode}	B. F.
Group 1	4	1	2	0.1317	0.0000-0.4852	4	2.778	0.3583	1.675
Group 2	4	2	1	0.1173	0.0000-0.4029	1	2.097	0.4344	2.304
Group 3	4	1	1	0.1014	0.0000-0.4706	1	1.726	0.4945	2.935
Group 1+2+3	12	2	2	**0.5549**	**0.2386-0.9048**	4	4.5390	0.2273	**3.231**
Group 1+2	8	2	2	**0.5316**	**0.2842-0.8219**	5	5.4702	0.3199	**3.292**
Group 2+3	8	2	1	**0.0917**	**0.0000-0.2644**	1	2.7730	0.3276	**3.409**

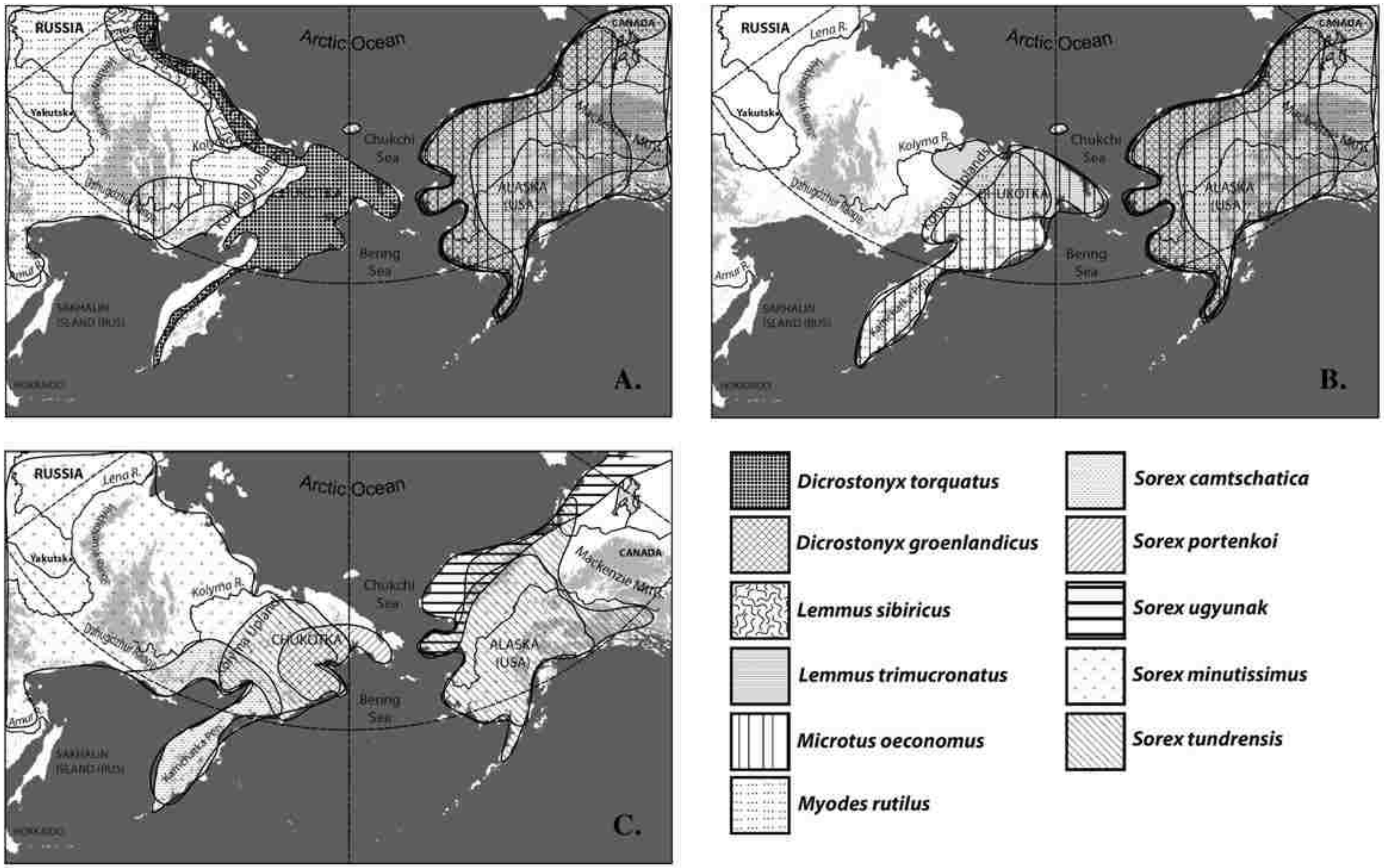

Figure 1. Maps of the study area. A) Group 1 taxon pairs; B) Group 2 taxon pairs; C) Group 3 taxon pairs. Shaded areas represent geographic extent within Beringia of the distinct populations (clades) used in this study, in many instances coincident with the geographic extent of the entire species. In Group 1, western Beringia portions of eastern populations (shown in B) are removed.

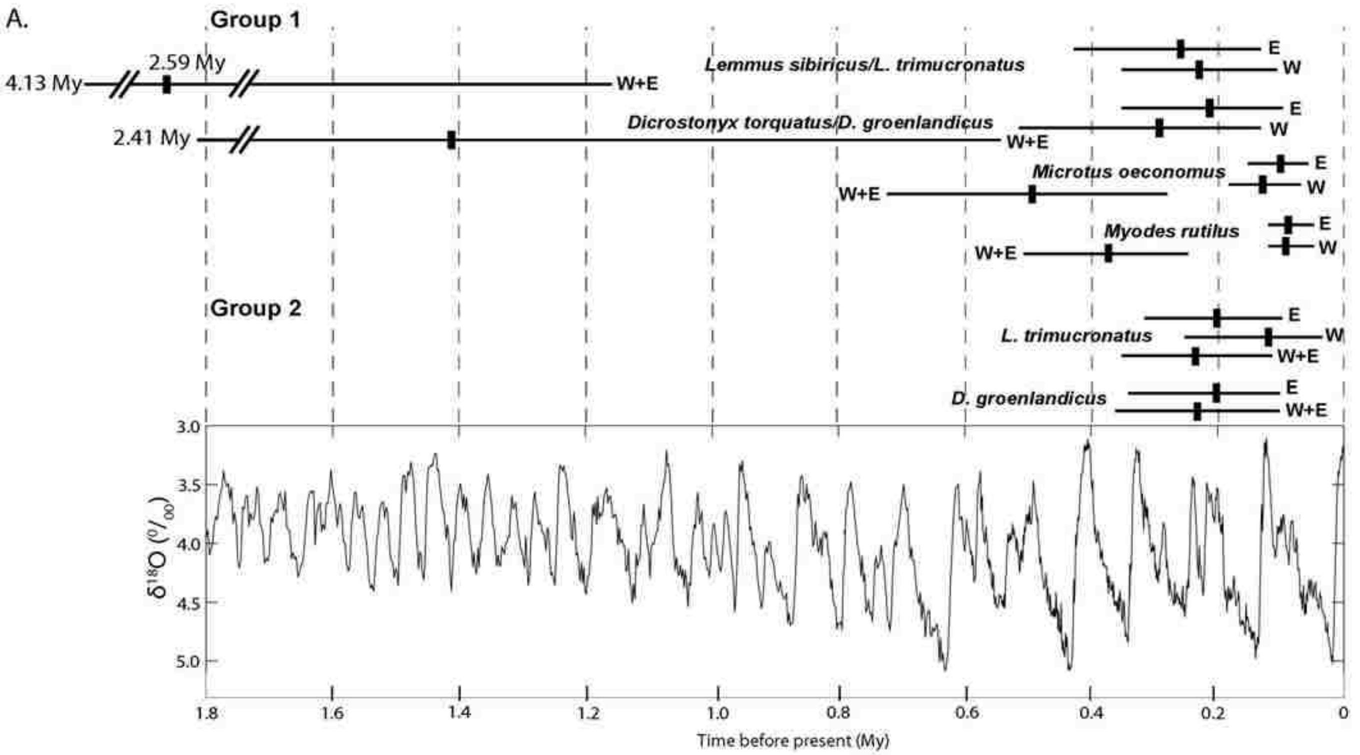

Figure 2A. Estimates for coalescence times (T_{MRCA}) for both combined taxon pairs and individual west and east populations. Solid vertical bars indicate median T_{MRCA} and horizontal lines indicate upper and lower confidence limits. T_{MRCA} estimates are plotted along a timeline that illustrates glacial cycling through the Pleistocene represented by the global oxygen isotope ratio ($\delta^{18}O$) record (adapted from Lisiecki and Raymo 2005). Lower values of $\delta^{18}O$ indicate warmer periods (top of trace) and higher values represent cooler periods (bottom of trace).

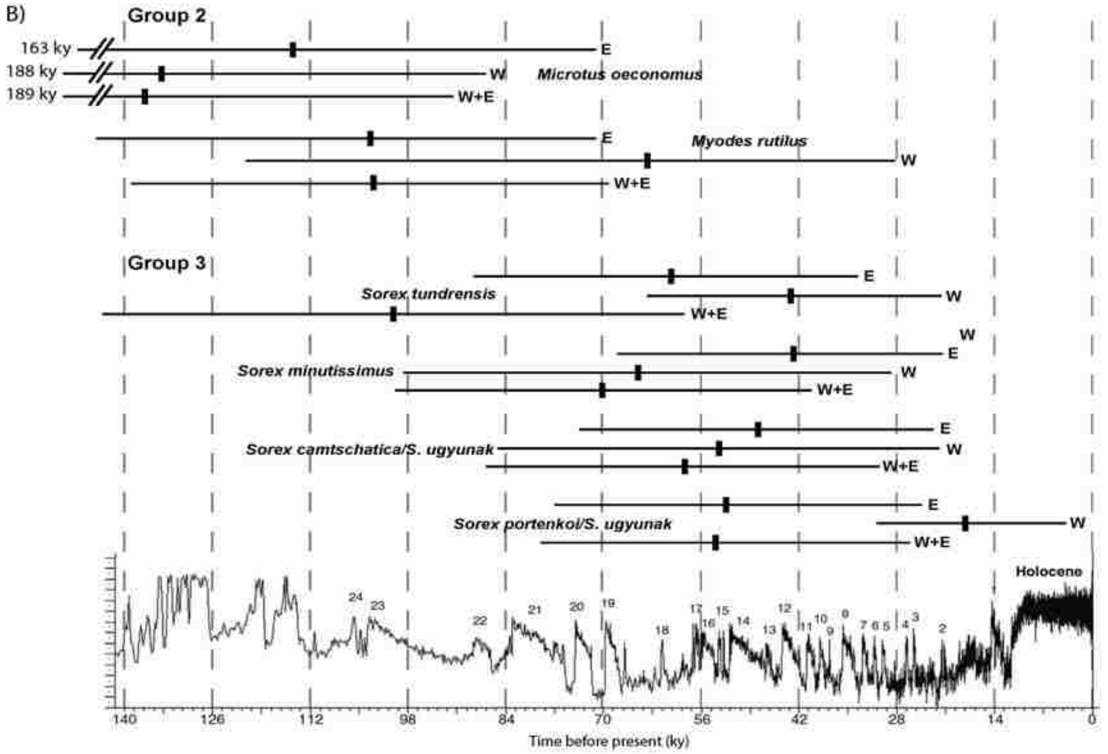

Figure 2B. Estimates for coalescence times (T_{MRCA}) for both combined taxon pairs and individual west and east populations. Solid vertical bars indicate median T_{MRCA} and horizontal lines indicate upper and lower confidence limits. T_{MRCA} estimates are plotted along a timeline that illustrates glacial cycling through the late-Pleistocene and Holocene represented by the global oxygen isotope ratio ($\delta^{18}O$) record (adapted from Hofreiter and Stewart 2009). Lower values of $\delta^{18}O$ indicate warmer periods (top of trace) and higher values represent cooler periods (bottom of trace).

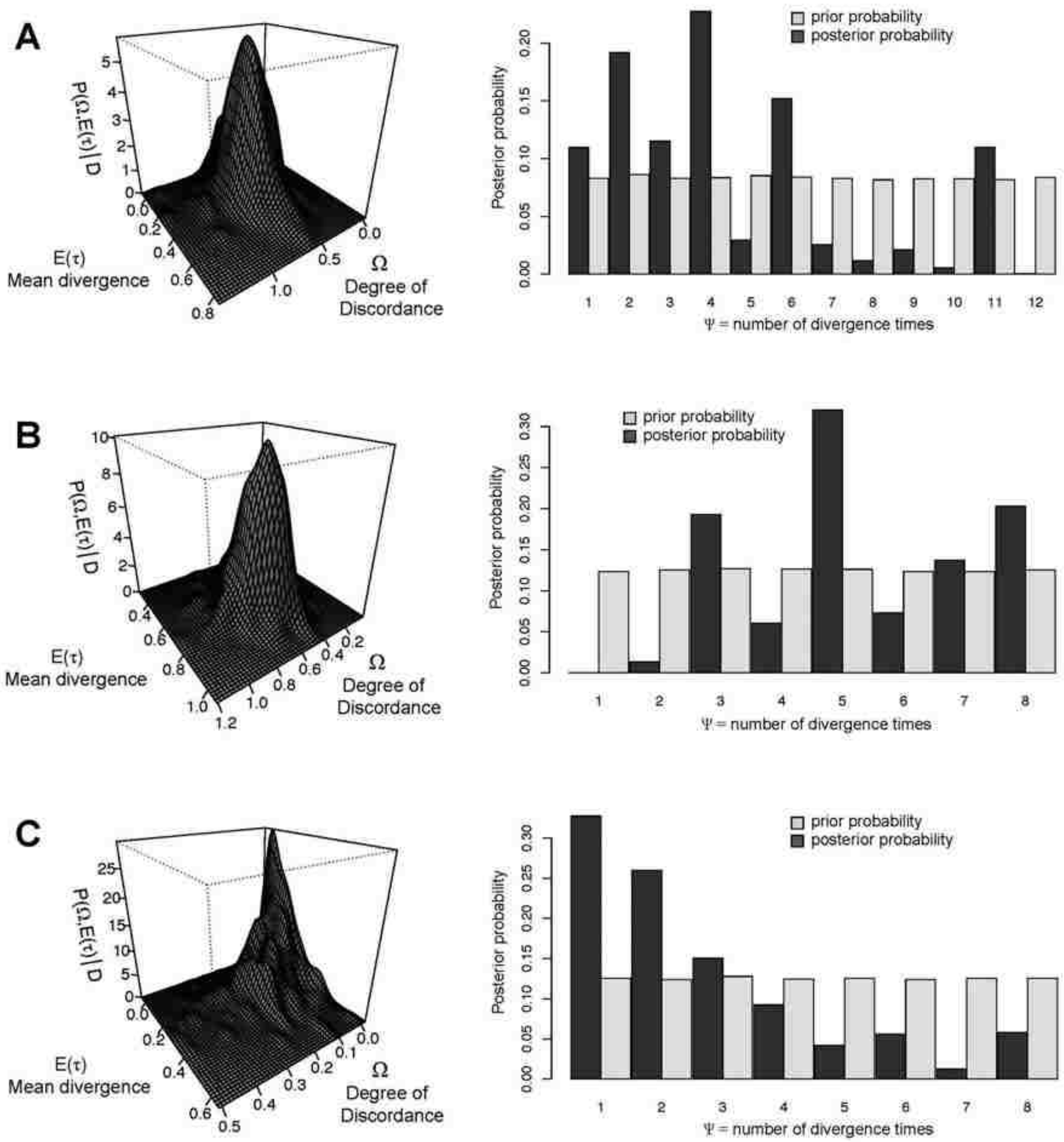

Figure 3. Posterior estimates of number of divergences across multiple taxon pairs for A) Group 1+2+3 (12 taxon pairs), B) Group 1+2 (8 taxon pairs), and C) Group 2+3 (8 taxon pairs). Plots on left represent joint posterior probability densities for *E(τ)* and on right represent posterior probability densities for *Ψ* (number of divergence times).

Appendix -- Specimen records included in this study. Collection and Tissue numbers, where given, correspond to Bayesian phylogenies (Fig. S1); specific localities are only provided for specimens sequenced for this study. All specimens are reported according to population (west or east), GenBank Accession, and the original publication for which they were sequenced. Numbers in parentheses following references refer to the full citation below.

Species	Tissue Number	Collection Number	Specific Locality	Population	GenBank Acc.	Reference
Dicrostonyx torquatus	N/A	N/A	N/A	West	AF119275	Conroy and Cook 1999 (1)
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ131439	Fedorov and Goropashnaya 1999 (2)
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ131440	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ131441	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ131442	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ238421	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ238422	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ238423	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ238424	Fedorov and Goropashnaya 1999
Dicrostonyx torquatus	N/A	N/A	N/A	West	AJ238425	Fedorov and Goropashnaya 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AF119268	Conroy and Cook 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AJ238427	Fedorov and Goropashnaya 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AJ131444	Fedorov and Goropashnaya 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AY159015	Fedorov and Stenseth 2002 (3)
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AJ238426	Fedorov and Goropashnaya 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AJ238428	Fedorov and Goropashnaya 1999
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AJ238429	Fedorov and Goropashnaya 1999

Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AY159006	Fedorov and Stenseth 2002
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AY159018	Fedorov and Stenseth 2002
Dicrostonyx groenlandicus	N/A	N/A	N/A	East	AY159019	Fedorov and Stenseth 2002
Dicrostonyx groenlandicus	N/A	N/A	N/A	West	AJ131443	Fedorov and Goropashnaya 1999
Lemmus sibiricus	N/A	N/A	N/A	West	AY219142	Fedorov et al. 2003 (4)
Lemmus sibiricus	N/A	N/A	N/A	West	AY219141	Fedorov et al. 2003
Lemmus sibiricus	N/A	N/A	N/A	West	AY219144	Fedorov et al. 2003
Lemmus sibiricus	N/A	N/A	N/A	West	AJ012678	Fedorov et al. 1999 (5)
Lemmus sibiricus	N/A	N/A	N/A	West	AJ012674	Fedorov et al. 1999
Lemmus sibiricus	N/A	N/A	N/A	West	AJ012673	Fedorov et al. 1999
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219148	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219146	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AF119276	Conroy and Cook 1999
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219153	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AJ012676	Fedorov et al. 1999
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219152	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219168	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219147	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219158	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219169	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219149	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	East	AY219171	Fedorov et al. 2003
Lemmus trimucronatus	N/A	N/A	N/A	West	FJ025982	Abramson et al. 2008 (6)
Lemmus trimucronatus	N/A	N/A	N/A	West	AJ012675	Fedorov et al. 1999
Microtus oeconomus	N/A	N/A	N/A	West	AY220015	Brunhoff et al. 2003 (7)

Microtus oeconomus	N/A	N/A	N/A	West	AY220016	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY220017	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY220018	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY220019	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY220020	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY305201	Galbreath and Cook 2004 (8)
Microtus oeconomus	N/A	N/A	N/A	West	AY305202	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305203	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305204	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305205	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305206	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305207	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305208	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305209	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305210	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305211	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305212	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305213	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305214	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305215	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305216	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305217	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305218	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305219	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305220	Galbreath and Cook 2004

Microtus oeconomus	N/A	N/A	N/A	West	AY305221	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305222	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305223	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305224	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305225	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305226	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305227	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305228	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305229	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305230	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305231	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305232	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305233	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305234	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305235	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305236	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305237	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305238	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305239	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305240	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305241	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305242	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305243	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305244	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305245	Galbreath and Cook 2004

Microtus oeconomus	N/A	N/A	N/A	West	AY305246	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305247	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305248	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305249	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305250	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305251	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305252	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305253	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305254	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305255	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305256	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305257	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305258	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305259	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305260	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305261	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305262	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305263	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY220025	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220026	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220028	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220029	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220030	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220031	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220034	Brunhoff et al. 2003

Microtus oeconomus	N/A	N/A	N/A	East	AY220035	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220040	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220041	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220042	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220043	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220044	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY220045	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	East	AY305100	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305116	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305117	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305118	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305119	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305120	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305121	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305122	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305123	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305124	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305125	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305126	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305127	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305128	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305129	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305130	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305131	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305132	Galbreath and Cook 2004

Microtus oeconomus	N/A	N/A	N/A	East	AY305133	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305134	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305135	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305136	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305137	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305138	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305139	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305140	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305141	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305142	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305143	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305144	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305145	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305146	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305147	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305148	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305149	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305150	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305151	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305152	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305153	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305154	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305155	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305156	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305157	Galbreath and Cook 2004

Microtus oeconomus	N/A	N/A	N/A	East	AY305158	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305159	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305160	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305173	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305174	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305175	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305176	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305177	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305178	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305179	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305180	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305181	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305182	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305189	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305190	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305191	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305192	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305193	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305194	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305195	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305196	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305197	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	East	AY305198	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY220021	Brunhoff et al. 2003
Microtus oeconomus	N/A	N/A	N/A	West	AY220022	Brunhoff et al. 2003

Microtus oeconomus	N/A	N/A	N/A	West	AY305090	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305091	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305092	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305093	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305094	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305095	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305096	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305097	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305098	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305099	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305101	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305102	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305103	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305183	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305184	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305185	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305186	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305187	Galbreath and Cook 2004
Microtus oeconomus	N/A	N/A	N/A	West	AY305188	Galbreath and Cook 2004
Myodes rutilus	N/A	N/A	N/A	West	AB072215	Iwasa et al. 2002 (9)
Myodes rutilus	N/A	N/A	N/A	West	AB072216	Iwasa et al. 2002
Myodes rutilus	N/A	N/A	N/A	West	AB072217	Iwasa et al. 2002
Myodes rutilus	N/A	N/A	N/A	West	AY309424	Cook et al. 2004 (10)
Myodes rutilus	N/A	N/A	N/A	West	AY309425	Cook et al. 2004
Myodes rutilus	NK123311	MSB:Mamm:144862	Russia, Republic of Sakha, Stokovo Station	West		Current Study

Myodes rutilus	NK123431	MSB:Mamm:144986	Russia, Republic of Sakha, Indigirka River Basin	West		Current Study
Myodes rutilus	NK123475	MSB:Mamm:145024	Russia, Republic of Sakha, Indigirka River Basin	West		Current Study
Myodes rutilus	NK126201	MSB:Mamm:148162	Russia, Magadanskaya Oblast, Buyunda	West		Current Study
Myodes rutilus	NK126211	MSB:Mamm:148174	Russia, Magadanskaya Oblast, Buyunda	West		Current Study
Myodes rutilus	NK126471	MSB:Mamm:148079	Russia, Magadanskaya Oblast, Omolon River	West		Current Study
Myodes rutilus	NK139113	MSB:Mamm:146675	Russia, Republic of Sakha, 4 km. W Yakutsk	West		Current Study
Myodes rutilus	NK139195	MSB:Mamm:146755	Russia, Republic of Sakha, Amga River	West		Current Study
Myodes rutilus	NK139270	MSB:Mamm:148526	Russia, Republic of Sakha, Amga River	West		Current Study
Myodes rutilus	NK139382	MSB:Mamm:148611	Russia, Republic of Sakha, Amga River	West		Current Study
Myodes rutilus	NK139394	MSB:Mamm:148647	Russia, Republic of Sakha, Amga River	West		Current Study
Myodes rutilus	NK139472	MSB:Mamm:148356	Russia, Republic of Sakha, Lena River Basin	West		Current Study
Myodes rutilus	NK139611	MSB:Mamm:148506	Russia, Republic of Sakha, Kenkeme River	West		Current Study
Myodes rutilus	NK139620	MSB:Mamm:148515	Russia, Republic of Sakha, Kenkeme River	West		Current Study
Myodes rutilus	NK139675	MSB:Mamm:148695	Russia, Republic of Sakha, Kenkeme River	West		Current Study
Myodes rutilus	NK158273	MSB:Mamm:149870	Russia, Magadanskaya Oblast, Chelomdzha	West		Current Study
Myodes rutilus	NK158278	MSB:Mamm:149876	Russia, Magadanskaya Oblast, Chelomdzha	West		Current Study
Myodes rutilus	N/A	N/A	N/A	East	AF119274	Conroy and Cook 1999
Myodes rutilus	N/A	N/A	N/A	East	AF272631	Cook et al. 2001 (11)
Myodes rutilus	N/A	N/A	N/A	East	AY309426	Cook et al. 2004
Myodes rutilus	N/A	N/A	N/A	East	AY309427	Cook et al. 2004
Myodes rutilus	NK123061	MSB:Mamm:143200	USA, Alaska, 120.5 mi. W Paxson on Denali Hwy.	East		Current Study
Myodes rutilus	NK123117	MSB:Mamm:143223	USA, Alaska, 10 mi. N, 1 mi. E Minto	East		Current Study
Myodes rutilus	NK123119	MSB:Mamm:143225	USA, Alaska, 10 mi. N, 1 mi. E Minto	East		Current Study
Myodes rutilus	NK123216	MSB:Mamm:143071	USA, Alaska, Fish Creek on Dalton Hwy.	East		Current Study
Myodes rutilus	NK123226	MSB:Mamm:143080	USA, Alaska, 2 mi. S Finger Mtn. on Dalton Hwy.	East		Current Study

Myodes rutilus	NK123250	MSB:Mamm:143088	USA, Alaska, 2 mi. S Finger Mtn. on Dalton Hwy.	East		Current Study
Myodes rutilus	NK123263	MSB:Mamm:143092	USA, Alaska, 2 mi. S Finger Mtn. on Dalton Hwy.	East		Current Study
Myodes rutilus	NK124507	MSB:Mamm:144060	USA, Alaska, Steese Hwy. 6, 35.5 mi. pond	East		Current Study
Myodes rutilus	NK124508	MSB:Mamm:144061	USA, Alaska, Steese Hwy. 6, 35.5 mi. pond	East		Current Study
Myodes rutilus	NK124509	MSB:Mamm:144062	USA, Alaska, Steese Hwy. 6, 35.5 mi. pond	East		Current Study
Myodes rutilus	NK124518	MSB:Mamm:144072	USA, Alaska, Steese Hwy. 6, 35.5 mi. pond	East		Current Study
Myodes rutilus	NK124548	MSB:Mamm:144023	USA, Alaska, Hwy. 2, 2 mi. W Dot Lake	East		Current Study
Myodes rutilus	NK124582	MSB:Mamm:144246	USA, Alaska, 3 mi. SW Eagle on Hwy. 5	East		Current Study
Myodes rutilus	NK124967	MSB:Mamm:144261	Canada, Yukon, 15 mi. W Stewart Crossing	East		Current Study
Myodes rutilus	NK125003	MSB:Mamm:145285	Canada, Yukon, McQuesten River on Hwy. 2	East		Current Study
Myodes rutilus	NK125152	MSB:Mamm:145671	Canada, Yukon, 2 mi. N Rock River on Hwy. 5	East		Current Study
Myodes rutilus	NK125231	MSB:Mamm:145660	Canada, Yukon, 0.25 mi. N Rock River on Hwy. 5	East		Current Study
Myodes rutilus	NK125245	MSB:Mamm:145332	Canada, Yukon, 0.25 mi. N Rock River on Hwy. 6	East		Current Study
Myodes rutilus	NK125259	MSB:Mamm:145615	Canada, Yukon, Rock River campground	East		Current Study
Myodes rutilus	NK125492	MSB:Mamm:145483	USA, Alaska, Portage Glacier Rd.	East		Current Study
Myodes rutilus	NK125581	MSB:Mamm:143159	USA, Alaska, Hess Creek on Dalton Hwy.	East		Current Study
Myodes rutilus	NK125582	MSB:Mamm:143160	USA, Alaska, Hess Creek on Dalton Hwy.	East		Current Study
Myodes rutilus	N/A	N/A	N/A	West	AB072220	Iwasa et al. 2002
Myodes rutilus	N/A	N/A	N/A	West	AB072221	Iwasa et al. 2002
Myodes rutilus	N/A	N/A	N/A	West	AB072222	Iwasa et al. 2002
Sorex camtschatica	AF32746	UAM:Mamm:73465	Russia, Kamchatskaya Oblast, Kronotskii Preserve	West		Current Study
Sorex camtschatica	AF41349	UAM:Mamm:80338	Russia, Magadanskaya Oblast, Alekchen Lakes	West		Current Study
Sorex camtschatica	AF6631	N/A	N/A	West	AY014917	Demboski and Cook 2003 (12)
Sorex camtschatica	AF6632	N/A	N/A	West	AY014918	Demboski and Cook 2003
Sorex camtschatica	AF6596	N/A	N/A	West	AY014919	Demboski and Cook 2003

Sorex camtschatica	ND3496	N/A	N/A	West	AY014920	Demboski and Cook 2003
Sorex camtschatica	IF5019	UAM:Mamm:84134	Russia, Magadanskaya Oblast, Gertnera Bay	West		Current Study
Sorex ugyunak	AF46229	UAM:Mamm:55850	USA, Alaska, W bank Rabbit Creek	East		Current Study
Sorex ugyunak	AF48342	UAM:Mamm:56384	USA, Alaska, Kaluich Creek Upland	East		Current Study
Sorex ugyunak	AF48601	UAM:Mamm:56475	USA, Alaska, Aniralik Lake	East		Current Study
Sorex ugyunak	AF58247	UAM:Mamm:82135	USA, Alaska, N side of Lake Tulilik	East		Current Study
Sorex ugyunak	AF58421	UAM:Mamm:82247	USA, Alaska, N side of Lake Tulilik	East		Current Study
Sorex ugyunak	AF58479	UAM:Mamm:81918	USA, Alaska, Lake Isiak	East		Current Study
Sorex ugyunak	AF58502	UAM:Mamm:82014	USA, Alaska, Lake Isiak	East		Current Study
Sorex ugyunak	AF58507	UAM:Mamm:82017	USA, Alaska, Lake Isiak	East		Current Study
Sorex ugyunak	AF58513	UAM:Mamm:82018	USA, Alaska, Lake Isiak	East		Current Study
Sorex ugyunak	AF58528	UAM:Mamm:82020	USA, Alaska, Lake Isiak	East		Current Study
Sorex ugyunak	AF7374	UAM:Mamm:46994	USA, Alaska, Kougarok Airfield, Taylor Hwy.	East		Current Study
Sorex ugyunak	NK123279	MSB:Mamm:143102	USA, Alaska, Finger Mtn. on Dalton Hwy.	East		Current Study
Sorex ugyunak	NK125515	MSB:Mamm:143121	USA, Alaska, Lake Galbraith campground	East		Current Study
Sorex ugyunak	AF11764	N/A	N/A	East	AY014927	Demboski and Cook 2003
Sorex ugyunak	AF7390	N/A	N/A	East	AY014928	Demboski and Cook 2003
Sorex ugyunak	AF7213	N/A	N/A	East	AY014929	Demboski and Cook 2003
Sorex ugyunak	AF7431	N/A	N/A	East	AY014930	Demboski and Cook 2003
Sorex ugyunak	BM39815	N/A	N/A	East	EU088307	Rausch et al. 2007 (13)
Sorex portenkoi	AF7467	N/A	N/A	West	AY014921	Demboski and Cook 2003
Sorex portenkoi	IF5187	UAM:Mamm:84327	Russia, Chukotka, confluence Volchya Ri., Liman Sea	West		Current Study
Sorex portenkoi	IF5222	UAM:Mamm:84282	Russia, Chukotka, confluence Volchya Ri., Liman Sea	West		Current Study
Sorex portenkoi	IF5228	UAM:Mamm:84286	Russia, Chukotka, confluence Volchya Ri., Liman Sea	West		Current Study
Sorex portenkoi	IF5243	UAM:Mamm:84290	Russia, Chukotka, confluence Volchya Ri., Liman Sea	West		Current Study

Sorex portenkoi	IF7561	UAM:Mamm:83828	Russia, Chukotka, Ulhum Ri., W Chaplino Village	West		Current Study
Sorex portenkoi	IF7570	UAM:Mamm:83837	Russia, Chukotka, Ulhum Ri., W Chaplino Village	West		Current Study
Sorex portenkoi	IF7573	UAM:Mamm:83840	Russia, Chukotka, Ulhum Ri., W Chaplino Village	West		Current Study
Sorex portenkoi	IF7584	UAM:Mamm:83851	Russia, Chukotka, Ulhum Ri., W Chaplino Village	West		Current Study
Sorex portenkoi	IF7585	UAM:Mamm:83852	Russia, Chukotka, Ulhum Ri., W Chaplino Village	West		Current Study
Sorex minutissimus	N/A	UAM:Mamm:29830	N/A	East	GU223639	Hope et al. 2010 (14)
Sorex minutissimus	N/A	UAM:Mamm:45820	N/A	East	GU223640	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:45841	N/A	East	GU223642	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:55806	N/A	East	GU223647	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:56130	N/A	East	GU223644	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:56133	N/A	East	GU223645	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:56157	N/A	East	GU223646	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:57104	N/A	East	GU223654	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:57111	N/A	East	GU223655	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:57142	N/A	East	GU223652	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:57395	N/A	East	GU223653	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:57531	N/A	East	GU223657	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:58567	N/A	East	GU223650	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:59401	N/A	East	HM002706	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:60167	N/A	East	GU223651	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:60281	N/A	East	GU223648	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:60566	N/A	East	GU223649	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:64945	N/A	East	GU223658	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:72928	N/A	East	GU223643	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:78467	N/A	East	GU223659	Hope et al. 2010

Sorex minutissimus	N/A	UAM:Mamm:91874	N/A	East	GU223660	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:91898	N/A	East	GU223661	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:93385	USA, AK, Waring Mtns.	East		Current Study
Sorex minutissimus	N/A	UAM:Mamm:93397	N/A	East	GU223663	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:93432	N/A	East	GU223664	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:94323	N/A	East	HM002707	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:94362	N/A	East	GU223662	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:144877	N/A	West	HM002704	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:144903	N/A	West	GU223631	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148033	N/A	West	GU223632	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148073	N/A	West	GU223633	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148416	N/A	West	HM002705	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148567	N/A	West	HM002694	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148592	N/A	West	GU223634	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148593	N/A	West	GU223635	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148650	N/A	West	GU223636	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:148651	N/A	West	GU223637	Hope et al. 2010
Sorex minutissimus	N/A	MSB:Mamm:94040	N/A	West	GU223629	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:37987	N/A	West	HM002702	Hope et al. 2010
Sorex minutissimus	N/A	UAM:Mamm:73463	N/A	West	GU223625	Hope et al. 2010
Sorex tundrensis	AF1043	UAM:Mamm:22042	N/A	East	HM992624	Hope et al. 2011 (15)
Sorex tundrensis	AF10537	UAM:Mamm:37961	N/A	East	HM992630	Hope et al. 2011
Sorex tundrensis	AF11343	UAM:Mamm:31687	N/A	East	HM992637	Hope et al. 2011
Sorex tundrensis	AF11686	UAM:Mamm:31395	N/A	East	HM992636	Hope et al. 2011
Sorex tundrensis	AF17866	UAM:Mamm:47524	N/A	East	HM992749	Hope et al. 2011

Sorex tundrensis	AF18632	UAM:Mamm:47527	N/A	East	HM992638	Hope et al. 2011
Sorex tundrensis	AF23468	UAM:Mamm:45203	N/A	East	HM992623	Hope et al. 2011
Sorex tundrensis	AF3486	UAM:Mamm:34064	N/A	East	HM992627	Hope et al. 2011
Sorex tundrensis	AF3490	UAM:Mamm:34065	N/A	East	HM992628	Hope et al. 2011
Sorex tundrensis	AF3533	UAM:Mamm:34142	N/A	East	HM992629	Hope et al. 2011
Sorex tundrensis	AF3539	UAM:Mamm:34067	N/A	East	HM992745	Hope et al. 2011
Sorex tundrensis	AF3543	UAM:Mamm:34068	N/A	East	HM992746	Hope et al. 2011
Sorex tundrensis	AF39125	UAM:Mamm:75505	N/A	East	HM992743	Hope et al. 2011
Sorex tundrensis	AF42720	UAM:Mamm:76157	N/A	East	HM992744	Hope et al. 2011
Sorex tundrensis	AF7389	UAM:Mamm:36758	N/A	East	HM992758	Hope et al. 2011
Sorex tundrensis	AF7457	UAM:Mamm:46991	N/A	East	HM992635	Hope et al. 2011
Sorex tundrensis	AF7476	UAM:Mamm:32957	N/A	East	HM992747	Hope et al. 2011
Sorex tundrensis	AF7483	UAM:Mamm:32959	N/A	East	HM992631	Hope et al. 2011
Sorex tundrensis	AF7484	UAM:Mamm:32960	N/A	East	HM992632	Hope et al. 2011
Sorex tundrensis	AF7485	UAM:Mamm:32961	N/A	East	HM992633	Hope et al. 2011
Sorex tundrensis	AF7487	UAM:Mamm:32963	N/A	East	HM992634	Hope et al. 2011
Sorex tundrensis	AF8909	UAM:Mamm:46825	N/A	East	HM992626	Hope et al. 2011
Sorex tundrensis	AF8927	UAM:Mamm:36746	N/A	East	HM992625	Hope et al. 2011
Sorex tundrensis	NK122184	MSB:Mamm:142945	N/A	East	HM992640	Hope et al. 2011
Sorex tundrensis	NK124651	MSB:Mamm:144200	N/A	East	HM992641	Hope et al. 2011
Sorex tundrensis	NK125145	MSB:Mamm:145646	N/A	East	HM992642	Hope et al. 2011
Sorex tundrensis	NK125518	MSB:Mamm:143124	N/A	East	HM992639	Hope et al. 2011
Sorex tundrensis	AF38150	UAM:Mamm:80449	N/A	West	HM992653	Hope et al. 2011
Sorex tundrensis	AF38220	UAM:Mamm:80496	N/A	West	HM992605	Hope et al. 2011
Sorex tundrensis	IF5115	UAM:Mamm:84242	N/A	West	HM992621	Hope et al. 2011

Sorex tundrensis	IF5144	UAM:Mamm:84247	N/A	West	HM992622	Hope et al. 2011
Sorex tundrensis	IF5156	UAM:Mamm:84310	N/A	West	HM992609	Hope et al. 2011
Sorex tundrensis	IF5161	UAM:Mamm:84260	N/A	West	HM992606	Hope et al. 2011
Sorex tundrensis	IF5164	UAM:Mamm:84313	N/A	West	HM992610	Hope et al. 2011
Sorex tundrensis	IF5167	UAM:Mamm:84315	N/A	West	HM992611	Hope et al. 2011
Sorex tundrensis	IF5172	UAM:Mamm:84265	N/A	West	HM992607	Hope et al. 2011
Sorex tundrensis	IF5180	UAM:Mamm:84322	N/A	West	HM992612	Hope et al. 2011
Sorex tundrensis	IF5181	UAM:Mamm:84269	N/A	West	HM992654	Hope et al. 2011
Sorex tundrensis	IF5183	UAM:Mamm:84270	N/A	West	HM992608	Hope et al. 2011
Sorex tundrensis	IF5209	UAM:Mamm:84277	N/A	West	HM992655	Hope et al. 2011
Sorex tundrensis	IF5237	UAM:Mamm:84362	N/A	West	HM992613	Hope et al. 2011
Sorex tundrensis	IF5259	UAM:Mamm:84375	N/A	West	HM992614	Hope et al. 2011
Sorex tundrensis	IF5262	UAM:Mamm:84378	N/A	West	HM992615	Hope et al. 2011
Sorex tundrensis	IF5273	UAM:Mamm:84388	N/A	West	HM992616	Hope et al. 2011
Sorex tundrensis	IF5280	UAM:Mamm:84395	N/A	West	HM992617	Hope et al. 2011
Sorex tundrensis	IF5285	UAM:Mamm:84400	N/A	West	HM992618	Hope et al. 2011
Sorex tundrensis	IF5292	UAM:Mamm:84407	N/A	West	HM992619	Hope et al. 2011
Sorex tundrensis	IF5294	UAM:Mamm:84409	N/A	West	HM992620	Hope et al. 2011
Microtus oeconomus	N/A	N/A	N/A	Outgroup	AY305163	Galbreath and Cook 2004
Myodes glareolus	N/A	N/A	N/A	Outgroup	AY309421	Cook et al. 2004
Sorex haydeni	AF23162	N/A	N/A	Outgroup	AY014939	Demboski and Cook 2003
Sorex minutissimus	N/A	N/A	N/A	Outgroup	HM002696	Hope et al. 2010
Sorex tundrensis	N/A	N/A	N/A	Outgroup	HM992660	Hope et al. 2011

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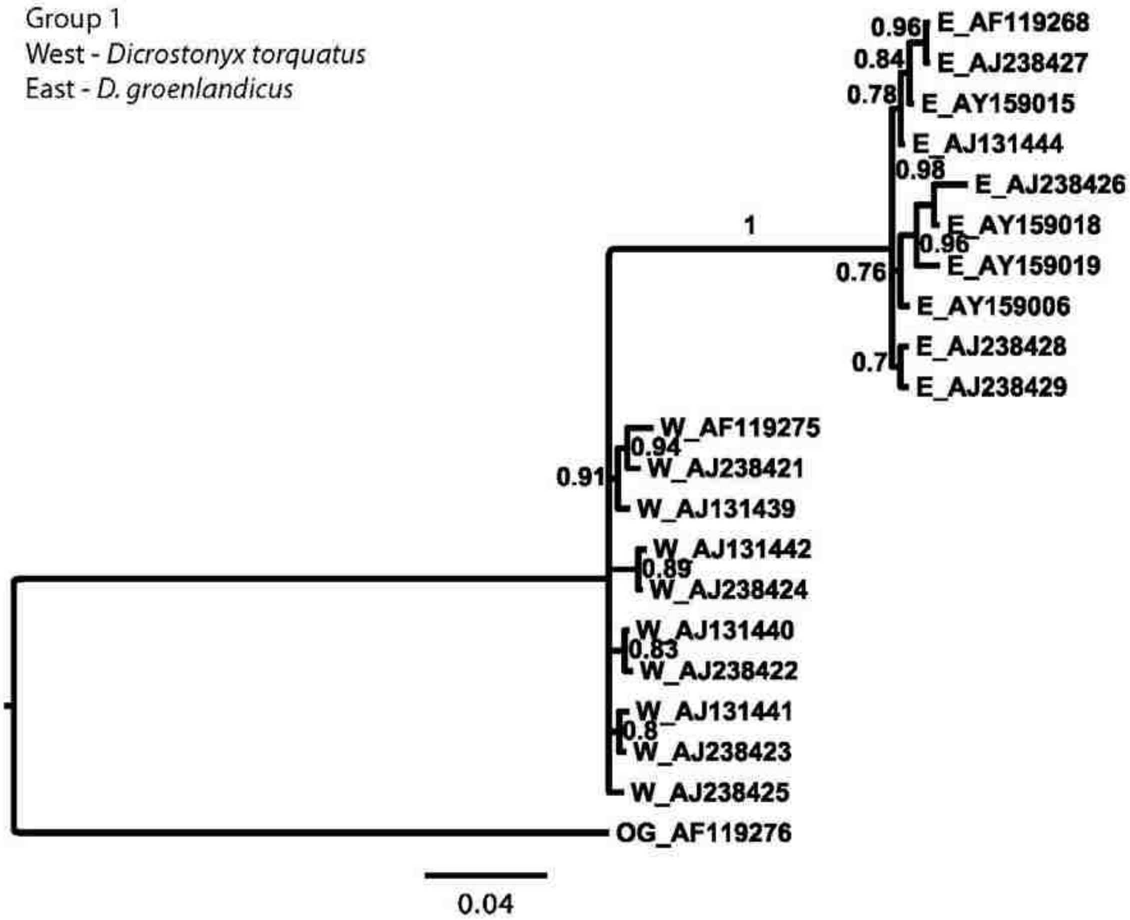


Figure S1A. Bayesian phylogeny including individuals from western populations prefixed with "W" and individuals from eastern populations prefixed with "E". Corresponding specimen information is provided in Appendix S1. Clade support values are represented by posterior probability values labeled at nodes.

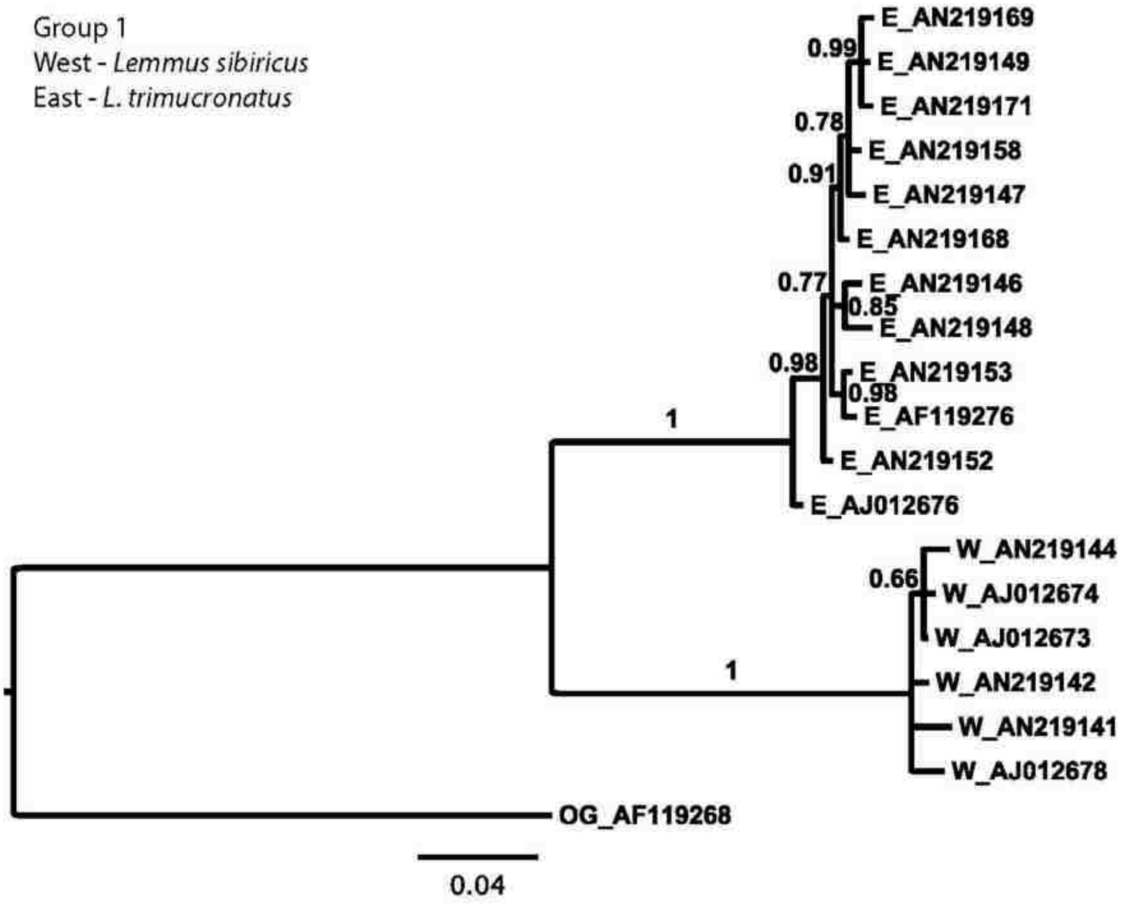
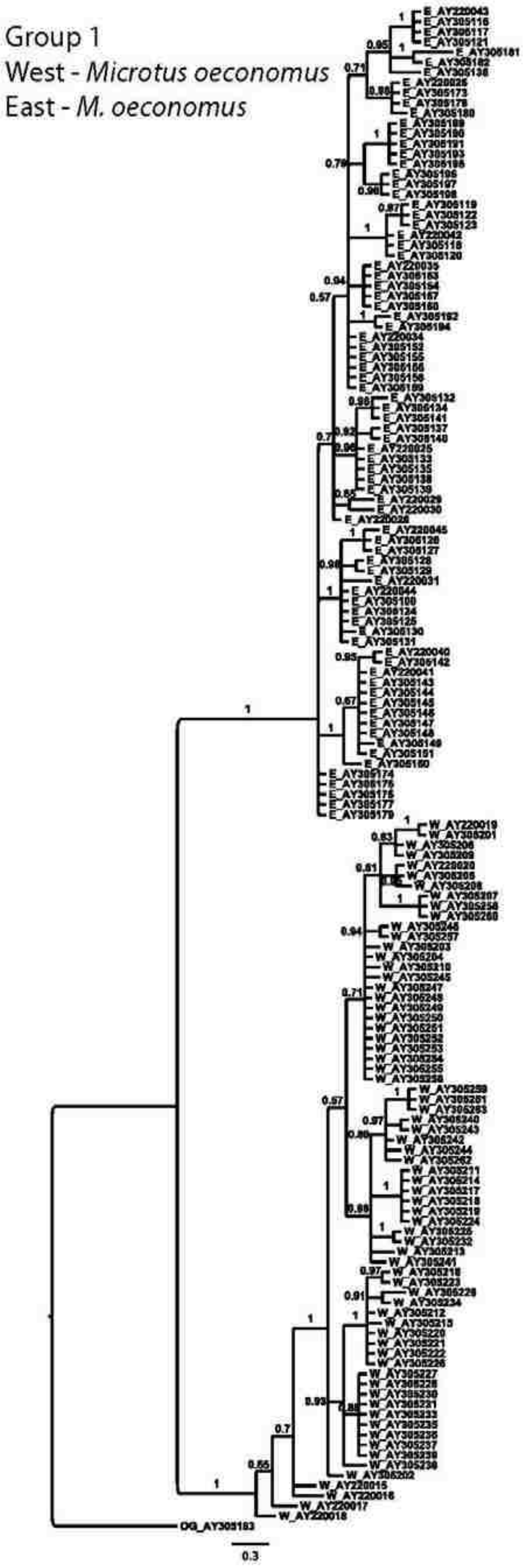

Group 1
West - *Lemmus sibiricus*
East - *L. trimucronatus*
E_AN219169
0.99
E_AN219149
E_AN219171
0.78
E_AN219158
0.91
E_AN219147
E_AN219168
0.77
E_AN219146
0.85
E_AN219148
0.98
E_AN219153
0.98
E_AF119276
1
E_AN219152
E_AJ012676
W_AN219144
0.66
W_AJ012674
W_AJ012673
1
W_AN219142
W_AN219141
W_AJ012678
OG_AF119268
0.04

Figure S1B.


Group 1
West - *Microtus oeconomus*
East - *M. oeconomus*
E_AY220043
E_AY305116
E_AY305117
E_AY305121
E_AY305181
E_AY305182
E_AY305136
E_AY220026
E_AY305173
E_AY305178
E_AY305180
E_AY305189
E_AY305190
E_AY305191
E_AY305193
E_AY305195
E_AY305196
E_AY305197
E_AY305198
E_AY305119
E_AY305122
E_AY305123
E_AY220042
E_AY305118
E_AY305120
E_AY220035
E_AY305153
E_AY305154
E_AY305157
E_AY305160
E_AY305192
E_AY305194
E_AY220034
E_AY305152
E_AY305155
E_AY305156
E_AY305158
E_AY305159
E_AY305132
E_AY305134
E_AY305141
E_AY305137
E_AY305140
E_AY220025
E_AY305133
E_AY305135
E_AY305138
E_AY305139
E_AY220029
E_AY220030
E_AY220028
E_AY220045
E_AY305126
E_AY305127
E_AY305128
E_AY305129
E_AY220031
E_AY220044
E_AY305100
E_AY305124
E_AY305125
E_AY305130
E_AY305131
E_AY220040
E_AY305142
E_AY220041
E_AY305143
E_AY305144
E_AY305145
E_AY305146
E_AY305147
E_AY305148
E_AY305149
E_AY305151
E_AY305150
E_AY305174
E_AY305176
E_AY305175
E_AY305177
E_AY305179
W_AY220019
W_AY305201
W_AY305206
W_AY305209
W_AY220020
W_AY305205
W_AY305208
W_AY305207
W_AY305258
W_AY305260
W_AY305246
W_AY305257
W_AY305203
W_AY305204
W_AY305210
W_AY305245
W_AY305247
W_AY305248
W_AY305249
W_AY305250
W_AY305251
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W_AY305253
W_AY305254
W_AY305255
W_AY305256
W_AY305259
W_AY305261
W_AY305263
W_AY305240
W_AY305243
W_AY305242
W_AY305244
W_AY305262
W_AY305211
W_AY305214
W_AY305217
W_AY305218
W_AY305219
W_AY305224
W_AY305225
W_AY305232
W_AY305213
W_AY305241
W_AY305216
W_AY305223
W_AY305229
W_AY305234
W_AY305212
W_AY305215
W_AY305220
W_AY305221
W_AY305222
W_AY305226
W_AY305227
W_AY305228
W_AY305230
W_AY305231
W_AY305233
W_AY305235
W_AY305236
W_AY305237
W_AY305239
W_AY305238
W_AY305202
W_AY220015
W_AY220016
W_AY220017
W_AY220018
OG_AY305183
0.3

Figure S1C.

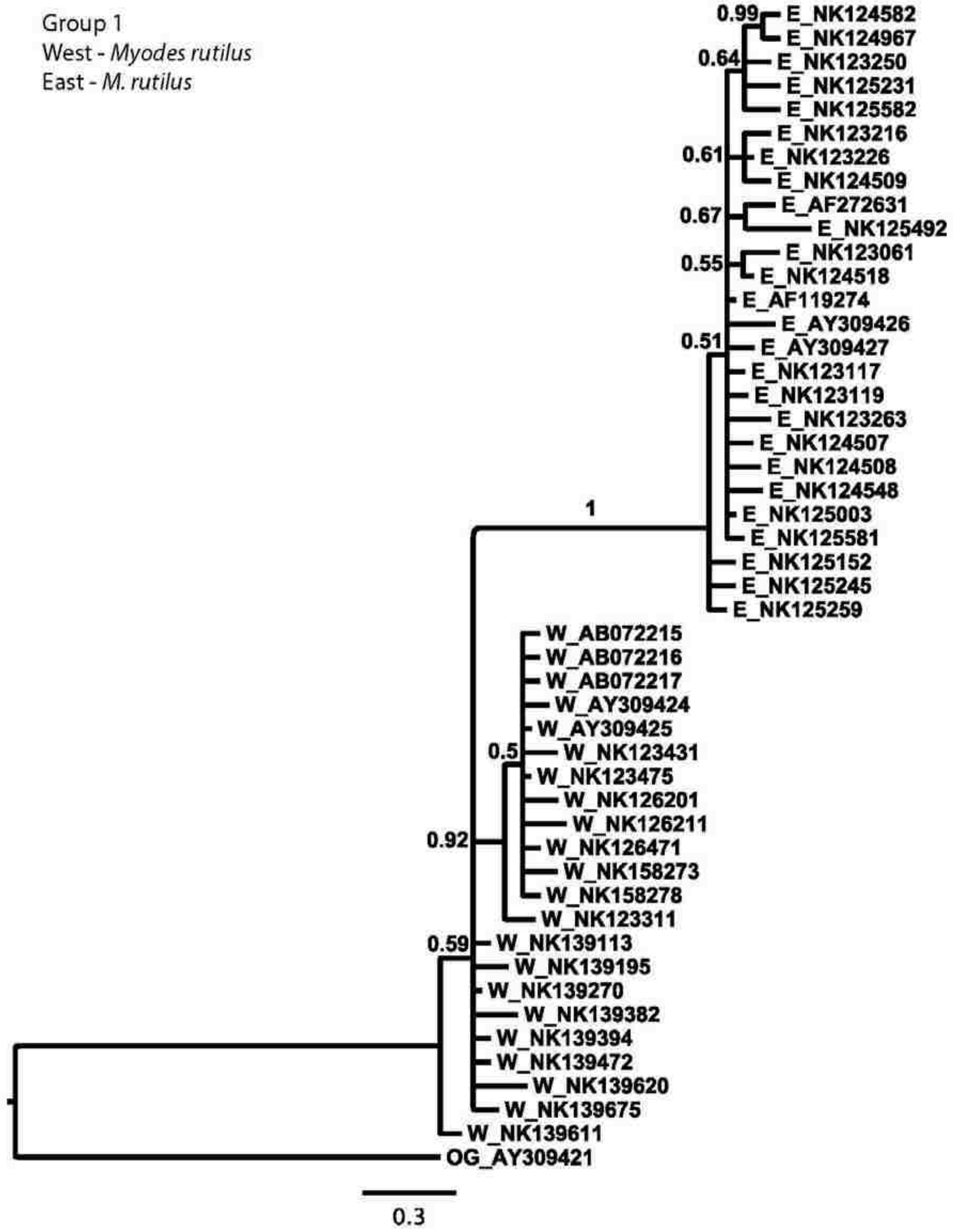
Group 1
West - *Myodes rutilus*
East - *M. rutilus*
0.99
0.64
0.61
0.67
0.55
0.51
1
0.5
0.92
0.59
E_NK124582
E_NK124967
E_NK123250
E_NK125231
E_NK125582
E_NK123216
E_NK123226
E_NK124509
E_AF272631
E_NK125492
E_NK123061
E_NK124518
E_AF119274
E_AY309426
E_AY309427
E_NK123117
E_NK123119
E_NK123263
E_NK124507
E_NK124508
E_NK124548
E_NK125003
E_NK125581
E_NK125152
E_NK125245
E_NK125259
W_AB072215
W_AB072216
W_AB072217
W_AY309424
W_AY309425
W_NK123431
W_NK123475
W_NK126201
W_NK126211
W_NK126471
W_NK158273
W_NK158278
W_NK123311
W_NK139113
W_NK139195
W_NK139270
W_NK139382
W_NK139394
W_NK139472
W_NK139620
W_NK139675
W_NK139611
OG_AY309421
0.3

Figure S1D.

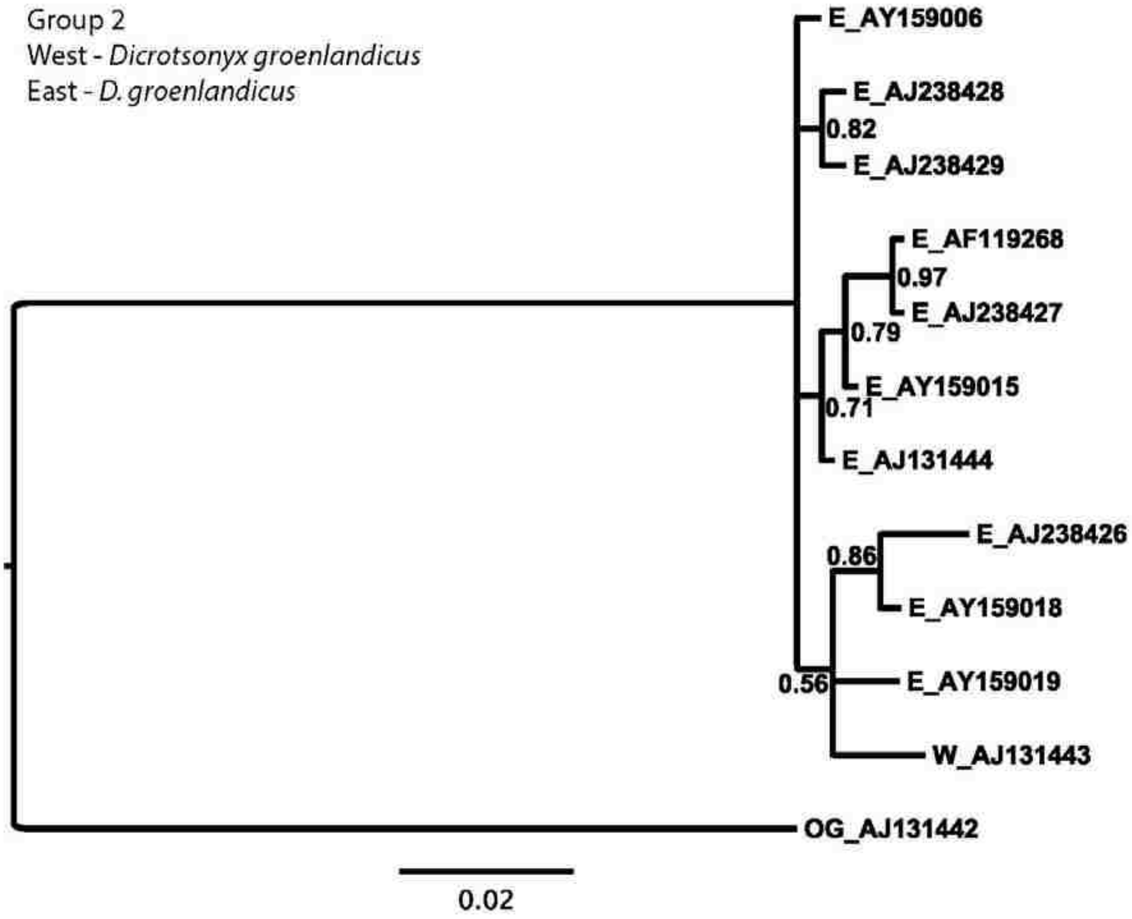
Group 2
West - *Dicrotsonyx groenlandicus*
East - *D. groenlandicus*
E_AY159006
E_AJ238428
0.82
E_AJ238429
E_AF119268
0.97
E_AJ238427
0.79
E_AY159015
0.71
E_AJ131444
E_AJ238426
0.86
E_AY159018
0.56
E_AY159019
W_AJ131443
OG_AJ131442
0.02

Figure S1E.

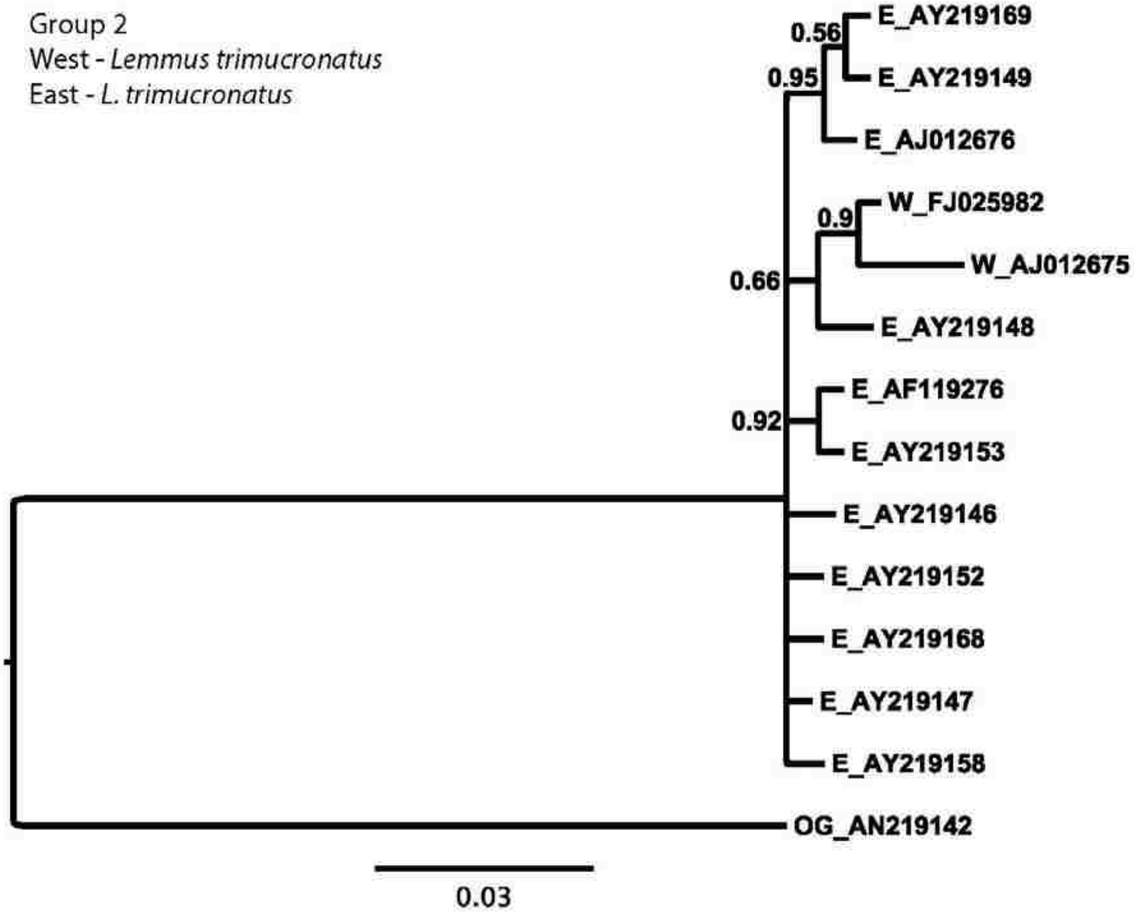
Group 2
West - *Lemmus trimucronatus*
East - *L. trimucronatus*
0.56
E_AY219169
0.95
E_AY219149
E_AJ012676
0.9
W_FJ025982
0.66
W_AJ012675
E_AY219148
E_AF119276
0.92
E_AY219153
E_AY219146
E_AY219152
E_AY219168
E_AY219147
E_AY219158
OG_AN219142
0.03

Figure S1F.

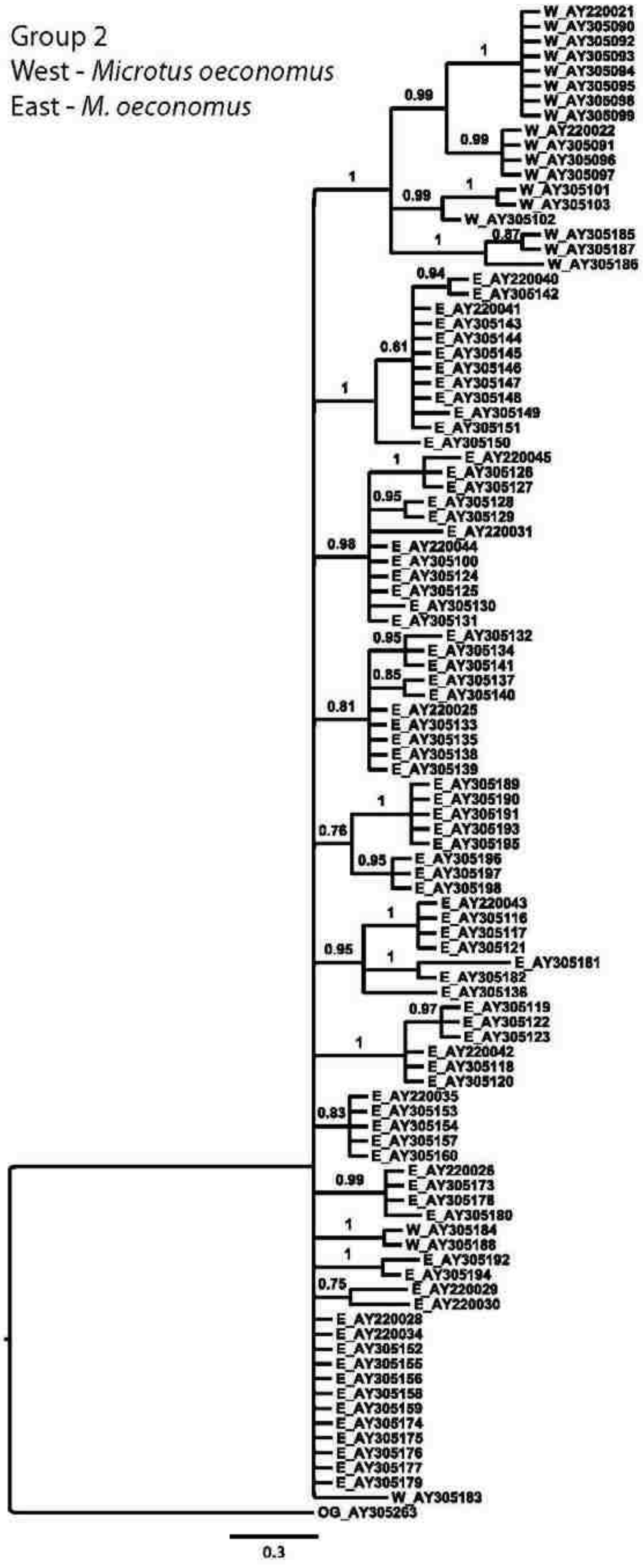
Group 2
West - *Microtus oeconomus*
East - *M. oeconomus*
1
0.99
1
W_AY220021
W_AY305090
W_AY305092
W_AY305093
W_AY305094
W_AY305095
W_AY305098
W_AY305099
0.99
W_AY220022
W_AY305091
W_AY305096
W_AY305097
0.99
1
W_AY305101
W_AY305103
W_AY305102
1
0.87
W_AY305185
W_AY305187
W_AY305186
1
0.61
0.94
E_AY220040
E_AY305142
E_AY220041
E_AY305143
E_AY305144
E_AY305145
E_AY305146
E_AY305147
E_AY305148
E_AY305149
E_AY305151
E_AY305150
0.98
1
E_AY220045
E_AY305126
E_AY305127
0.95
E_AY305128
E_AY305129
E_AY220031
E_AY220044
E_AY305100
E_AY305124
E_AY305125
E_AY305130
E_AY305131
0.81
0.95
E_AY305132
E_AY305134
E_AY305141
0.85
E_AY305137
E_AY305140
E_AY220025
E_AY305133
E_AY305135
E_AY305138
E_AY305139
0.76
1
E_AY305189
E_AY305190
E_AY305191
E_AY305193
E_AY305195
0.95
E_AY305196
E_AY305197
E_AY305198
0.95
1
E_AY220043
E_AY305116
E_AY305117
E_AY305121
1
E_AY305181
E_AY305182
E_AY305136
1
0.97
E_AY305119
E_AY305122
E_AY305123
E_AY220042
E_AY305118
E_AY305120
0.83
E_AY220035
E_AY305153
E_AY305154
E_AY305157
E_AY305160
0.99
E_AY220026
E_AY305173
E_AY305178
E_AY305180
1
W_AY305184
W_AY305188
1
E_AY305192
E_AY305194
0.75
E_AY220029
E_AY220030
E_AY220028
E_AY220034
E_AY305152
E_AY305155
E_AY305156
E_AY305158
E_AY305159
E_AY305174
E_AY305175
E_AY305176
E_AY305177
E_AY305179
W_AY305183
OG_AY305263
0.3

Figure S1G.

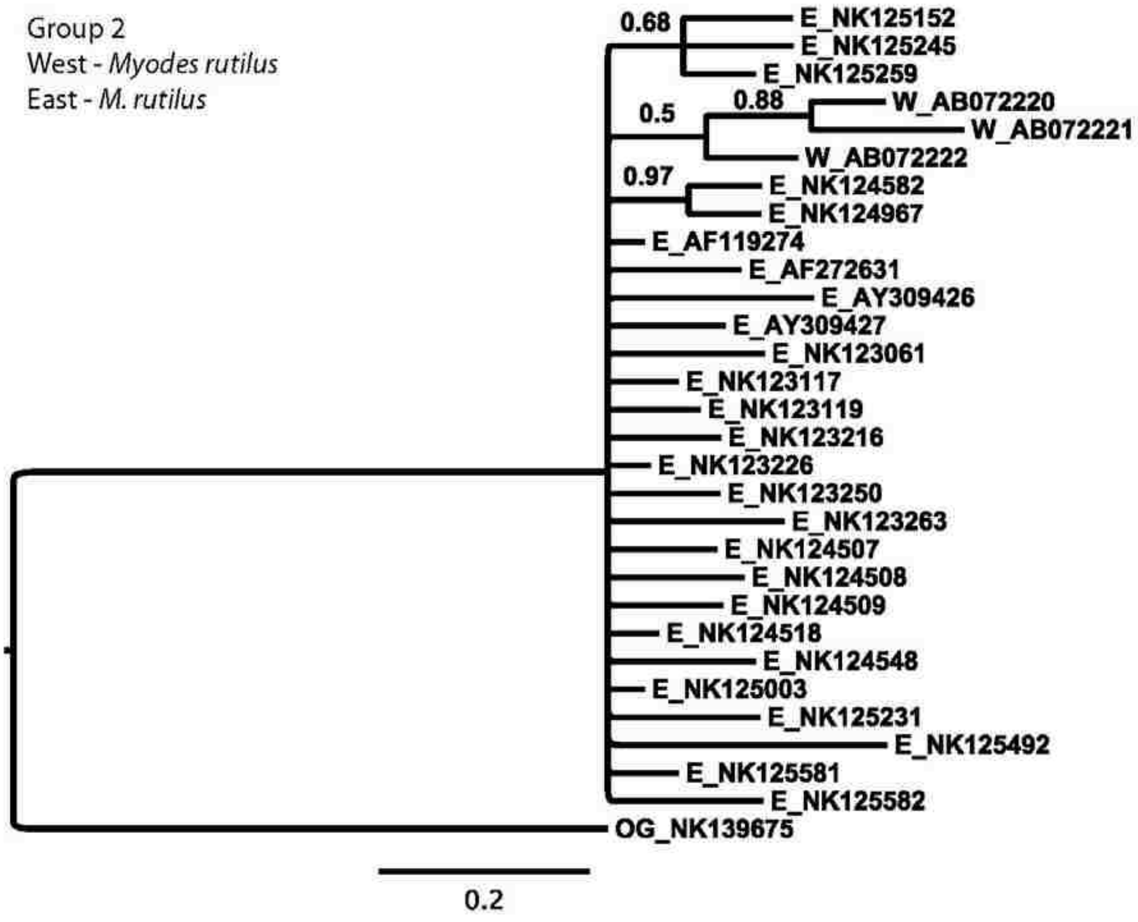
Group 2
West - *Myodes rutilus*
East - *M. rutilus*
0.68
E_NK125152
E_NK125245
E_NK125259
0.5
0.88
W_AB072220
W_AB072221
W_AB072222
0.97
E_NK124582
E_NK124967
E_AF119274
E_AF272631
E_AY309426
E_AY309427
E_NK123061
E_NK123117
E_NK123119
E_NK123216
E_NK123226
E_NK123250
E_NK123263
E_NK124507
E_NK124508
E_NK124509
E_NK124518
E_NK124548
E_NK125003
E_NK125231
E_NK125492
E_NK125581
E_NK125582
OG_NK139675
0.2

Figure S1H.


Group 3
West - *Sorex camtschatica* + *S. portenkoi*
East - *S. ugyunak*
0.89
W2_IF5187
W2_IF5222
W2_IF5228
0.55
W2_AF7467
W2_IF5243
W2_IF7561
W2_IF7570
W2_IF7573
W2_IF7584
W2_IF7585
0.62
W_AF6631
W_AF6632
W_AF6596
W_ND3496
W_IF5019
0.85
W_AF41349
0.54
E_AF48342
E_BM39815
0.52
E_AF46229
E_AF58528
E_AF48601
E_AF58247
E_AF58421
E_AF58479
E_AF58502
E_AF58507
E_AF58513
E_AF7374
E_NK123279
E_NK125515
E_AF11764
E_AF7390
E_AF7213
E_AF7431
W_AF32746
OG_AF23162
0.2

Figure S1I.

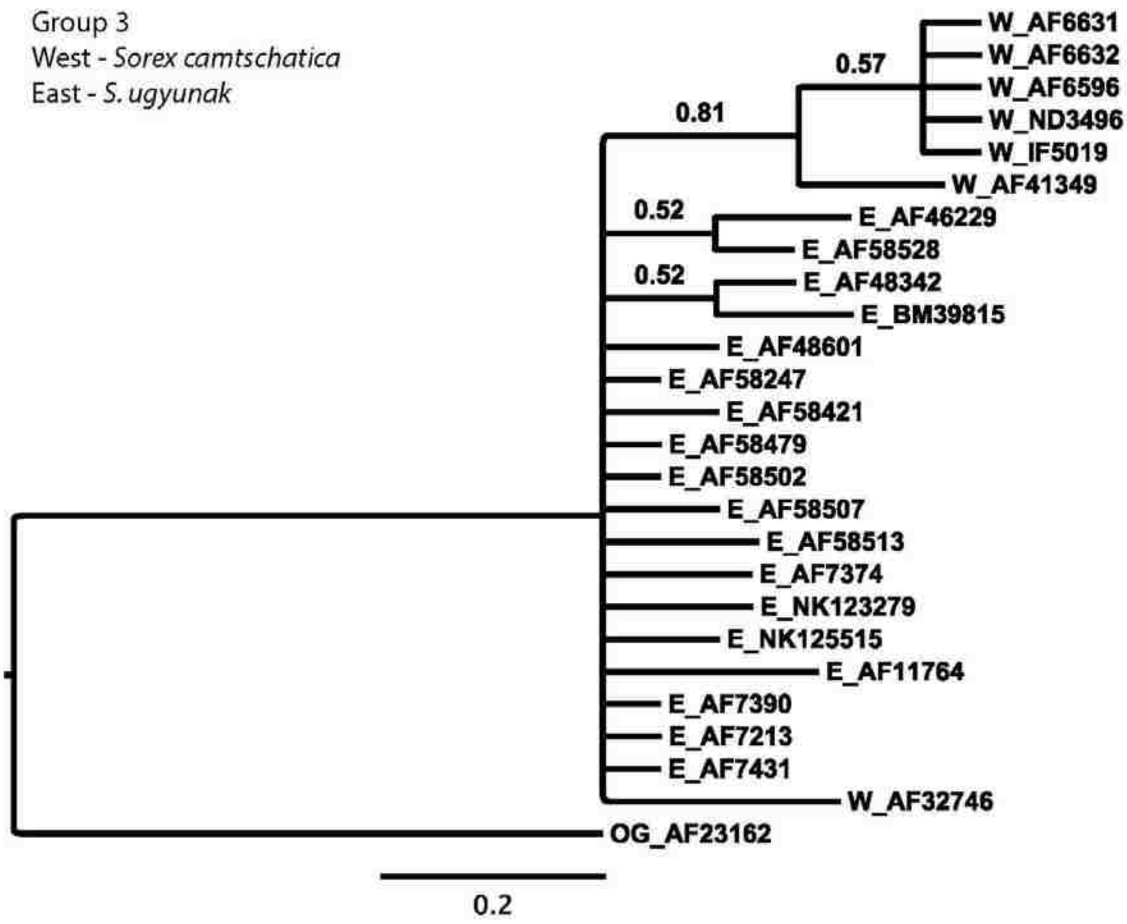
Group 3
West - *Sorex camtschatica*
East - *S. ugyunak*
0.57
0.81
0.52
0.52
W_AF6631
W_AF6632
W_AF6596
W_ND3496
W_IF5019
W_AF41349
E_AF46229
E_AF58528
E_AF48342
E_BM39815
E_AF48601
E_AF58247
E_AF58421
E_AF58479
E_AF58502
E_AF58507
E_AF58513
E_AF7374
E_NK123279
E_NK125515
E_AF11764
E_AF7390
E_AF7213
E_AF7431
W_AF32746
OG_AF23162
0.2

Figure S1J.

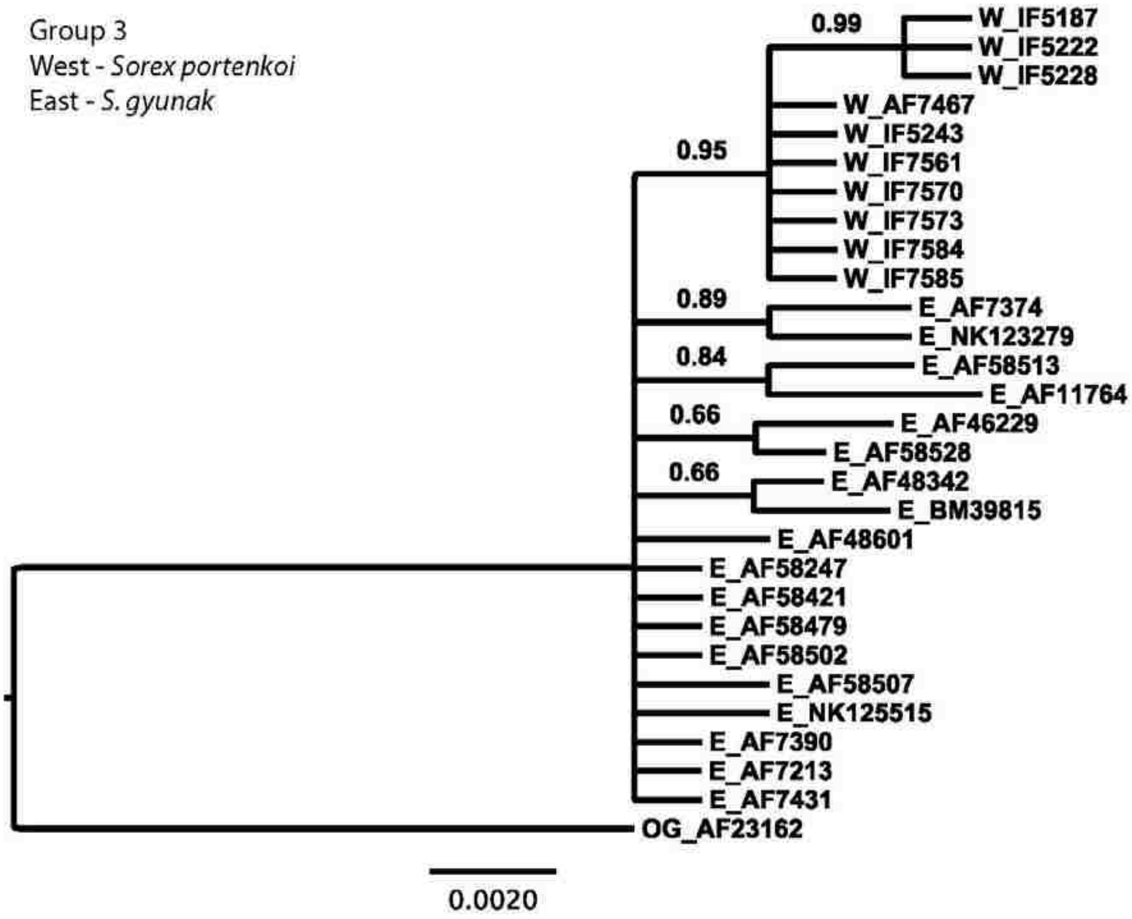
Group 3
West - *Sorex portenkoi*
East - *S. gyunak*
0.99
W_IF5187
W_IF5222
W_IF5228
W_AF7467
0.95
W_IF5243
W_IF7561
W_IF7570
W_IF7573
W_IF7584
W_IF7585
0.89
E_AF7374
E_NK123279
0.84
E_AF58513
E_AF11764
0.66
E_AF46229
E_AF58528
0.66
E_AF48342
E_BM39815
E_AF48601
E_AF58247
E_AF58421
E_AF58479
E_AF58502
E_AF58507
E_NK125515
E_AF7390
E_AF7213
E_AF7431
OG_AF23162
0.0020

Figure S1K.

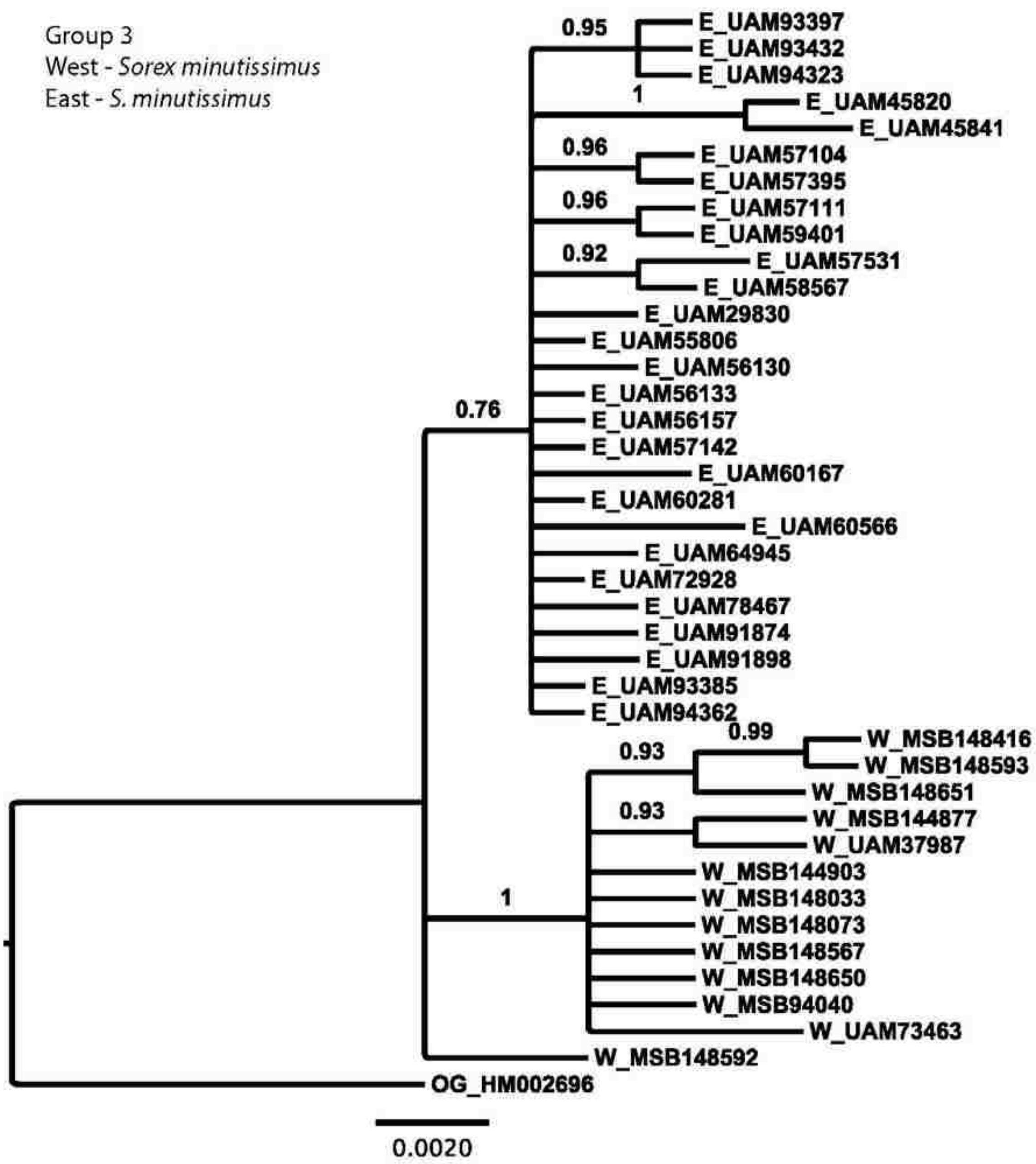
Group 3
West - *Sorex minutissimus*
East - *S. minutissimus*
0.95
E_UAM93397
E_UAM93432
E_UAM94323
1
E_UAM45820
E_UAM45841
0.96
E_UAM57104
E_UAM57395
0.96
E_UAM57111
E_UAM59401
0.92
E_UAM57531
E_UAM58567
E_UAM29830
E_UAM55806
E_UAM56130
E_UAM56133
0.76
E_UAM56157
E_UAM57142
E_UAM60167
E_UAM60281
E_UAM60566
E_UAM64945
E_UAM72928
E_UAM78467
E_UAM91874
E_UAM91898
E_UAM93385
E_UAM94362
0.99
W_MSB148416
0.93
W_MSB148593
W_MSB148651
0.93
W_MSB144877
W_UAM37987
W_MSB144903
1
W_MSB148033
W_MSB148073
W_MSB148567
W_MSB148650
W_MSB94040
W_UAM73463
W_MSB148592
OG_HM002696
0.0020

Figure S1L.

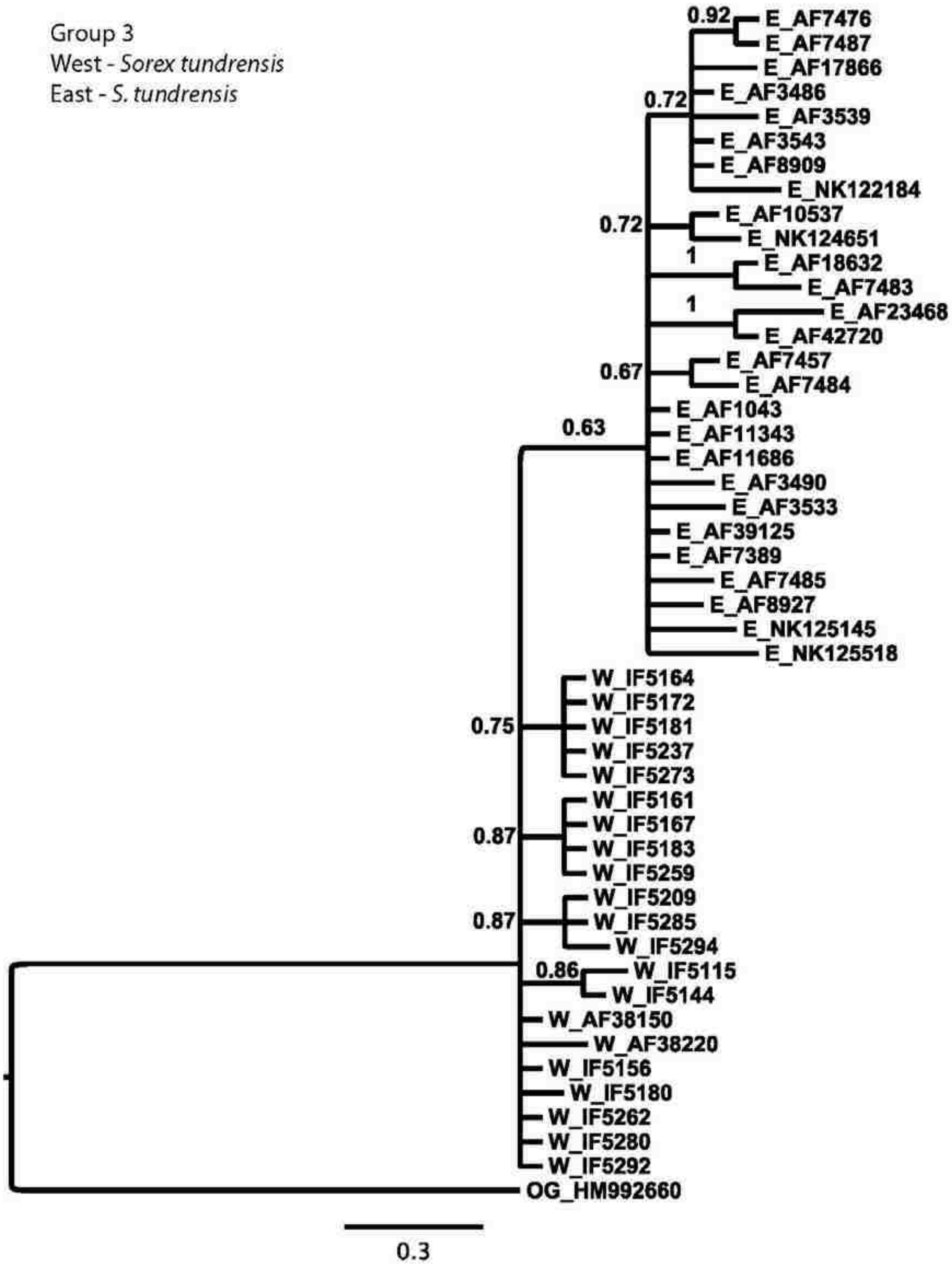
Group 3
West - Sorex tundrensis
East - S. tundrensis
0.92
E_AF7476
E_AF7487
E_AF17866
0.72
E_AF3486
E_AF3539
E_AF3543
E_AF8909
E_NK122184
0.72
E_AF10537
E_NK124651
1
E_AF18632
E_AF7483
1
E_AF23468
E_AF42720
0.67
E_AF7457
E_AF7484
E_AF1043
0.63
E_AF11343
E_AF11686
E_AF3490
E_AF3533
E_AF39125
E_AF7389
E_AF7485
E_AF8927
E_NK125145
E_NK125518
W_IF5164
W_IF5172
0.75
W_IF5181
W_IF5237
W_IF5273
W_IF5161
W_IF5167
0.87
W_IF5183
W_IF5259
W_IF5209
0.87
W_IF5285
W_IF5294
0.86
W_IF5115
W_IF5144
W_AF38150
W_AF38220
W_IF5156
W_IF5180
W_IF5262
W_IF5280
W_IF5292
OG_HM992660
0.3

Figure S1M.

Group 1

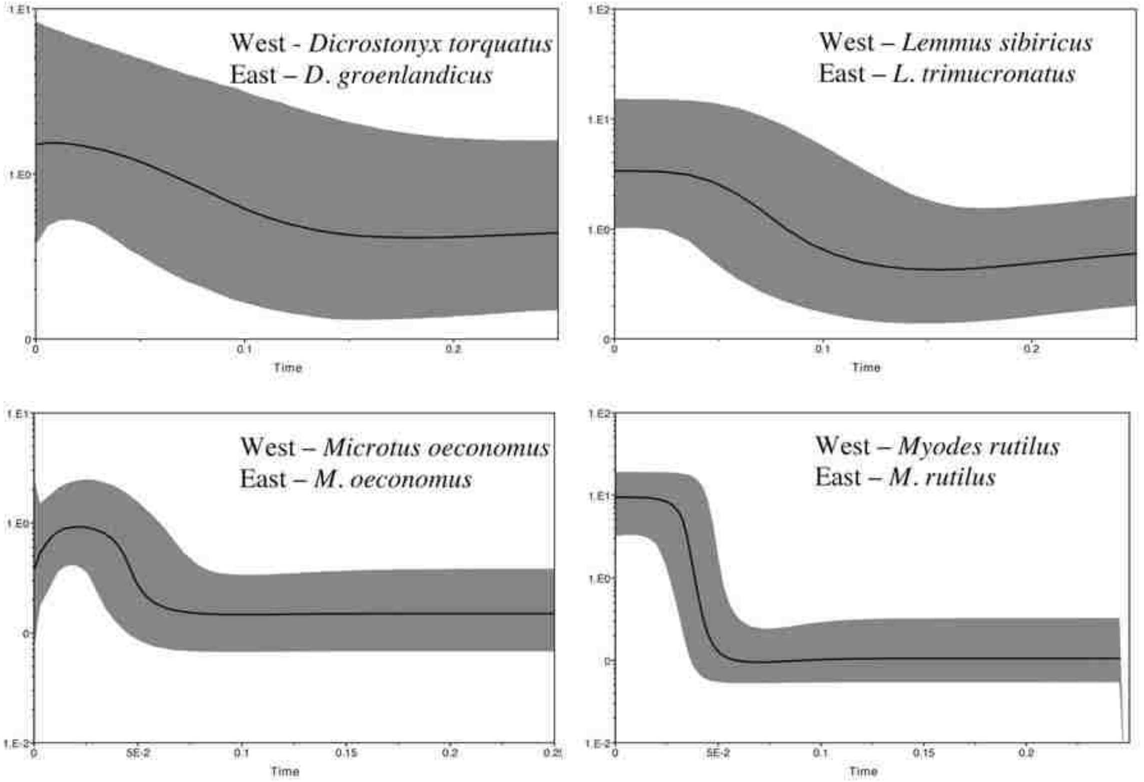

Figure S2A. Bayesian skyline plots for combined taxon pairs of Group 1. Solid lines represent median effective population size change through time (past on the right, present on the left). Shaded interval represents the 95% highest probability distribution. Horizontal axis is time (millions of years); vertical axis is log-transformed and represents τ (tau; a measure of the effective population size as a function of generation time and mutation rate).

Group 2

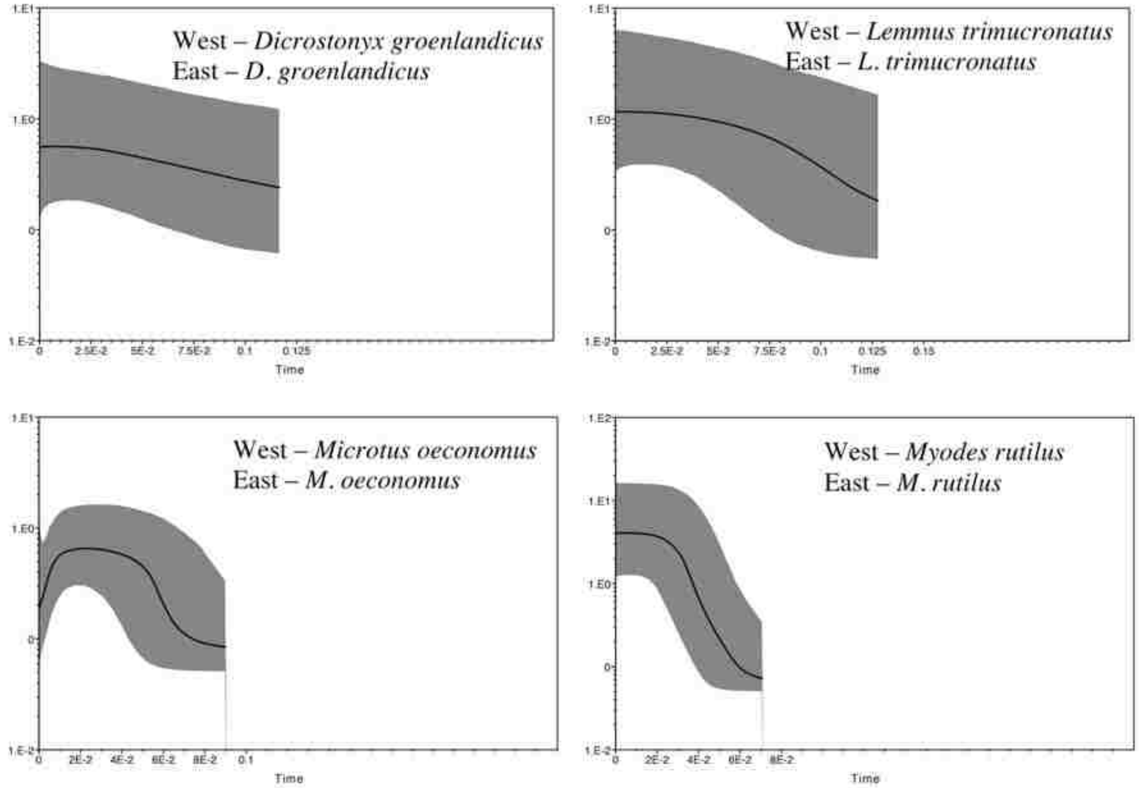

Figure S2B. Bayesian skyline plots for combined taxon pairs of Group 2.

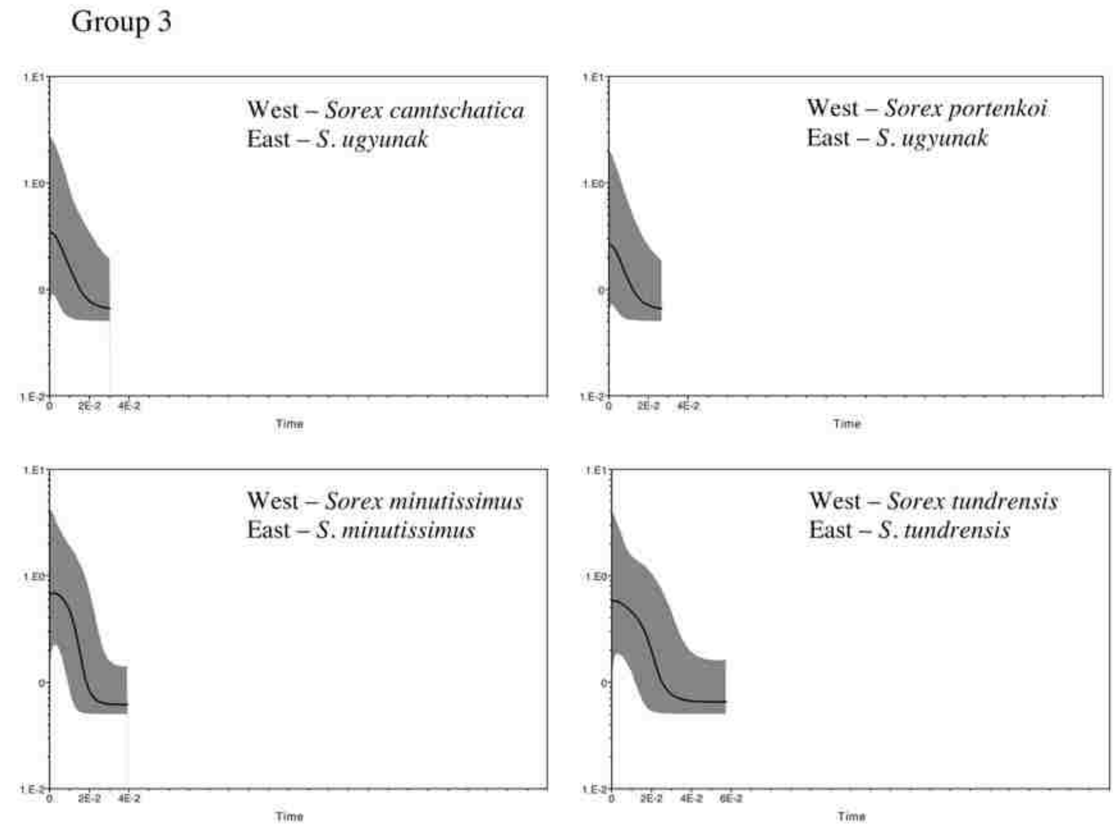

Figure S2C. Bayesian skyline plots for combined taxon pairs of Group 3.

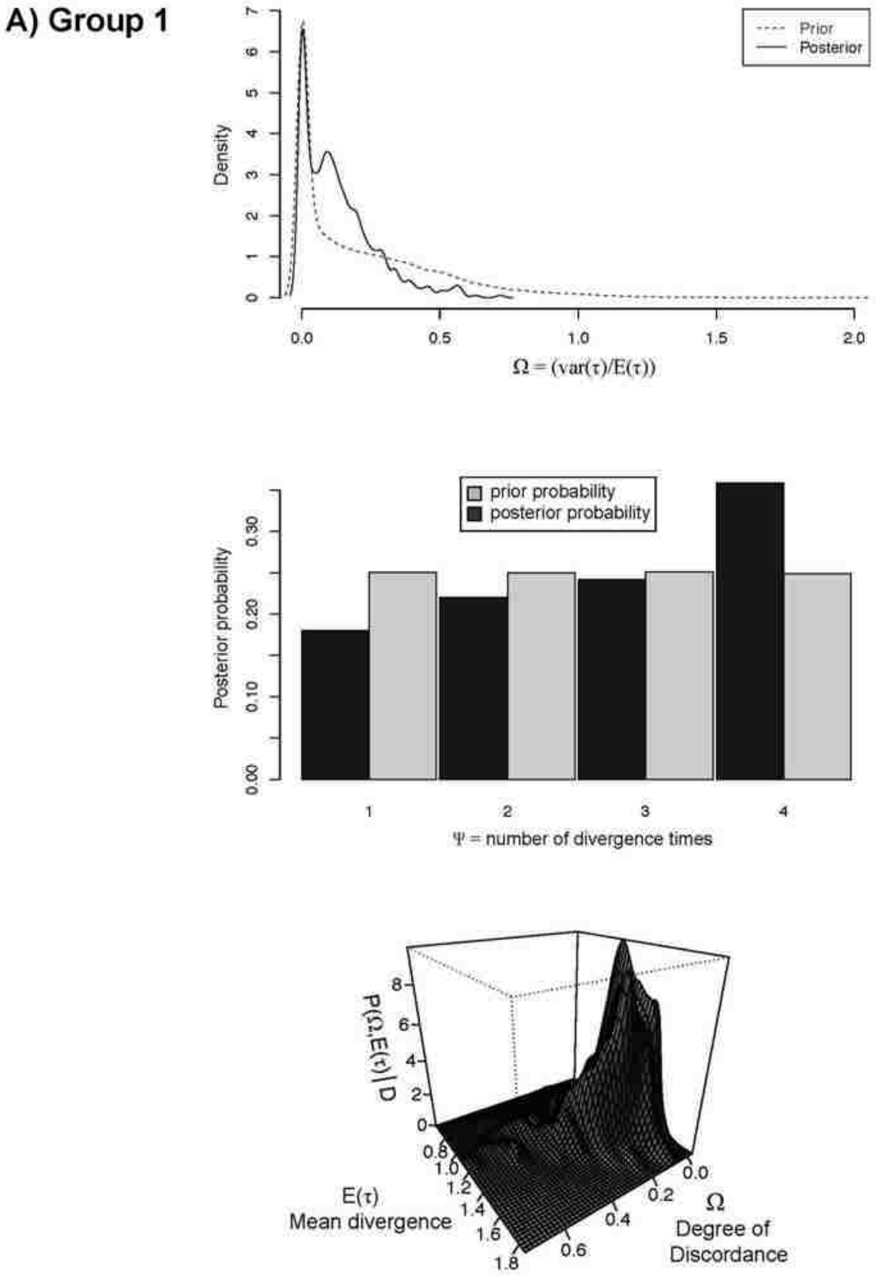

Figure S3A. Posterior estimates of number of divergences across multiple taxon pairs for Group 1 (4 vole taxon pairs). Top: posterior credible interval for simultaneous divergence; Middle: posterior probability densities for Ψ (number of divergence times); Bottom: joint posterior probability densities for $E(\tau)$.

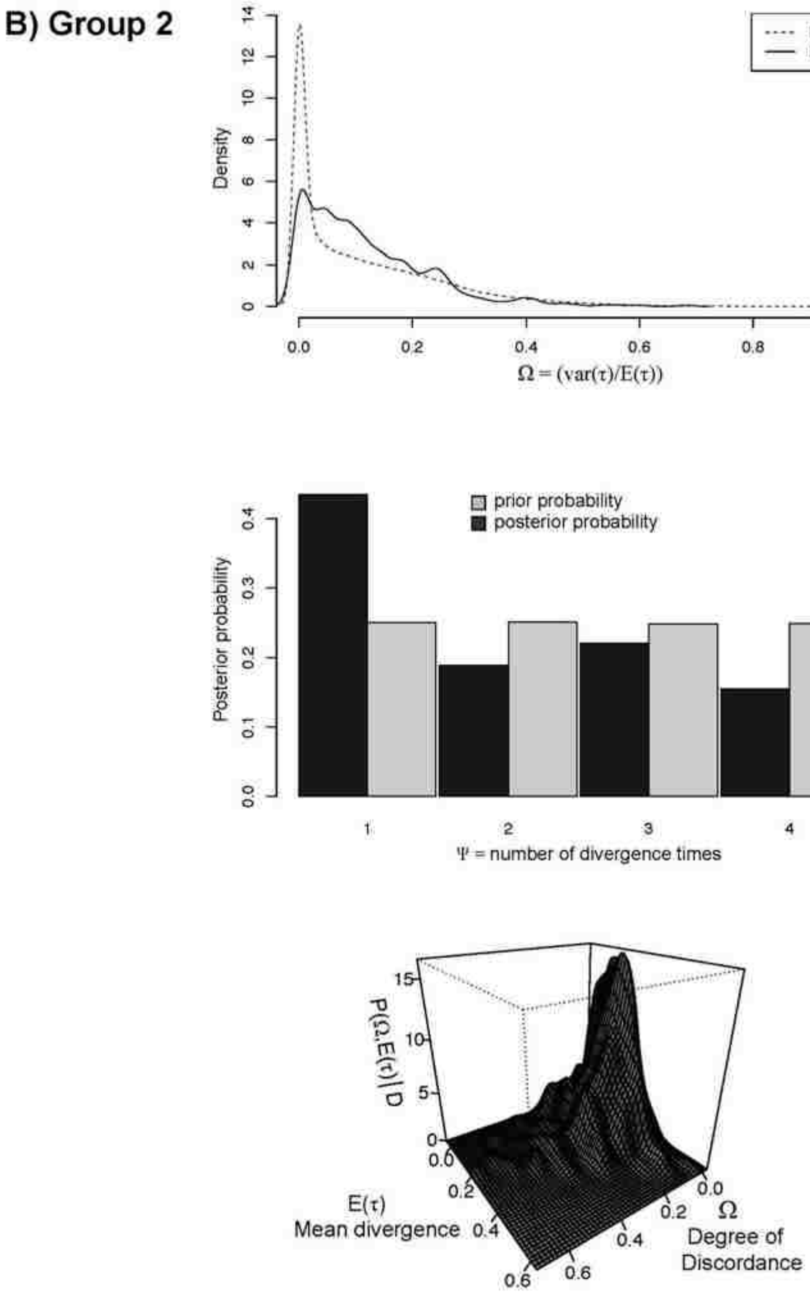

Figure S3B. Posterior estimates of number of divergences across multiple taxon pairs for Group 2 (4 recent vole taxon pairs).

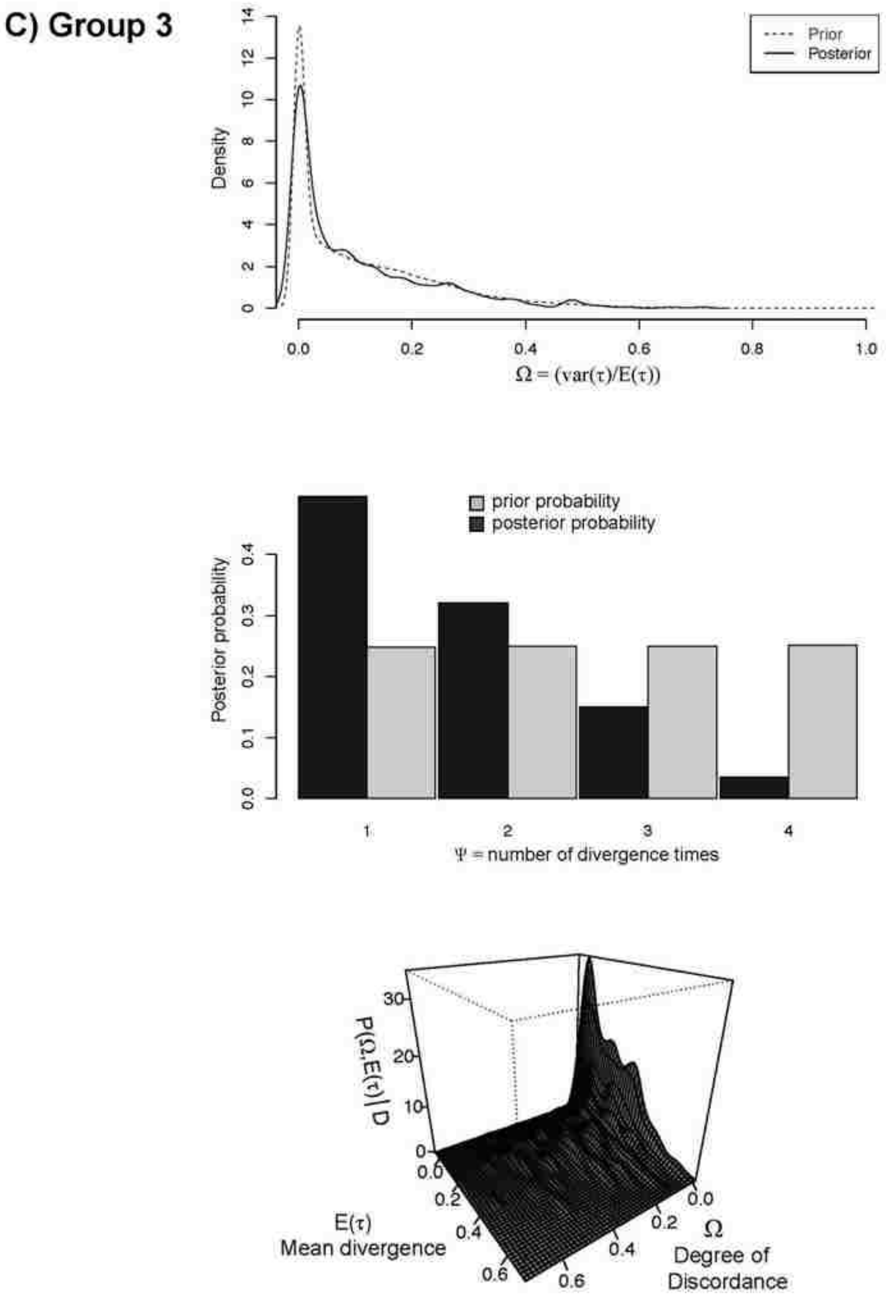

Figure S3C. Posterior estimates of number of divergences across multiple taxon pairs for Group 3 (4 shrew taxon pairs).

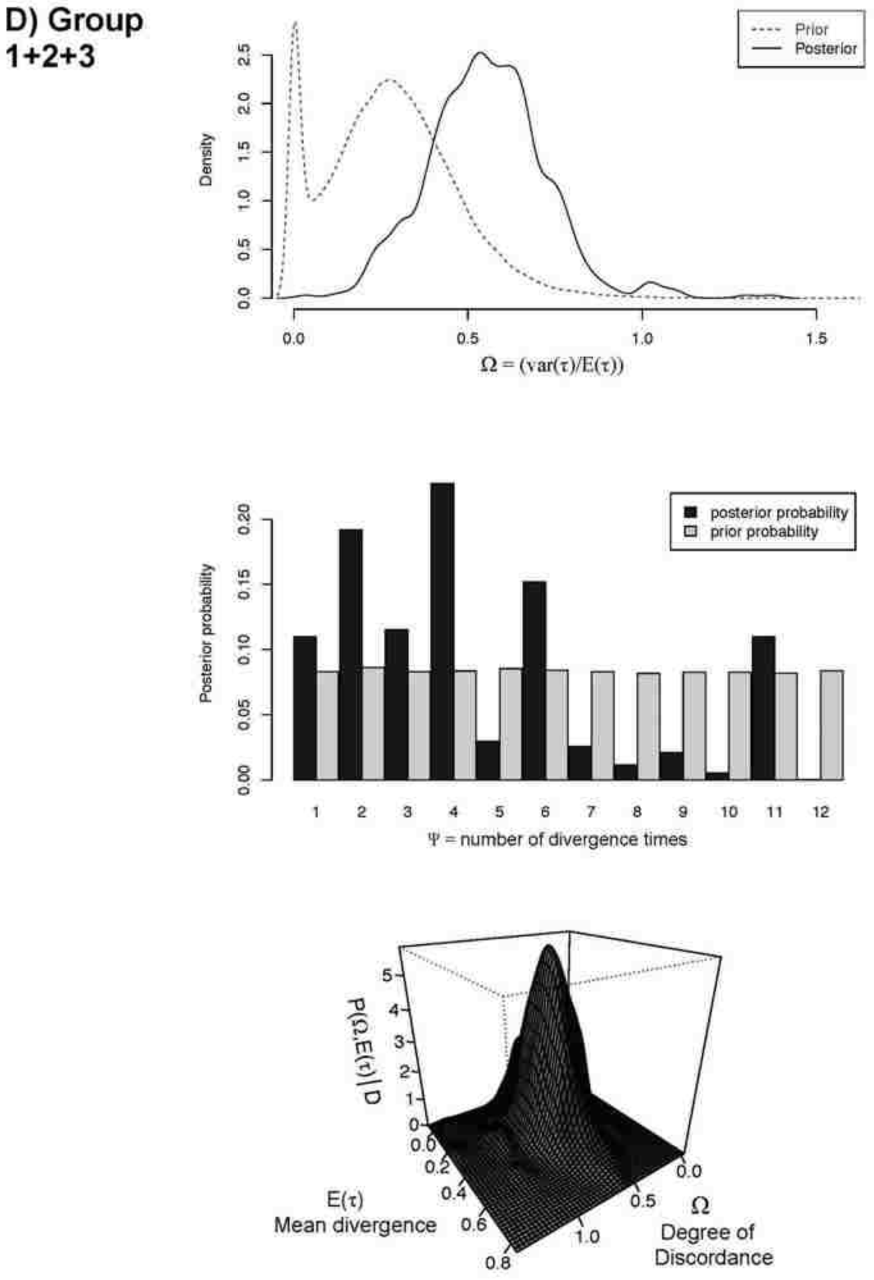

Figure S3D. Posterior estimates of number of divergences across multiple taxon pairs for Group 1+2+3 (12 taxon pairs).

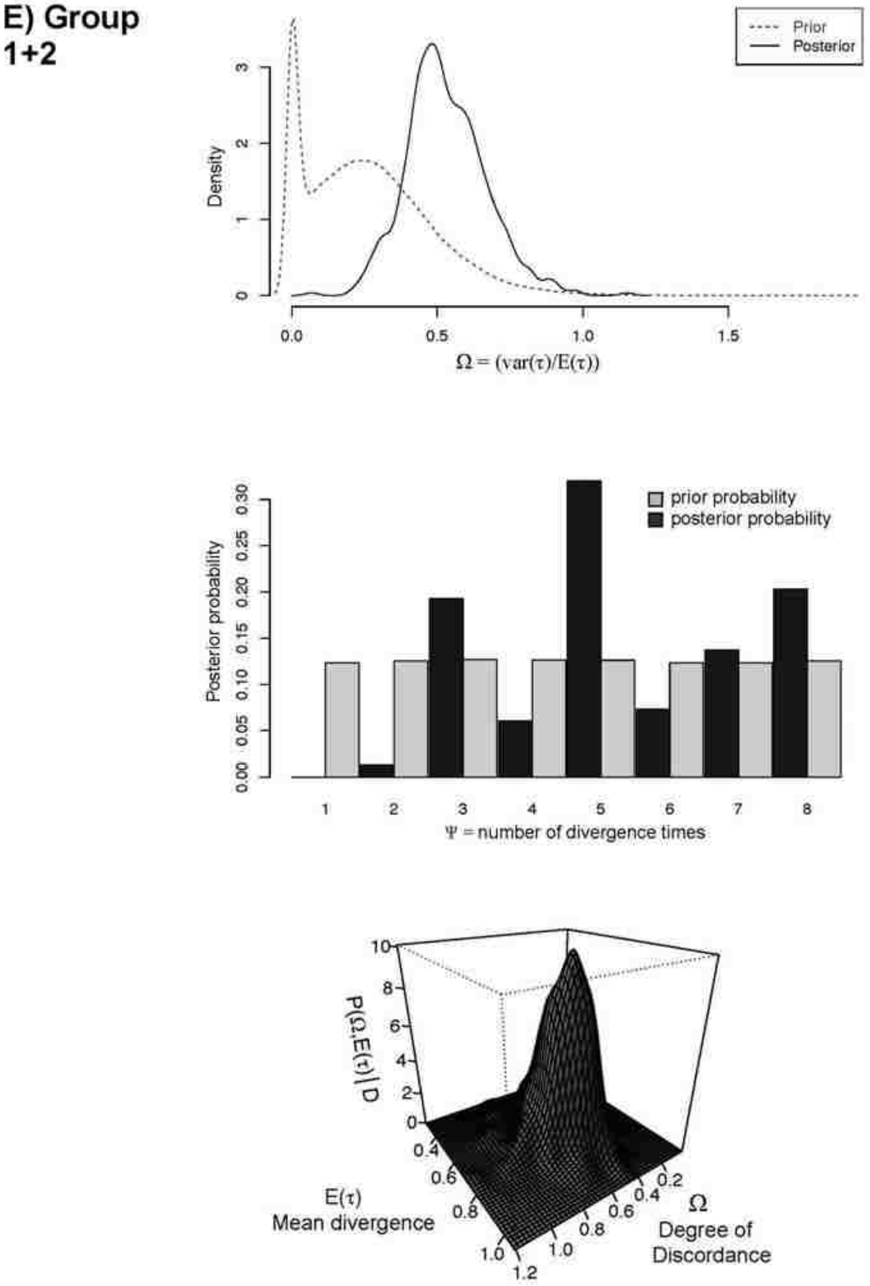

Figure S3E. Posterior estimates of number of divergences across multiple taxon pairs for Group 1+2 (8 vole taxon pairs).

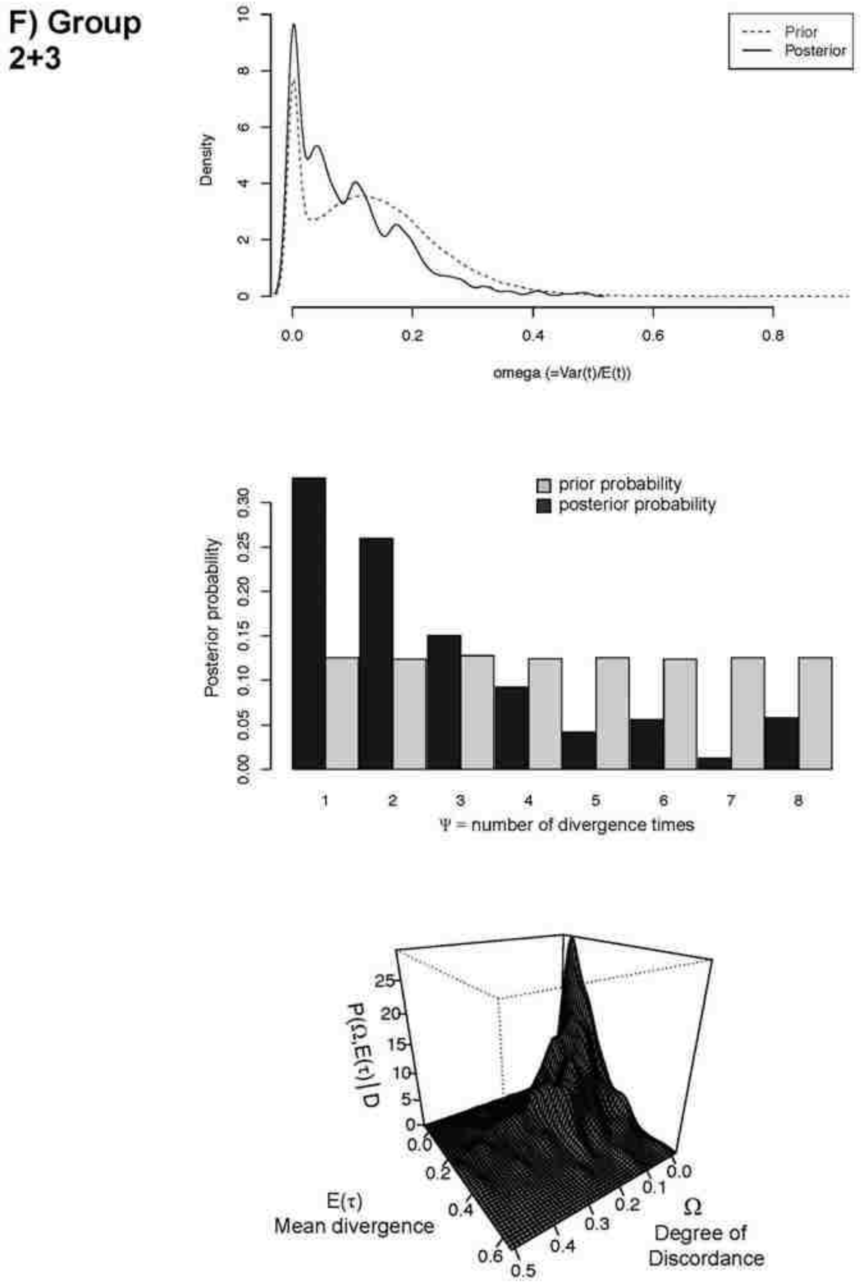

Figure S3F. Posterior estimates of number of divergences across multiple taxon pairs for Group 2+3 (4 recent vole + 4 shrew taxon pairs).

CHAPTER 4

A climate for speciation: rapid spatial diversification among the *Sorex cinereus* complex of shrews.

Running Title: Rapid speciation of *cinereus* complex shrews

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ABSTRACT

The cyclic climate regime of the Pleistocene caused dramatic environmental change at high latitudes. Although these events may have been brief in periodicity from an evolutionary standpoint, multiple episodes of allopatry and divergence have been implicated in rapid radiations of a number of organisms. Shrews of the *Sorex cinereus* complex have long challenged taxonomists due to similar morphology and often-contiguous geographic ranges. Here, multi-locus phylogenetic and demographic assessments using a coalescent framework were combined to investigate spatiotemporal evolution of 13 nominal species with a widespread distribution throughout North America and across Beringia into Siberia. For these species, we first test a hypothesis of recent differentiation in response to Pleistocene climate versus more ancient divergence that would coincide with pre-Pleistocene perturbations and then investigate the processes driving diversification over a vast geographic area. Demography within and among species indicates both regional stability and rapid expansion with divergence linked to ancestral ecological differentiation coincident with early cladogenesis within the group. Our genetic analyses highlight novel diversity within these morphologically conserved mammals, helping to clarify relationships between geographic distribution and evolutionary history. Evolution within the *cinereus* complex constitutes a spatial model for rapid sequential diversification spanning multiple continents and a valuable template for future comparative assessments.

1. Introduction

The history of diversification among the extant North American biota has been strongly influenced by geologic and climate change over broad latitudinal and longitudinal gradients, coupled with intermittent transcontinental biotic exchange through the Neogene period (the last 23 million years [My]) across the Beringian Isthmus in the north, and a more recent connection across the Isthmus of Panama in the south. As such, the relative influence of different drivers of evolution related to environmental change through time has been of interest when considering variable genetic responses. Independent phylogeographic studies have revealed substantial population structure and in some cases speciation as a consequence of late Pleistocene climate change (e.g. Brochmann and Brysting, 2008; Egan and Crandall, 2008; Hewitt, 2004; Weir and Schluter, 2004), particularly at higher latitudes. Conversely, it has been posited that Pleistocene periodicity was too brief to promote speciation in many instances due to repeated reconnection and admixture of allopatric populations (e.g. Petit et al., 2003). Particularly at lower latitudes, geologic change as a consequence of tectonic movement is invoked as the major cause of cladogenesis working over a deeper timeframe (Riddle, 1995, 1998). The wide latitudinal range of North America means that the relative severity and influence of climate versus geophysical change on patterns of diversification may vary considerably from north to south (Weir and Schluter, 2007). In addition, major geologic change during the Neogene has been significantly more pronounced in western North America than in the east (Finarelli and Badgley, 2010). Although tectonic movement is ongoing, major geologic features influencing the North American biota were in place by onset of the Pleistocene. Finally, advances in comparative phylogeographic approaches have improved our understanding of common geographic and climatic elements through North America that influenced patterns of diversification, including phylogeographic breaks, barriers to dispersal, areas of endemism, refugia, or zones of contact over multiple taxa (Burbrink et al., 2008; Swenson and Howard, 2005). With a growing knowledge of the factors influencing evolutionary patterns in North America, we can now form and test predictions for sequential diversification within a given taxonomic group over this broad study area. We use genetic information from multiple independent loci to investigate the history of speciation within the *Sorex cinereus* complex (*cinereus* complex), a widespread and diverse suite of closely related shrews occurring throughout North America and westward into Siberia.

The recent geologic history of North America sets the evolutionary stage for diversification. Beginning in the middle Miocene (15 My), initial formation of the Basin and Range province in the western U.S. was followed by uplift of the Cascade and Sierra Nevada Ranges around 10 My and then further development of the Rocky Mountains (first formed in the Eocene) and Colorado Plateau (for detailed citations see Brunsfeld et al., 2006; Riddle, 1995). Uplift in concert with aridification of western and central North America contributed to the formation of the grasslands of the Great Plains, shrublands of the Columbia Plateau/Basin, and the extensive deserts (Hafner and Riddle, 2005) as evidenced by molecular analyses of disparate floral and faunal groups (e.g. Jaeger et al., 2005; Houston et al., 2010; Neiswenter and Riddle, 2010; Riddle and Hafner, 2006). Highly heterogeneous physiography as a consequence of geologic change influenced diversification both independently and in combination with climatic variability.

Mountain ranges, generally orientated north/south, fragment desert ecosystems while montane forest ecosystems are isolated by intervening arid-lands (Brunsfeld et al., 2006). Eastern geologic history over this time frame was much less variable, perhaps contributing to comparatively lower diversity estimates compared with western North America (Badgley, 2010), and yet major biogeographic provinces in the East are associated with more ancient features such as the Appalachian Range, the Atlantic-Gulf of Mexico divide, and various riverine systems (Soltis et al., 2006). By the late Pliocene (3 My), a cooling trend allowed formation of permafrost at the highest latitudes and the associated tundra biome (Matthews, 1979). Glacial cycling during the Pleistocene epoch (2.5 My) caused repeated climate fluctuations that increased in intensity due to onset of 100 ky cycles by 0.8 My (Lisiecki and Raymo, 2005). These glaciations shunted the biota dramatically and were major drivers of diversification. Connection of Eurasia and North America through Beringia provided multiple opportunities for transcontinental exchange and divergence (e.g. Waltari et al., 2007). Members of the *cinereus* complex collectively exhibit broad ecological associations and a vast geographic distribution, providing an excellent and rare opportunity to investigate spatial and temporal evolution across the latitudinal and longitudinal extent of North America and eastern Siberia (e.g. Pigot et al., 2010).

Systematic relationships within the *cinereus* complex are unresolved despite previous studies of variation in morphology, chromosomes, allozymes, and mitochondrial DNA (mtDNA; see Demboski and Cook, 2003 for overview). The complex now comprises 13 species in the subgenus *Otisorex* (Hutterer, 2005) including the recently allied *Sorex emarginatus* (Esteva et al., 2010). Members occupy most terrestrial ecosystems in North America, except southwestern deserts, and stretch across the Bering Strait into Siberia. The species complex is split into 2 major clades described as Beringian and Southern (van Zyll de Jong, 1991; Table 1). The Beringian clade contains 8 species, 6 of which occupy the tundra and taiga ecosystems of the Arctic: *Sorex ugyunak* occurs in tundra of northernmost Alaska and Canada, having expanded eastward out of the Beringian refugium following retreat of continental ice sheets since the Last Glacial Maximum (LMG) to occupy its current distribution. *Sorex jacksoni* (St. Lawrence Island) and *Sorex pribilofensis* (St. Paul Island) are Bering Strait endemics in tundra habitat and represent remnants of a previously more widespread distribution across the Beringian Isthmus before recent inundation (10,000-16,000 BP; Hopkins et al., 1982). *Sorex portenkoi* occupies tundra within portions of Chukotka and northern Kamchatka in Siberia and *Sorex camtschatica* is found in tundra and taiga both on the Kamtchatka Peninsula and southern Magadanskaya Region, Russia. *Sorex leucogaster* is an insular endemic known only from Paramushir Island within the Kurile group. Although these northernmost forms are described as separate species, their taxonomic status is still debated (Demboski and Cook, 2003). Divergence of mtDNA is minimal suggesting a recent common ancestor. Other members of the Beringian clade occur further south in North America: *Sorex haydeni* occupies grasslands of the northern and central prairies and to a lesser extent deciduous forest. *Sorex preblei* occupies arid sagebrush shrubland centered on the Columbia Basin. Indications from mtDNA of an early dichotomy within the Beringian clade separate *S. preblei* from other members, followed by *S. haydeni*.

The Southern clade is represented by 5 nominal species (Hutterer 2005): *Sorex* *cinereus* (*sensu stricto*) is the most widespread shrew in North America occupying most available boreal coniferous forest in the west and north, and deciduous forests of the east (Whitaker, 2004). Occurrence of *S. cinereus* in the southwestern United States comprises isolated mountaintop sky island populations within remnant patches of previously more widespread forest. Along both Pacific and Atlantic coasts, *S. cinereus* is represented by multiple land-bridge island populations, although there are few systematic assessments of these populations (e.g. Stewart and Baker, 1992) and their history poorly known. *Sorex cinereus* has also spread northward to treeline to occupy much of Canada and Alaska reflecting a rapid range expansion from the south following continental ice sheet retreat (Demboski and Cook, 2003). *Sorex cinereus* does not occur in Oregon or California, but *Sorex lyelli* has a limited distribution in eastern California including mid- to high-elevation arid habitats of the Sierra Nevada Range. In the eastern United States, *Sorex longirostris* occurs in the southern Appalachian deciduous forests near bogs and marshes. Finally, both *Sorex milleri* and *Sorex emarginatus* form isolated populations in montane forests in central eastern and central western Mexico, respectively (Esteva et al., 2010).

We present 1) a multi-locus temporal assessment of sequential evolution among the *Sorex cinereus* complex by testing explicit predictions; 2) a review of the major features in North America and Beringia that have driven geographic speciation within this group; and 3) evidence for a contemporary rapid radiation among this widely distributed suite of small mammals. Low genetic divergence (~6% uncorrected sequence divergence in the cytochrome *b* [Cyt *b*] gene; Demboski and Cook, 2003) among the whole complex presents an excellent opportunity to investigate the evolutionary drivers of this contemporary radiation (Egan and Crandall, 2008).

2. Methods

2.1. Taxonomic and genetic sampling

Over all analyses, we included 374 specimens (59 from GenBank) representing 6 outgroups, all recognized species within the *cinereus* complex (Table 2; Appendix A), and populations within the widespread *S. cinereus* (*sensu stricto*) that are coincident with distinct geographic regions (Fig. 1). Outgroups were *Sorex fumeus*, *Sorex monticolus*, *Sorex nanus*, *Sorex palustris*, *Sorex rohweri*, and *Sorex trowbridgii* based on close phylogenetic relationships with the *cinereus* complex (George, 1988) and availability of tissue samples. All belong within the subgenus *Otisorex* (Hutterer, 2005). For specimens sequenced, heart, liver, or skin was obtained from frozen (stored at -80℃), ethanol preserved, or dried samples. Genomic DNA was obtained through standard salt extraction, PCR, and cycle sequencing methods (Hope et al., 2010). We amplified variable lengths of the Cyt *b* gene (430-1140bp). A single primer pair for the entire Cyt *b* gene was used for frozen high quality samples (MSB05/MSB14; Hope et al., 2010). For degraded DNA samples, multiple species-specific internal primers were developed (Table 3). To improve DNA amplification from degraded DNA samples, we modified protocols of Hope et al. (2010) by substituting AmpliTaq Gold® DNA polymerase and 10x PCR buffer Gold. Automated sequencing of complementary strands was conducted using an Applied Biosystems 3110 DNA sequencer (Molecular Biological Facility, UNM). Complementary strands of DNA were compared and sequences were deposited in GenBank (Appendix A). We also sequenced 99 individuals of the *cinereus* complex and

11 outgroup specimens representing *S. monticolus*, *S. nanus*, *S. palustris*, *S. rohweri*, and *S. trowbridgii* for 4 nuclear loci including 2 nuclear exons (500 bp of the apolipoprotein B gene [ApoB] and 397 bp of the breast cancer susceptibility 1 gene [BRCA1]) found to be phylogenetically informative for other *Sorex* species (Dubey et al., 2007; Hope et al., 2010) and 2 nuclear introns (345 bp of the interferon 1 gene [IFN1] and 326 bp of the myosin heavy chain 1 gene [MYH2]; Lyons et al., 1997; Appendix A). Primer pairs ApoBF/ApoBR and BRCA1F/BRCA1R (Dubey et al., 2006, 2007) were used to amplify and sequence ApoB and BRCA1 genes, respectively, and IFN1F/IFN1R and MYH2F/MYH2R (Lyons et al., 1997) were used to sequence the IFN1 and MYH2 genes, respectively.

Sequences were edited and aligned in SEQUENCHER 4.8 (Genecodes, Ann Arbor, Michigan) and checked by eye. Sequences for all coding regions were translated to amino acids and examined for internal stop codons, rates of transition/transversion changes, and relative first, second and third position changes in codons that might indicate a pseudogene. Alleles of nuclear heterozygotes were inferred using PHASE (Stephens et al., 2001; Stephens and Scheet, 2005). PHASE implements a Bayesian method for reconstructing haplotypes from nuclear sequences that include multiple heterozygous base sites within individuals. To estimate allele frequencies, PHASE was run 5 times. The run with best goodness-of-fit to an approximate coalescent model was retained, resulting in 2 nuclear haplotype sequences or alleles per individual for all independent nuclear genealogies using the same individuals (n_{tot} = 220).

2.2. Phylogeny Reconstruction

We estimated a phylogeny using Bayesian methods for variable lengths of the Cyt *b* gene (430-1140 bp; *n* = 164) representing all species within the *cinereus* complex and outgroup species. We included partial sequences amplified from poor quality samples to maximize sequence diversity for the mitochondrial locus. The best model of DNA substitution was determined using MrModeltest v2.3 (Nylander, 2004) under the Akaike information criterion. Markov Chain Monte Carlo (MCMC) searches of tree space were performed in MrBayes v3.1 (Ronquist and Huelsenbeck, 2003) to estimate phylogenies. Two separate runs were conducted with sequences partitioned by codon position. Each run computed 10 million generations, sampling every 100 generations, with 5 independent chains, and the first 10,000 trees discarded as burn in. Convergence of MCMC runs was assessed in Tracer v1.4 (Rambaut and Drummond, 2007). The resulting phylogram with posterior probabilities was visualized in FigTree v1.2.2 (Rambaut, 2009).

2.3. Species Tree Estimation from Multiple Loci

Evidence from multiple independent genes is critical to inferring species relationships (Edwards and Beerli, 2000) because gene tree/species tree discord can result from gene duplication, introgression, sorting of ancestral polymorphism or rapid fixation of linked loci through selective sweeps (Carstens and Knowles, 2007). For species tree estimation, we used a method involving coalescent coestimation of multiple gene trees embedded within a corresponding species tree topology using *BEAST (Heled and Drummond, 2010) and implemented in the program BEAST v1.6.1 (Drummond and Rambaut, 2007). This method uses a Bayesian MCMC technique. Independent loci were partitioned (unlinked) according to substitution models estimated for each locus (Table 4), molecular clock model, and gene tree estimation. A strict molecular clock was employed and mutation rates for the 4 nuclear loci were estimated based on a Cyt *b* mutation rate for *Sorex* of 5.5% My^{-1} (Hope et al., 2010). A Species Tree: Yule Process tree prior was assigned for all 5 loci with a piecewise linear & constant root population size model. Initial tree root height was estimated and default settings were used for all priors and operators. The MCMC chain was run for 100 million iterations. Resulting tree files were annotated in TreeAnnotator v1.6.1 (part of the BEAST software package) and the species tree topology visualized in Figtree v1.2.2. Independent genealogies for each locus were also estimated in MrBayes v3.1 utilizing methods identical to the expanded mitochondrial phylogeny but employing models of evolution specific to each locus (Table 4).

2.4. Population demographics

Populations for demographic analyses were expanded where possible to include additional Cyt *b* sequences ($n_{tot} = 361$; Table 2) and were assigned based not only on previous studies but also on the results of our Cyt *b* Bayesian phylogeny as a null estimate of relationships within the species complex (Table 5). Species designations within this complex have undergone numerous changes as a result of limited geographic sampling, low genetic and/or morphological differentiation (Demboski and Cook, 2003), and instances of purported hybridization (Brunet et al., 2002; Stewart and Baker, 1997). We therefore retained each nominal species (Hutterer 2005) as a separate group, and also included several populations that may represent new taxa. Demboski and Cook (2003) recognized a population of shrews from the Jemez Mountains of New Mexico that were genetically similar to *S. haydeni* based on mtDNA. We subsequently expanded sampling from this area (*S. sp. SW*; Table 2). In addition, multiple samples collected from riparian and arid sagebrush habitats in the central Rocky Mountains form one or more seemingly distinct evolutionary lineages (*S. sp. RM*; Table 2). All species of the Beringian clade (Demboski and Cook 2003) were closely allied so within this clade we designated 3 subgroups to investigate demography independent of the recognized taxonomy. The first subgroup includes 3 arid-land forms that consistently are associated on the basis of the nuclear loci (*S. lyelli*, *S. sp. SW*, *S. Sp. RM*). We also grouped all high-latitude tundra/taiga species (*S. ugyunak*, *S. pribilofensis, S. jacksoni, S. portenkoi, S. camtschatica,* and *S. leucogaster*) and all Siberian species (*S. portenkoi, S. camtschatica,* and *S. leucogaster*). We grouped all species within the Southern clade (Demboski and Cook 2003), and additionally separated *S. cinereus* (*sensu stricto*) into 4 subgroups reflecting a western clade, a southwestern clade, a midwestern clade, and an eastern clade, with the latter equivalent to the nominal species *S. fontinalis* (George, 1988; Hollister, 1911). Summary statistics were calculated in DnaSP (Librado and Rozas, 2009) for each population to assess genetic diversity: segregating sites (*S*); haplotype diversity (*Hd*); and nucleotide diversity (π). Uncorrected pairwise sequence divergence between populations was calculated as percentage divergence My^{-1}.

For tests of demographic expansion, we used DnaSP to calculate Tajima's *D* (Tajima, 1989), Fu's *Fs* (Fu, 1997), and *R2* (Ramos-Onsins and Rozas, 2002) and assessed significance with 10,000 coalescent simulations. In addition we assessed pairwise mismatch distributions to investigate potential demographic expansion of each major group (samples ≥7) from a small ancestral population. Assuming panmixia with an infinite-sites model of neutral nucleotide substitution (Rogers and Harpending, 1992; Slatkin and Hudson, 1991), a smooth unimodal distribution would indicate sudden population expansion whereas a ragged distribution would reflect stable or contracting populations. Multimodal distributions may indicate either multiple expansions or alternatively subdivision within the complex. All groups and loci were assessed for potential selection using the McDonald-Kreitman test (McDonald and Kreitman, 1991). Summary statistics, genetic diversity indices, and tests of demographic expansion also were completed for each nuclear locus recognizing 3 groups: the entire *cinereus* complex, the Beringian clade, and the Southern clade.

3. Results

3.1 Phylogenies

The Cyt *b* phylogeny is largely coincident with earlier interpretations of the *cinereus* complex (Demboski and Cook, 2003), although new relationships are identified (Fig. 2). A well-supported (PP = 1.00) group within the Beringian clade consists of high-latitude species including *S. ugyunak* in Alaska and Canada; *S. pribilofensis* and *S. jacksoni* from islands in the Bering Strait; and *S. portenkoi, S. camtschatica*, and *S. leucogaster* in Siberia. Within these tundra/taiga species, relationships are poorly resolved due to low levels of divergence. *Sorex leucogaster* is nested within *S. ugyunak* while *S. ugyunak* is paraphyletic with respect to other species. Only *S. portenkoi* and *S. pribilofensis* are monophyletic. Lower-latitude members of the Beringian clade include *S. lyelli* (previously allied to the Southern clade) as sister-taxon to *S. sp. RM* (which consists of specimens that were previously considered to be *S. preblei*); both *S. lyelli* and *S. sp. RM* are closely allied to high-latitude species. Specimens from the southwestern United States (Jemez and San Juan Mtns.; *S. sp. SW*) are reciprocally monophyletic (*Cyt b*) with *S. haydeni* from the central Great Plains, a relationship first described by Demboski and Cook (2003). *Sorex preblei* is basal but paraphyletic with respect to the remainder of the Beringian clade. Within the Southern clade, there is ambiguity with respect to recognized taxonomic relationships. *Sorex emarginatus* is significantly divergent from other species in this clade, but the other Mexican endemic (*S. milleri*) is nested within *S. cinereus*. *Sorex longirostris* and *S. cinereus* (east) are divergent from other clades within *S. cinereus*, including well-supported west, midwest, and southwest clades (Fig. 2).

For the species phylogeny, the 4 nuclear loci varied in estimated mutation rate (0.7%-1.7%), models of evolution, and associated observed base frequencies (Table 4). Species tree relationships were broadly concordant with the mitochondrial topologies (expanded Cyt *b* dataset [Fig. 2]; multi-locus Cyt *b* dataset [Fig. S1]), with a few notable differences (Fig. 3). The *cinereus* complex as a whole is well supported (PP = 1.00) with *S. longirostris* sister to all other species. The Southern clade is paraphyletic but the Beringian clade and a sub-clade consisting of all the high-latitude tundra/taiga species are well supported. *Sorex haydeni* is weakly allied with the tundra/taiga species. All the arid-land species (*S. lyelli*, *S. sp. RM*, and *S. sp. SW*), together with *S. preblei*, form a weakly supported clade. *Sorex cinereus* (*sensu stricto*) forms a distinct monophyletic clade with little support of geographic populations (Fig. 3). Among the outgroup taxa, *S. rohweri* is sister to the *cinereus* complex. *Sorex monticolus* and *S. palustris* are consistently grouped over all loci as previously reported (Demboski and Cook, 2001), and *S. trowbridgii* is consistently the most distant outgroup (Fig. 3).

Coalescence times indicate time to most recent common ancestor (T_{MRCA}) and are estimated at roughly 60 ky for all *S. cinereus* and 43 ky for all the tundra/taiga species (Fig. 3). The Beringian clade is dated to 130 ky. The *cinereus* complex excluding *S. longirostris* is dated to 170 ky and including *S. longirostris*, T_{MRCA} is 308 ky. The *cinereus* complex and *S. rohweri* coalesce at ~850 ky and the root of the tree is estimated at 2.7 My. Confidence intervals surrounding the most recent estimates in some instances overlap (Fig. 3), although they are narrow compared with confidence surrounding basal tree relationships.

3.2 Diversity and Demography

No locus exhibited evidence of selection based on the McDonald-Kreitman test. Nucleotide diversity and haplotype diversity for the Cyt *b* gene varied considerably among groups (Table 5). Nucleotide diversity and haplotype diversity were consistently lowest among species of the Beringian clade, particularly the tundra/taiga species at highest latitudes. Within the Southern clade, each population exhibited high nucleotide diversity. Among nuclear loci, MHY2 exhibited the highest nucleotide diversity. Diversity indices were lower for the Beringian clade than the Southern clade over all loci except BRCA1 (Table 5).

A range of 0.1%-13.8% uncorrected pairwise divergence was found for Cyt *b* for the entire *cinereus* complex (Table 6). Highest and lowest divergence values are exhibited by *S. emarginatus* and *S. leucogaster* respectively from other members of the complex (Table 6). Divergence within both the Beringian and Southern clades ranged from ~1-3%, and between any species ranged from 4.6-6.8%, in both comparisons excluding the outlying species *S. emarginatus* and *S. leucogaster* (Table 6). Within the Beringian clade, the tundra/taiga species exhibited divergence of <1%. Among populations of *S. cinereus*, divergence ranged from 1.1-2.7%, values comparable with distances between arid-land species (Table 6).

Demographic expansion was generally not significant for species within the Beringian clade (Table 5), with the exception of *S. ugyunak*. Within the Southern clade, *S. cinereus* (west) and *S. cinereus* (midwest) exhibited significant signals of expansion. Mismatch distributions for *S. ugyunak* and west and midwest clades of *S. cinereus* illustrate a unimodal distribution also indicating population expansion, whereas other species exhibit ragged distributions apart from *S. pribilofensis* and *S. portenkoi*, species with extremely low nucleotide diversity (Fig. 4). Multi-modal (ragged) distributions for all subgroups are indicative of population subdivision or multiple expansion events (Fig. 4).

4. Discussion

There are few instances where complexes of closely related species occupy such a broad range of geography and climate as *cinereus* shrews, whose largely parapatric distributions reflect a high degree of ecological diversification exemplified by an initial mesic/xeric split between the Beringian and Southern clades (Table 1). Initial divergence in this shrew complex may have been pre-Pleistocene, possibly associated with Miocene/Pliocene geologic change and followed by differentiation during the Pleistocene glacial regime associated with multiple episodes of allopatric differentiation (Demboski and Cook, 2003). Riddle (1995) asserts that diversification in response to climate cycling generally should follow onset of the more extreme 100 ky periodicity of the mid- to late-Pleistocene (about 700,000 ybp). Alternatively, van Zyll de Jong (1982, 1991) proposed that diversification within the entire complex was as recent as the latest Wisconsinan glaciation. Our results strongly indicate that diversification of the entire complex is well within the boundaries of the Pleistocene with an eight-fold decrease of mutation rate for the Cyt *b* gene (~0.7% My^{-1}) necessary to allow a coalescence time for the entire complex that would coincident with onset of the Pleistocene. The mutation rate of 5.5% My^{-1} we use is a point estimate, that is based on vicariance of two sister species in the sub-genus *Sorex* and our focal taxa should share similar mutation rates (Kumar and Subramanian 2002). Although fossil *Sorex* are available, identification and dating of fossils has been problematic (e.g. Harris, 1998; Kurtén and Anderson, 1980; Rzebik-Kowalska, 2005), and only applied to questions related to deeper structure within soricomorphs (e.g. Dubey et al., 2007; Esselstyn and Brown, 2009).

4.1 Rapid Speciation

The history of the *cinereus* complex spans only 3 glacial cycles (Fig. 3; $T_{MRCA} = 0.308 \pm 0.1$ My) during the late-Pleistocene and Holocene, representing a relatively rapid mammalian radiation. Considering the extensive combined range, higher speciation rates are reasonable as the probability of speciation is dependent on the range of the species (Rosenzweig, 1975). Speciation rate has been shown to decrease through time as a consequence of allopatric splitting of the geographic range of sister species resulting in multiple successively smaller ranges each with a lowered probability of future speciation (Waldron, 2007; Weir, 2006). However, if the species expand following allopatry, geographic range for each sibling species will remain large and overall speciation rate high (Pigot et al., 2010). Such geographic speciation due to peripatric or allopatric divergence followed by range expansion (Pigot et al. 2010) may characterize the evolutionary history of the *cinereus* complex.

Among outgroup taxa, coalescence of *S. trowbridgii* and other species in the subgenus *Otisorex* is estimated at ~2.7 My, with a confidence interval that encompasses the onset of the Pleistocene (Fig. 3). *Sorex trowbridgii* has recently been closely allied to a large clade of *Sorex* mostly occurring in Mexico (Esteva et al. 2010). Remaining species within the subgenus *Otisorex* comprise the other major clade of *Sorex* with a Nearctic origin. Onset of Pleistocene glaciations (~2.5 My) may be the primary driver of this early dichotomy in North America. Similarly, diversification among many of the Eurasian shrews in the sub-genus *Sorex* have been dated to within the Pleistocene (Hope et al. 2011) suggesting that high diversity within the entire genus (77 recognized species;

Hutterer, 2005) was driven largely by major Pleistocene climate episodes and not geophysical change during the Miocene and Pliocene. We estimated a date of 850 ky for the T_{MRCA} of *S. rohweri* and the *cinereus* complex (Fig 3), nearly coincident with onset of 100 ky glacial periodicity. The entire *cinereus* complex coalesces at ~310 ky, coincident with the middle Yarmouth interglacial at which time *S. longirostris* diverges, likely in eastern North America. Well-differentiated eastern clades also characterize other North American organisms due to postulated barriers such as the huge glacial-melt outflow from the Laurentide ice sheet through much of the Pleistocene that became the Mississippi River and may have isolated populations latitudinally (Avise and Walker, 1998; Avise et al., 1998). Southern and Beringian clades (excluding *S. longirostris*) are estimated to have split during the Illinoian glacial period (~170 ky). We postulate that ancestors of the Southern clade were situated in south and central U. S. and Mexico, whereas ancestors of the Beringian clade were isolated west of the Rocky Mountains and south of the Cordilleran ice sheet, likely in cold peri-glacial habitats. Few fossil shrews are available, however "*S. cinereus*" were found in several localities in Texas dated to the Late Pleistocene (Kurten and Anderson, 1980) and also in Mexico (Esteva et al. 2005). This is also plausibly the period at which a major ecological division within the *cinereus* complex occurred. Members of the Southern clade are closely associated with coniferous forests and other mesic habitats whereas members of the Beringian clade are more closely associated with xeric and cold environments.

The Sangamon interglacial (~130 ky) is coincident with division of the Beringian clade into high-latitude and mid-latitude species, with the former rapidly expanding northward following glacial retreat. These Bering ancestors would have been peri-glacial and moved north preceding boreal forest expansion that ultimately formed a forest barrier between high- and mid-latitude Beringian populations. This habitat barrier, much as at present, would have been continent-wide across most of of Canada, effectively causing allopatric divergence of non-forest species to north and south. Concurrently however, *S. cinereus* likely expanded northward through this boreal forest belt.

Onset of the Wisconsinan glacial (~75 ky) would have allowed the high-latitude species to expand at some point across the Beringian Isthmus due to lowered sea levels to occupy Siberia, possibly in multiple episodes through this most recent glacial phase (Dokuchaev, 1997). Mid-latitude species such as *S. preblei* and the arid-land group likely expanded to occupy western North America at lower elevations where forests were scarce. Further differentiation was influenced by geographic features such as immense pluvial lakes or glaciated mountain ranges. *Sorex cinereus* receded to the south. Eastern *S. cinereus* was likely pushed south through New England to be isolated in the eastern United States as has been postulated for other species such as *Sorex palustris* (Stewart et al. 2002). Greater divergence of *S. cinereus* (east) from other regional populations (Fig. 2) is likely due to strict allopatry whereas other distinct populations within *S. cinereus* experienced gene flow for longer, even intermittently through the Wisconsinan glacial phase. Since the LGM (21 ky), the established ecological differences between Beringian and Southern species resulted in fragmentation of *S. sp. RM*, *S. sp. SW*, and *S. lyelli* (arid-land forms), but allowed expansion of *S. cinereus* (forest). These demographic changes are reflected by mismatch distributions and expansion statistics (Fig. 4; Table 5) where *S. cinereus* (west) and *S. cinereus* (midwest) rapidly expanded northwards, but arid-land species exhibit ragged distributions indicating stable or contracting populations. A signal of expansion in the tundra associated *S. ugyunak* may reflect population growth eastward from the Beringian refugium to occupy newly available tundra following glacial retreat.

Diversification among the *cinereus* complex is linked closely to repeated climate-forced allopatry followed by range fluctuation (Jansson and Dynesius, 2002). Importantly, the early ecological split means that diversification between Beringian and Southern clades was out of phase with respect to climate cycles. Such a staggered rapid radiation resulted in *S. cinereus* diversifying in forest refugia during the Wisconsinan glacial period followed by isolation and divergence of high-latitude Beringian species since the LGM when fragmented by the sundering of Beringia, as recently as 11 ky (e.g. Fedorov et al., 1999). Contact zones between species of this complex always consist of a Southern (i.e. *S. cinereus, sensu stricto*) and a Beringian clade species. *Sorex cinereus* has been collected sympatrically with *S. haydeni* at the forest-grassland interface in Minnesota (Brunet et al., 2002), with *S. sp. RM* at the forest-sagebrush interface in Idaho, Montana, and Wyoming (Kirkland et al., 1997; pers. obs.), and with *S. ugyunak* at the forest-tundra interface within Alaska. The extent of divergence between Southern and Beringian clades may be sufficient to prevent significant hybridization. Habitats associated with these major clades appear to constitute barriers so that niche conservatism has maintained population isolation and divergence following initial episodes of allopatry (Weins and Graham, 2005).

Hybridization within the *cinereus* complex has been recorded on at least one occasion between *S. cinereus* and *S. haydeni* (Brunet et al., 2002) although the extent of introgression appears limited to a narrow hybrid zone. Multiple instances of apparent incomplete lineage sorting among the nuclear genealogies (Fig. S1) could reflect historic hybridization or the slower sorting of nuclear alleles. With such a shallow history for the complex, hybridization likely occurred repeatedly potentially leading to the underestimation of coalescence times among clades (Hewitt, 2011; Petit et al. 2003). In particular, ancient introgression in the history of the complex likely left signatures through disparate lineages that might impact phylogenies (e.g. Demboski and Cook, 2001; Good et al., 2003; Runck et al., 2009).

4.2 Systematics

Demboski and Cook (2003) assessed genetic relationships among 9 of the 13 currently recognized species within the *cinereus* complex using two mtDNA loci. Subsequently Esteva et al. (2010) recognized the close alignment of *S. milleri* and *S. emarginatus* with *S. cinereus,* also using mtDNA. This study reports the first molecular sequences from both *S. leucogaster* and *S. lyelli*, and also includes *S. rohweri*, a recently described species and potential sister taxon to the *cinereus* complex (Nagorsen and Panter, 2009; Rausch et al., 2007). This significantly expanded dataset increases specimen and locality representation within species, particularly *S. cinereus* as suggested by Demboski and Cook (2003), and has highlighted new and old systematic issues. Demboski and Cook (2003) described two specimens from the Jemez Mountains of New Mexico that represented a disjunct and genetically distinct population of *S. haydeni*. Multiple loci and expanded sampling (Table 2; Fig. 2) emphasize that this population (*S. sp. SW*), previously identified as *S. haydeni* (mtDNA; Demboski and Cook, 2003), *S. cinereus* (Findley et al., 1975), and *S. preblei* (Kirkland and Findley, 1996), is a member of the

Beringian clade of shrews and most closely allied to *S. lyelli* (Fig. 3). *Sorex lyelli* is associated with the Beringian clade for the first time, suggesting that no member of the Southern clade has ever occurred within Cascade and Sierra Nevada forests of westernmost North America. *Sorex lyelli* likely shifted in elevation to inhabit the Sierra Nevada as surrounding areas of the Great Basin were desertified in the Holocene. A recognized phylogeographic break for other mammals north of the Cascade Range in Washington State (e.g. Arbogast and Kenagy, 2001) is coincident with the western distributional limit of *S. cinereus,* although suitable forest habitat is continuous through this area and southward. *Sorex preblei* has been associated with arid sagebrush habitats from southern British Columbia (Nagorsen et al. 2001) through the Columbia Basin of Oregon and south to northern California (Shohfi et al., 2006) and eastward to Utah, Idaho, Montana, and Wyoming (Cornely et al., 1992). Populations east of Oregon may represent an incipient species (*S. sp. RM*) that is most closely related to *S. lyelli* (Fig. 2; 3). Systematic relationships among the high-latitude species of the Beringian clade remain unresolved, but the limited divergence indicates a recent history of diversification (<50 ky; Fig. 3).

Within the Southern clade, relatively high mitochondrial divergence of eastern populations of *S. cinereus* from other *S. cinereus* (Table 6) is consistent with George's (1988) conclusion that these are a separate species (*S. fontinalis*). However, nuclear variation indicated that *S. cinereus* (east) is well supported within *S. cinereus* (*sensu stricto*; Fig. 3). *Sorex milleri* was found to be allied to *S. cinereus* (Esteva et al., 2010) and this relationship is supported, but we suggest that the validity of this species is questionable, as it is nested within *S. cinereus* (Fig. 2). Poor quality DNA from these specimens limited the number of recovered loci however, and similarly the status of *S. emarginatus* should be further clarified although it appears to be a member of the *cinereus* complex. *Sorex longirostris* has been considered a member of the Southern clade based on allozymes (George, 1988) and mitochondrial DNA (Demboski and Cook, 2003; Fig. 2). However, our analyses suggest it is the most basal member of the species complex (Fig. 3; Fig. S1). Finally, *S. rohweri* was suggested to be closely related to the *cinereus* complex (Nagorsen and Panter, 2009; Rausch et al., 2007) and over all loci except ApoB (Fig. S1), *S. rohweri* was consistently sister to the *cinereus* complex (Fig. 3). However, in general higher-level relationships were not consistent across independent gene genealogies.

5. Conclusions

This study characterizes a radiation of shrews that is driven by cyclical environmental change, and facilitated by early ecological differentiation between the major clades of this complex. Differentiation is stimulated by allopatry and subsequent rapid range change (Pigot et al., 2010). A combination of abiotic (climate and geography) and biotic (habitat) factors can thus drive dramatic distributional and genetic change over brief time periods, even among the smallest non-volant mammals.

This scenario for sequential evolution within the *cinereus* complex presents multiple avenues for future research,including further consideration of taxonomy. Although we do not formally recommend taxonomic revision, extremely low genetic diversity among all high-latitude Beringian species is less than intra-specific differences seen among other high-latitude shrew species (e.g. Hope et al., 2010; 2011). Similarly, the Mexican species *S. milleri* does not form a reciprocally monophyletic relationship with *S. cinereus* and as such may not warrant distinct species recognition. Conversely, two distinct evolutionary units, previously considered *S. preblei*, approach inter-specific levels of divergence that characterize other nominal shrews. Although initial morphological analyses formed the basis of species descriptions associated with this complex, our genetic assessment points toward the need for a comprehensive comparative revision. Additional specimens from poorly represented taxa (*S. emarginatus*, *S. leucogaster*, *S. lyelli*, *S. milleri*, *S. preblei*) will allow for more detailed demographic and evolutionary analyses. Finally, novel methods for analysis of multi-locus data should provide more powerful views of historical demography, species relationships and spatiotemporal diversification (e.g. reviewed in Hickerson et al. 2010).

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Table 1

Major clades, general habitat affinities, and distributions of species within the *Sorex cinereus* complex.

Clade*/Species**	Habitat	Distribution
Beringian Clade	Generally xeric	
Sorex camtschatica	Tundra/taiga	learctic: Russia: Magadan region and Kamchatka Pen.
Sorex leucogaster	Tundra	Palearctic: Russia: Paramushir Is., Kuriles
Sorex portenkoi	Tundra	Palearctic: Russia: Chukotka
Sorex jacksoni	Tundra	Bering Strait: St. Lawrence Is.
Sorex pribilofensis	Tundra	Bering Strait: St. Paul Is.
Sorex ugyunak	Tundra	Nearctic: northernmost Alaska and Canada
Sorex haydeni	Grassland	Nearctic: Great Plains of Canada and USA
Sorex preblei	Sagebrush shrubland	Nearctic: western North America: Columbia Basin
Southern Clade	Generally mesic	
Sorex cinereus	Coniferous forest	Nearctic: widespread
Sorex lyelli	Coniferous forest, shrubland	Nearctic: California: eastern Sierra Nevada Mtns.

Sorex emarginatus	Coniferous forest	Nearctic: Mexico: Sierra Madre Occidental
Sorex milleri	Coniferous forest	Nearctic: Mexico: Sierra Madre Oriental
Sorex longirostris	Deciduous forest, marsh, bog	Nearctic: southeast United States

*Clade relationships first described by van Zyll de Jong (1991).

**Assignment to clades based on van Zyll de Jong (1991), Demboski and Cook (2003), and Esteva et al. (2010).

Table 2

Sample sizes (excluding outgroup taxa) used for independent analyses including estimation of the mitochondrial cytochrome *b* genealogy, the multi-locus species tree, and population demographic statistics including genetic diversity indices.

Species/population	*Cyt b* gene	Species Tree	Population Demographics
All	151	99	361
Beringia Clade	78	49	129
S. preblei	7	2	9
S. haydeni	6	5	11
S. lyelli	2	2	2
S. sp. RM	12	11	25
S. sp. SW	9	8	22
S. ugyunak	11	8	23
S. pribilofensis	6	5	9
S. jacksoni	7	1	7
S. portenkoi	9	4	11
S. camtschatica	8	3	9
S. leucogaster	1	0	1
Southern Clade	73	50	232
S. emarginatus	1	0	1
S. milleri	9	0	7
S. cinereus (All)	53	40	214

S. cinereus (west)	19	14	122
S. cinereus (southwest)	17	12	40
S. cinereus (midwest)	10	8	21
S. cinereus (east)	7	6	31
S. longirostris	10	10	10

Table 3

Primers developed for amplification of the cytochrome *b* gene. Degraded DNA was amplified using multiple primer pairs; complete sequences were obtained from high quality DNA using only MSB05/MSB14, developed previously (Hope et al. 2010). Primers St1, St2, St7 were developed for use with other shrew species (Hope et al. 2011).

	Forward			Reverse		
Pair	Name	Sequence	Start	Name	Sequence	Start
1	MSB05	GACATGAAAAATCATTGTTGTAATTC	-43	MVZ06S	TGTGTCTGATGTGTAGTGTA	177
2	St1	CTCATCATGGTGAAACTTCG	81	St2	CCGATATAAGGGATTGCTGA	470
3	ScFa	CGCAGTAATAGCAACTGCC	363	ScRa	CTGGGTCGCCTAGTAAGTC	762
4	ScFb	GGTCTCCTACTCATTTTAG	694	ScRb	GTGTGAGAAGGTCTGCTAC	1005
5	St7	TAATATTCCGCCCATTTAGCC	944	MSB14	CCCATCTCTGGTTTACAAGAC	1186

Table 4

Characteristics of five genetic loci. Cyt *b* = mitochondrial cytochrome *b* gene; ApoB = apolipoprotein B gene; BRCA1 = breast cancer susceptibility 1 gene; IFN1 = interferon 1 gene; MYH2 = myosin heavy chain 2 gene. Characteristics include mutation rate My^{-1} with 95% confidence intervals, relative base frequencies, evolutionary model as estimated using MrModeltest, and transition/transversion ratio where applicable.

Locus	Mutation Rate (C.I.)	F(A)	F(C)	F(G)	F(T)	Model	Ti/Tv
Cyt *b*	0.0550 (0.0280-0.0890)	0.286	0.303	0.134	0.278	GTR+I+G	N/A
ApoB	0.0087 (0.0064-0.0113)	0.296	0.229	0.141	0.334	GTR+G	N/A
BRCA1	0.0070 (0.0047-0.0094)	0.416	0.179	0.177	0.229	HKY+G	2.727
IFN1	0.0094 (0.0065-0.0124)	0.295	0.231	0.236	0.238	K80+G	2.025
MYH2	0.0167 (0.0116-0.0220)	0.257	0.222	0.353	0.169	GTR+I+G	N/A

Table 5

Demographic statistics for members of the *cinereus* complex. Values were calculated for the cytochrome *b* gene except where indicated otherwise (ApoB = apolipoprotein B gene; BRCA1 = breast cancer susceptibility 1 gene; IFN1 = interferon 1 gene; MYH2 = myosin heavy chain 2 gene). Summary statistics include *n* = sample size; *S* = segregating sites; *h* = number of haplotypes; *Hd* = haplotype diversity; π = nucleotide diversity. Population growth statistics include Tajima's *D*, Fu's *Fs*, and Ramos-Onsins and Rozas' *R2*. Significance of *D* is reported in parentheses and significance of *Fs* and *R2* are indicated by asterisks (* P ≤0.05; **P ≤0.01***P ≤0.001).

Species/group	*N*	Length (bp)	*S*	*h*	*Hd*	π	*D (P)*	*Fs*	*R2*
All	361	859	190	163	0.985	0.0315	-0.517 (0.357)	-34.076**	0.070
Beringia Clade	129	947	85	46	0.960	0.0137	-0.731 (0.255)	-7.758	0.075
S. preblei	9	726	3	4	0.778	0.0014	-0.359 (0.373)	-1.039	0.167
S. haydeni	11	821	6	6	0.855	0.0031	0.890 (0.815)	-0.976	0.200
Arid-land species	49	957	35	18	0.893	0.0108	0.943 (0.864)	0.486	0.144
S. lyelli	2	1044	0	1	N/A	N/A	N/A	N/A	N/A

S. sp. RM	25	1030	15	13	0.890	0.0032	-0.622 (0.306)	-4.686*	0.099
S. sp. SW	22	957	9	7	0.645	0.0020	-0.695 (0.263)	-1.077	0.104
Tundra/taiga species	60	847	26	20	0.904	0.0040	-1.247 (0.077)	-7.415**	0.060
S. ugyunak	23	847	13	12	0.739	0.0017	-2.073 (0.007)	-9.209***	0.050***
S. pribilofensis	9	981	1	2	0.222	0.0002	-1.088 (0.151)	-0.263	0.314
S. jacksoni	7	1044	5	3	0.524	0.0016	-1.024 (0.184)	0.904	0.284
Siberia species	21	941	7	6	0.779	0.0026	0.808 (0.830)	0.314	0.167
S. portenkoi	11	941	1	2	0.509	0.0005	1.186 (0.867)	1.023	0.255
S. camtschatica	9	1044	5	4	0.583	0.0017	-0.270 (0.421)	0.077	0.152
S. leucogaster	1	634	0	1	N/A	N/A	N/A	N/A	N/A
Southern Clade	232	853	143	119	0.977	0.0133	-1.717 (0.005)	-107.569***	0.038*
S. emarginatus	1	827	0	1	N/A	N/A	N/A	N/A	N/A
S. milleri	7	388	0	1	N/A	N/A	N/A	N/A	N/A
S. cinereus (All)	214	859	129	112	0.975	0.0122	-1.688 (0.012)	-100.859***	0.038*

S. cinereus (west)	122	851	73	58	0.955	0.0039	-2.434 (<0.001)	-70.110***	0.021***
S. cinereus (southwest)	40	894	32	18	0.865	0.0057	-1.200 (0.108)	-4.397	0.071
S. cinereus (midwest)	21	1034	27	17	0.976	0.0038	-1.847 (0.018)	-11.764***	0.067***
S. cinereus (east)	31	919	56	26	0.983	0.0122	-0.907 (0.190)	-10.796***	0.083
S. longirostris	10	755	16	10	1.000	0.0057	-1.137 (0.143)	-6.603***	0.083***
ApoB All	200	500	40	42	0.883	0.0057	-1.721 (0.017)	-31.691***	0.035*
ApoB Beringia Clade	102	500	18	19	0.710	0.0033	-1.585 (0.030)	-11.251***	0.044
ApoB Southern Clade	98	500	28	29	0.885	0.0070	-1.068 (0.121)	-14.557***	0.061
BRCA1 All	200	397	26	27	0.889	0.0082	-0.741 (0.271)	-8.565**	0.062
BRCA1 Beringia Clade	102	397	19	17	0.747	0.0051	-1.280 (0.085)	-6.492*	0.052
BRCA1 Southern Clade	98	397	12	13	0.833	0.0042	-0.749 (0.218)	-4.026*	0.069
IFN1 All	200	345	34	28	0.635	0.0071	-1.695 (0.013)	-14.023***	0.036*
IFN1 Beringia Clade	102	345	12	9	0.169	0.0010	-2.269 (<0.001)	-9.199***	0.033
IFN1 Southern Clade	98	345	28	23	0.887	0.0110	-0.946 (0.182)	-6.313*	0.069

MYH2 All	200	326	47	51	0.920	0.0177	-0.826 (0.224)	-24.543***	0.060
MYH2 Beringia Clade	102	326	27	18	0.798	0.0122	-0.706 (0.284)	-2.210	0.072
MYH2 Southern Clade	98	326	33	38	0.944	0.0163	-0.522 (0.327)	-19.257***	0.078

Table 6

Uncorrected sequence divergence expressed as percentage divergence My^{-1} for the mitochondrial cytochrome *b* gene between each designated species or population within the *Sorex cinereus* complex.

Species/group	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.
1. All	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
2. Beringia Clade	--	--	--	--	--	--	--	--	--	--	--	--	--	5.4	10.4	5.8	5.3	5.5	5.1	5.3	5.4	5.7
3. *S. preblei*	3.2	2.8	3.1	2.7	2.9	2.8	2.7	3.2	2.8	2.8	2.9	2.7	3.2	4.9	13.8	5.5	4.8	5.0	4.5	4.7	4.6	4.9
4. *S. haydeni*	--	1.9	2.6	2.4	1.1	2.0	2.0	2.7	2.3	2.3	2.3	2.3	1.6	5.4	13.5	6.8	5.3	5.5	5.1	5.8	5.8	5.8
5. Arid-land species	--	--	--	--	--	1.3	1.2	1.7	1.4	1.3	1.4	1.3	1.0	5.2	10.7	5.8	5.1	5.4	4.9	5.2	5.3	5.6
6. *S. lyelli*	--	--	--	0.7	2.0	1.1	1.0	1.6	1.2	1.1	1.2	1.0	0.4	5.4	11.2	5.9	5.4	5.5	5.2	5.5	5.4	5.5
7. *S. sp. RM*	--	--	--	--	1.8	0.8	0.7	1.4	1.0	0.8	0.9	0.9	0.5	5.0	11.0	5.7	5.0	5.2	4.9	5.2	5.1	5.3
8. *S. sp. SW*	--	--	--	--	--	1.8	1.7	2.1	1.9	1.9	1.9	1.8	1.6	5.3	10.8	6.0	5.3	5.5	5.0	5.3	5.4	5.8
9. Tundra/taiga species	--	--	--	--	--	--	--	--	--	--	--	--	--	5.6	10.9	5.7	5.6	5.5	5.3	5.1	5.5	5.8
10. *S. ugyunak*	--	--	--	--	--	--	--	0.7	0.3	0.3	0.2	0.4	0.1	5.5	10.8	5.6	5.5	5.4	5.2	5.1	5.4	5.7
11. *S. pribilofensis*	--	--	--	--	--	--	--	--	0.7	0.7	0.7	0.8	0.6	5.7	11.7	6.1	5.7	5.8	5.5	5.6	5.8	6.4
12. *S. jacksoni*	--	--	--	--	--	--	--	--	--	0.4	0.4	0.3	0.3	5.5	11.4	5.7	5.5	5.6	5.3	5.3	5.4	5.9
13. Siberia species	--	--	--	--	--	--	--	--	--	--	--	--	--	5.4	11.3	5.7	5.3	5.5	5.2	5.2	5.3	5.6

14.	*S. portenkoi*	--	--	--	--	--	--	--	--	--	--	--	0.4	0.2	5.5	11.3	5.8	5.5	5.6	5.3	5.3	5.4	5.7
15.	*S. camtschatica*	--	--	--	--	--	--	--	--	--	--	--	--	0.2	5.2	11.3	5.5	5.2	5.3	5.0	5.0	5.1	5.5
16.	*S. leucogaster*	--	--	--	--	--	--	--	--	--	--	--	--	--	5.7	10.7	5.8	5.7	5.9	5.4	5.3	5.7	6.6
17.	Southern Clade	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
18.	*S. emarginatus*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	7.9	7.9	7.6	8.5	8.3	8.0	7.9
19.	*S. milleri*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.8	1.9	1.5	1.4	2.7	3.0
20.	*S. cinereus* (All)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.8
21.	*S. cinereus* (W)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.3	1.7	2.2	2.9
22.	*S. cinereus* (SW)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.1	2.2	2.8
23.	*S. cinereus* (MW)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.2	2.8
24.	*S. cinereus* (E)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.8
25.	*S. longirostris*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

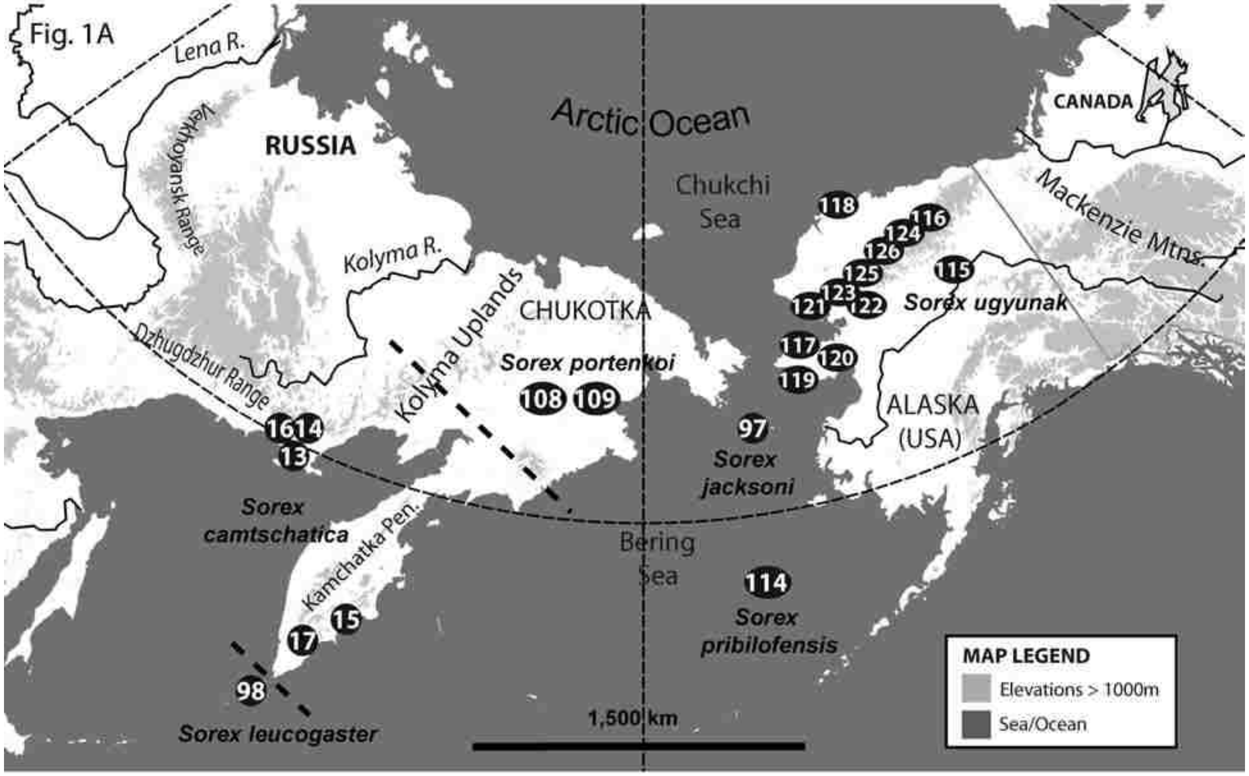

Fig. 1A. Map of the study area (Beringia) indicating localities by number coincident with Appendix A. Map illustrates the distribution of high-latitude Beringian clade species including *S. camtschatica* (13-17), *S. portenkoi* (108, 109), *S. leucogaster* (98), *S. pribilofensis* (114), *S. jacksoni* (97), and *S. ugyunak* (115-126).

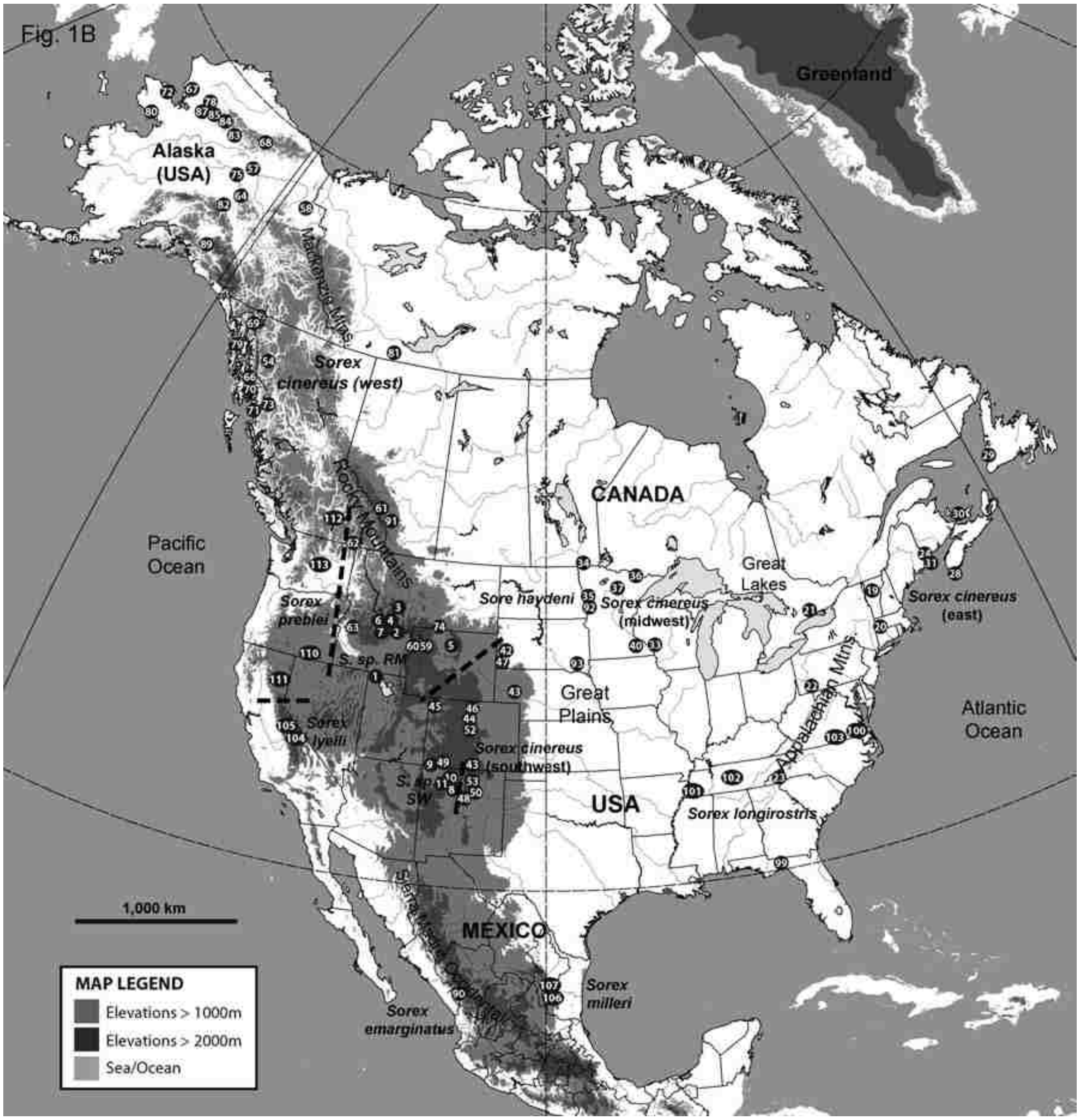

Fig. 1. Maps of the study area (North America) indicating localities by number coincident with Appendix A. Map illustrates the distribution of lower-latitude Beringian clade species including *S. sp. RM* (1-7), *S. preblei*, (110-113), *S. lyelli* (104, 105), *S. sp. SW* (8-11), *S. haydeni* (91-93 95, 96), and distributions of Southern clade species including *S. cinereus* (west; 2, 3, 6, 7, 54, 57-64, 66-75, 78-87, 89), *S. cinereus* (southwest; 42-53), *S. cinereus* (midwest; 32-39), *S. cinereus* (east; 19-27), *S. longirostris* (99-103), *S. emarginatus* (90), *S. milleri* (106, 107).

Fig. 2

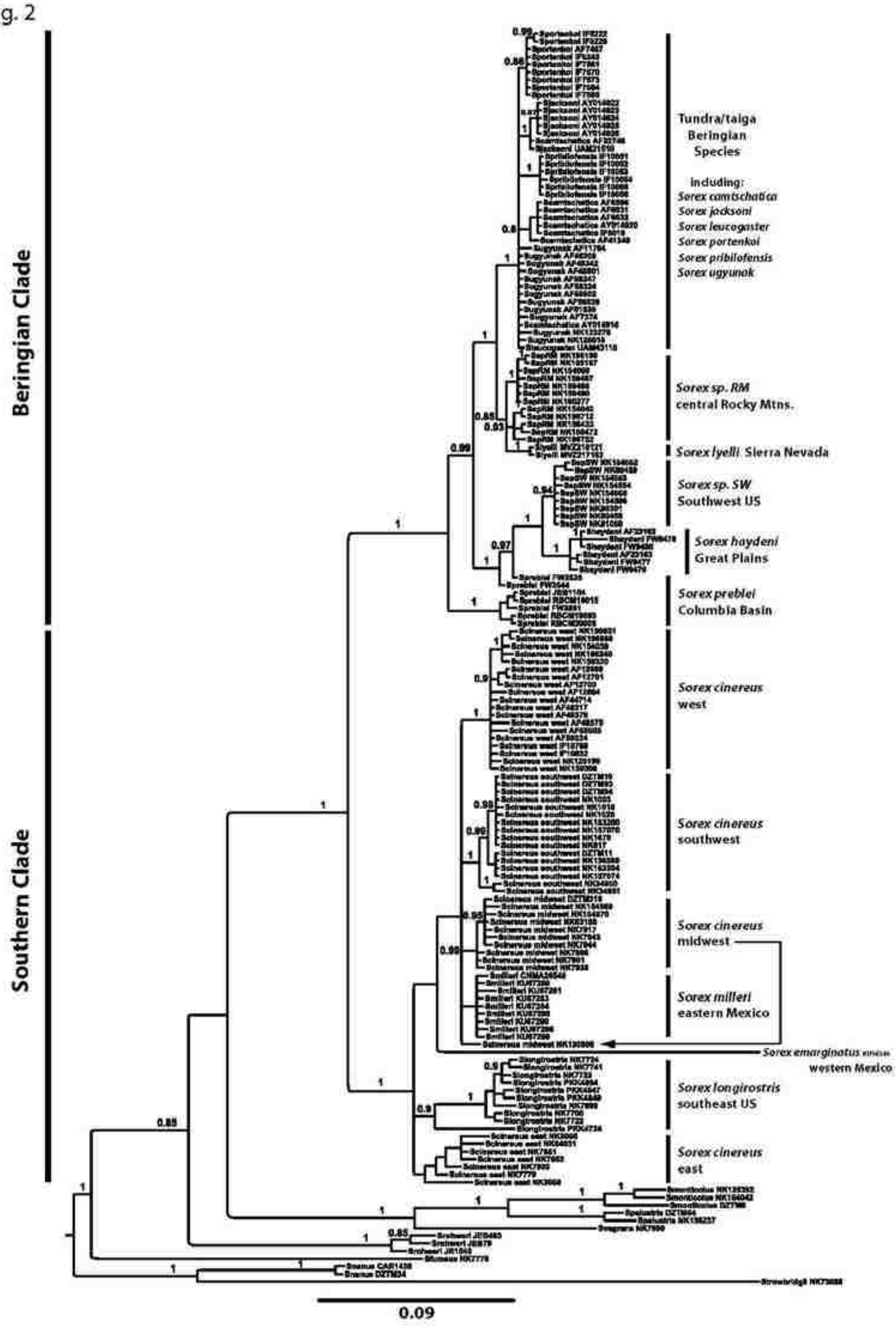

Fig. 2. Mitochondrial cytochrome *b* Bayesian phylogeny for the *cinereus* complex of shrews and associated outgroups. Specimen numbers are coincident with Appendix A. Posterior probability nodal support values <0.8 are not provided.

Fig. 3

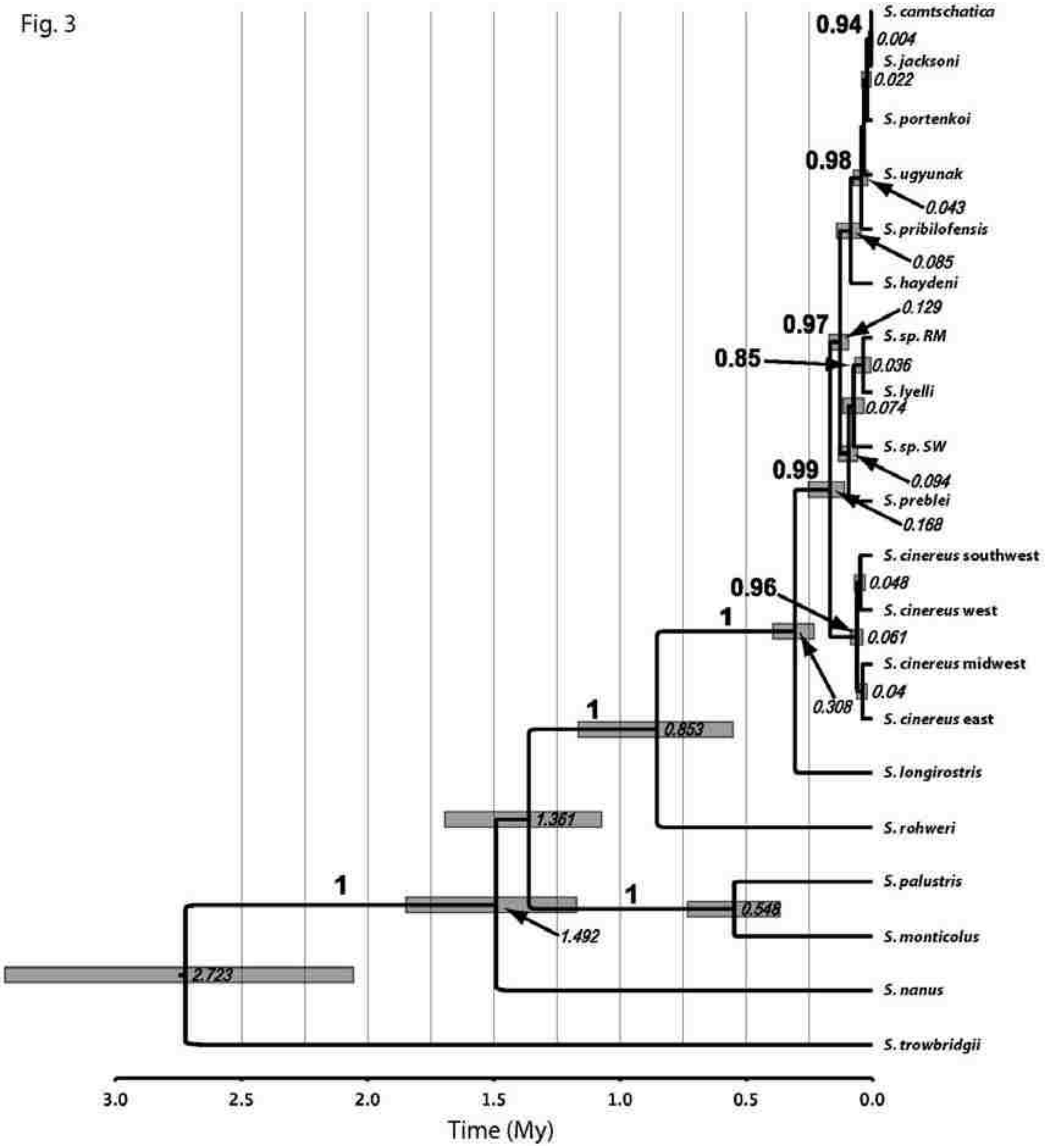

Fig. 3. Species tree estimation from 5 independent loci including mtDNA Cyt *b* gene, and nuclear ApoB, BRCA1, IFN1, and MYH2 genes. Phylogeny provides both posterior probability nodal support values (bold, left of node) and coalescence times (millions of years; italics, right of node). Shaded bars around nodes indicate 95% confidence intervals for coalescence estimates. The topology is presented as ultrametric and proportional to an evolutionary timeline (bottom) that extends from the present (right) to the past (left).

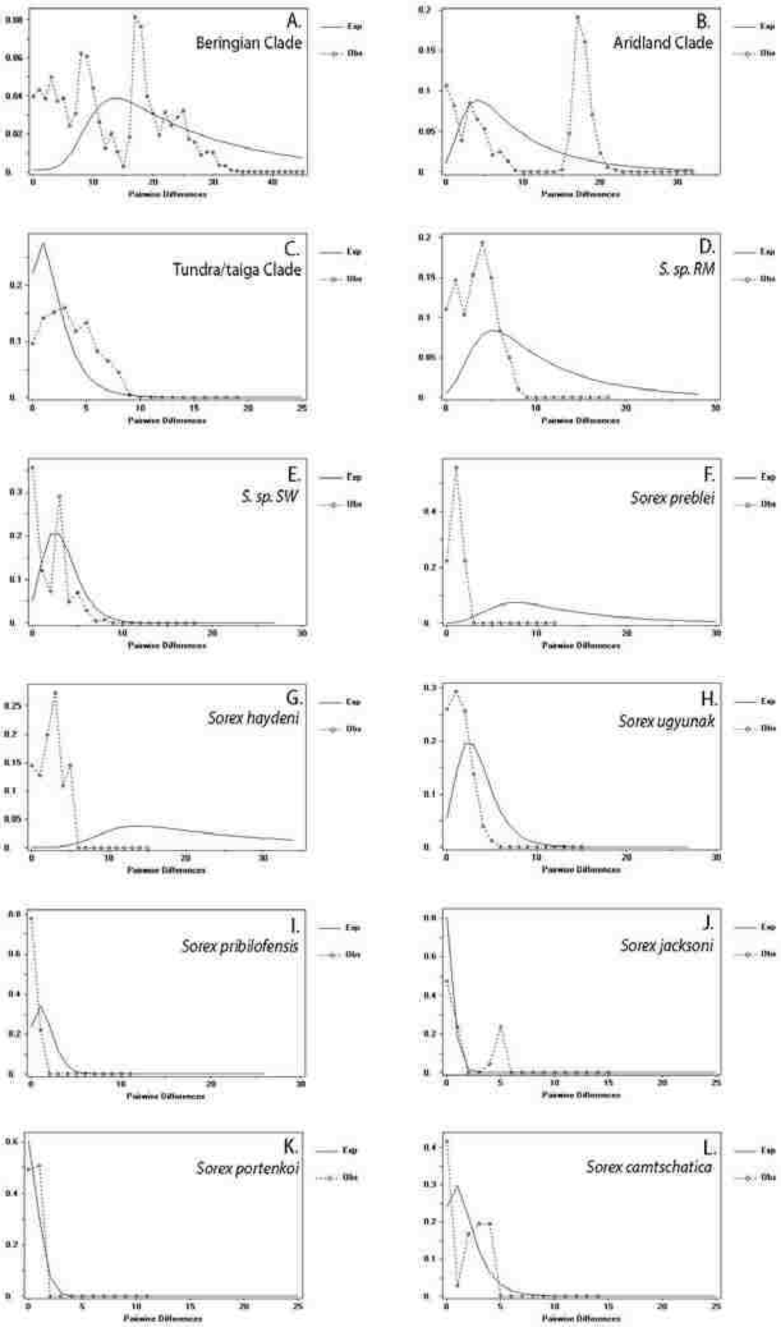

Fig. 4A. Pairwise mismatch distributions for all groups designated within the *cinereus* complex (n ≥7). Y-axis = proportion of DNA sequences that differ by a given number of sites as represented on the x-axis (= number of pairwise differences). Solid lines indicate expected distributions and dotted lines with data points indicate observed distributions.

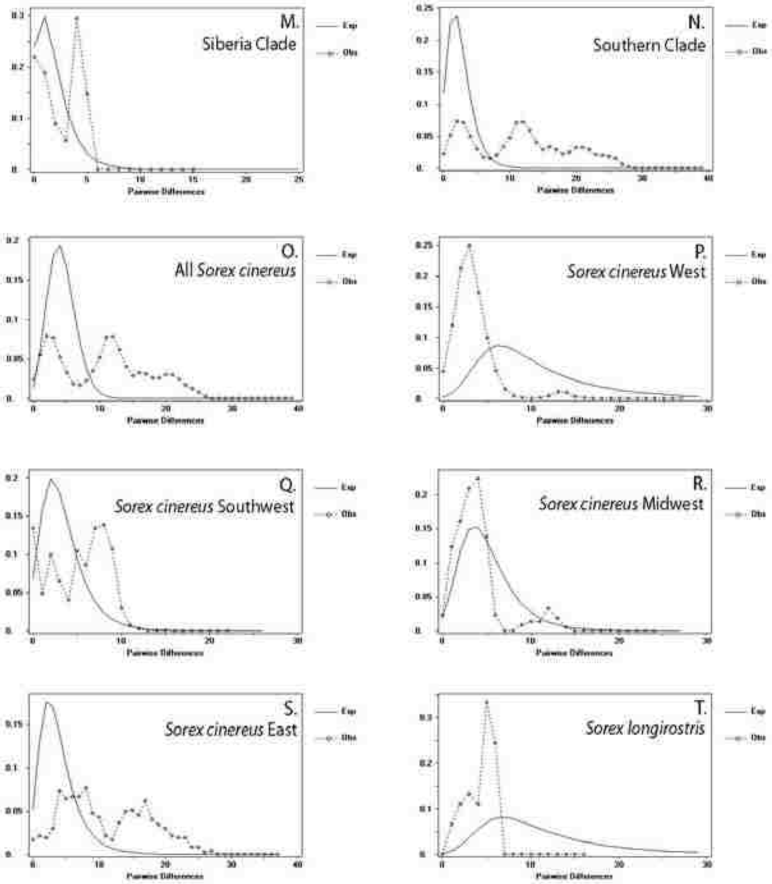

Fig. 4B. Pairwise mismatch distributions for all groups designated within the *cinereus* complex (n ≥7). Y-axis = proportion of DNA sequences that differ by a given number of sites as represented on the x-axis (= number of pairwise differences). Solid lines indicate expected distributions and dotted lines with data points indicate observed distributions.

Appendix -- Specimens examined. Locality numbers correspond to Fig. 1. Specimen and museum catalog numbers correspond to specimens within phylogeny reconstructions.

Species	Specimen #	Museum #	Country	Specific Locality	Locality	Lat	Long	GenBank
S. sp. RM	NK156472	MSB:Mamm:155228	USA	Utah, Raft River, 12 km. W. Yost	1	41.9529	-113.6765	
S. sp. RM	NK156433	MSB:Mamm:155341	USA	Utah, Raft River, 12 km. W. Yost	1	41.9529	-113.6765	
S. sp. RM	NK154058	MSB:Mamm:156236	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417	
S. sp. RM	NK154040	MSB:Mamm:156239	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417	
S. sp. RM	NK159490	MSB:Mamm:156442	USA	Montana, Camp Creek, 23 mi. S, 6 mi. W Butte	3	45.6468	-112.6351	
S. sp. RM	NK159491	MSB:Mamm:156443	USA	Montana, Camp Creek, 23 mi. S, 6 mi. W Butte	3	45.6468	-112.6351	
S. sp. RM	NK159487	MSB:Mamm:156563	USA	Montana, Camp Creek, 23 mi. S, 6 mi. W Butte	3	45.6468	-112.6351	
S. sp. RM	NK159488	MSB:Mamm:156564	USA	Montana, Camp Creek, 23 mi. S, 6 mi. W Butte	3	45.6468	-112.6351	
S. sp. RM	NK195260	MSB:Mamm:224087	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195259	MSB:Mamm:224088	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195278	MSB:Mamm:224090	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195270	MSB:Mamm:224093	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195277	MSB:Mamm:224113	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195276	MSB:Mamm:224116	USA	Montana, Dyce Creek, 4 mi. N, 20 mi. W Dillon	4	45.2788	-113.0364	
S. sp. RM	NK195166	N/A	USA		5			
S. sp. RM	NK195167	N/A	USA		5			
S. sp. RM	NK195218	N/A	USA		5			

S. sp. RM	NK196696	N/A	USA	Idaho, Lemhi Co.	6	44.9355	-113.5533	
S. sp. RM	NK196712	N/A	USA	Idaho, Lemhi Co.	6	44.9436	-113.5532	
S. sp. RM	NK196731	N/A	USA	Idaho, Lemhi Co.	7	44.9759	-113.516	
S. sp. RM	NK196752	N/A	USA	Idaho, Lemhi Co.	6	44.9516	-113.6154	
S. sp. RM	NK196770	N/A	USA	Idaho, Lemhi Co.	7	44.9651	-113.6083	
S. sp. RM	NK196771	N/A	USA	Idaho, Lemhi Co.	7	44.9651	-113.6083	
S. sp. RM	NK196777	N/A	USA	Idaho, Lemhi Co.	7	44.9651	-113.6083	
S. sp. RM	NK196781	N/A	USA	Idaho, Lemhi Co.	7	44.9651	-113.6083	
S. sp. SW	NK80301	DGR:Mamm:31812	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	8	35.8074	-106.5078	
S. sp. SW	NK80460	DGR:Mamm:31942	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	8	35.8074	-106.5078	
S. sp. SW	MSB112714	MSB:Mamm:112714	USA	Colorado, 8 mi N Red Feather Lakes along Sheep Creek	N/A	40.8	-105.59	
S. sp. SW	MSB114228	MSB:Mamm:114228	USA	Colorado, Mesa Verde National Park	9	37.17	-108.42	
S. sp. SW	MSB114845	MSB:Mamm:114845	USA	Colorado, Mesa Verde National Park	9	37.17	-108.42	
S. sp. SW	NK36365	MSB:Mamm:121500	USA	Colorado, Mesa Verde National Park, Waters Canyon	9	37.17	-108.42	
S. sp. SW	NK154552	MSB:Mamm:140357	USA	New Mexico, Jemez Mtns., Santa Clara Peak Rd.	10	36.1692	-106.3598	
S. sp. SW	NK154553	MSB:Mamm:140358	USA	New Mexico, Jemez Mtns.m 7 mi. N, 2 mi. E Jemez Springs	11	35.8686	-106.6271	
S. sp. SW	NK154554	MSB:Mamm:140359	USA	New Mexico, Jemez Mtns., Twin Cabins Canyon	11	35.9896	-106.6347	
S. sp. SW	NK154555	MSB:Mamm:140360	USA	New Mexico, Jemez Mtns., Twin Cabins Canyon	11	35.9896	-106.6347	
S. sp. SW	NK154586	MSB:Mamm:140391	USA	New Mexico, Valles Caldera National Preserve, Valle Toledo	11	35.9722	-106.4722	
S. sp. SW	NK80304	MSB:Mamm:140803	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	12	35.8074	-106.5078	
S. sp. SW	NK80463	MSB:Mamm:140813	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	12	35.8074	-106.5078	
S. sp. SW	NK80458	MSB:Mamm:140819	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	12	35.8074	-106.5078	
S. sp. SW	NK80459	MSB:Mamm:140820	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	12	35.8074	-106.5078	
S. sp. SW	NK42552	MSB:Mamm:141114	USA	New Mexico, 3.2 km N, 16.2 km E Jemez Springs	12	35.8074	-106.5079	AY014935

S. sp. SW	NK42570	MSB:Mamm:87746	USA	New Mexico, 3.2 km N, 16.2 km E Jemez Springs	12	35.8074	-106.5079	
S. sp. SW	NK42640	MSB:Mamm:89326	USA	New Mexico, 3.2 km N, 16.2 km E Jemez Springs	12	35.8074	-106.5079	AY014934
S. sp. SW	NK81059	MSB:Mamm:91007	USA	New Mexico, 3.5 km. N, 16.4 km. E Jemez Springs	12	35.8074	-106.5078	
S. sp. SW	CAR1582	N/A	USA	New Mexico, Sandoval County	12	35.8814	-106.3771	
S. sp. SW	CAR1592	N/A	USA	New Mexico, Sandoval County	12	35.8814	-106.3771	
Sorex camtschatica	AY014920	N/A	Russia	Magadanskaya Oblast, Magadan	13	59.55	150.84	AY014920
Sorex camtschatica	AF6596	UAM:Mamm:29148	Russia	Magadanskaya Oblast, 18 km. N Magadan, Snow Valley	14	59.7333	150.8667	AY014919
Sorex camtschatica	AF6631	UAM:Mamm:29149	Russia	Magadanskaya Oblast, 18 km. N Magadan, Snow Valley	14	59.7333	150.8667	AY014917
Sorex camtschatica	AF6632	UAM:Mamm:29150	Russia	Magadanskaya Oblast, 18 km. N Magadan, Snow Valley	14	59.7333	150.8667	AY014918
Sorex camtschatica	AF32746	UAM:Mamm:73465	Russia	Kamchatskaya Oblast, Kronotskii Preserve	15	54.6667	160.25	
Sorex camtschatica	AF41349	UAM:Mamm:80338	Russia	Magadanskaya Oblast, Alekchen Lakes	16	60.7567	151.7839	
Sorex camtschatica	IF5019	UAM:Mamm:84134	Russia	Magadanskaya Oblast, 28 km. N Gertnera Bay	14	59.7167	150.85	
Sorex camtschatica	AY014916	UWBM:Mamm:39234	Russia	Kamchatskaya Oblast, Kamchatca Peninsula	17	53.25	158.183	AY014916
Sorex cinereus (east)	NK3058	MSB:Mamm:43340	USA	Vermont, 5.8 mi. N Stowe on Hwy 100	19	44.5276	-72.6183	
Sorex cinereus (east)	NK3056	MSB:Mamm:43344	USA	Vermont, 6 mi. N Stowe on Hwy 100	19	44.5302	-72.6167	
Sorex cinereus (east)	NK9136	MSB:Mamm:46895	USA	Massachusetts, 0.3 mi. N, 0.2 mi. W Whately Center	20	42.44	-72.63	
Sorex cinereus (east)	NK7852	MSB:Mamm:53128	Canada	Ontario, Limerick Township, 0.5 mi. N, 3 mi. W Gilmour	21	44.8008	-77.672	
Sorex cinereus (east)	NK7851	MSB:Mamm:53129	Canada	Ontario, Limerick Township, 0.5 mi. N, 3 mi. W Gilmour	21	44.8008	-77.672	
Sorex cinereus (east)	NK7779	MSB:Mamm:53148	USA	Pennsylvania, 2.75 mi. S, 1 mi. W Rector	22	40.1568	-79.2578	
Sorex cinereus (east)	NK7803	MSB:Mamm:53165	USA	Pennsylvania, 2.75 mi. S, 1 mi. W Rector	22	40.1568	-79.2578	
Sorex cinereus (east)	NK64031	MSB:Mamm:74017	USA	North Carolina, Great Smoky Mountain National Park	23	35.6	-83.4167	
Sorex cinereus (east)	DQ788817	N/A	Canada	New Brunswick, Campobello Island	24	44.88	-66.98	DQ788817
Sorex cinereus (east)	NK191334	N/A	USA		25			
Sorex cinereus (east)	NK191335	N/A	USA		26			

Sorex cinereus (east)	NK191336	N/A	USA		27			
Sorex cinereus (east)	NK191339	N/A	USA					
Sorex cinereus (east)	NK191341	N/A	USA					
Sorex cinereus (east)	NK191342	N/A	USA					
Sorex cinereus (east)	NK191343	N/A	USA					
Sorex cinereus (east)	NK191346	N/A	USA					
Sorex cinereus (east)	NK191347	N/A	USA					
Sorex cinereus (east)	NK191349	N/A	USA					
Sorex cinereus (east)	NK191350	N/A	USA					
Sorex cinereus (east)	NK191360	N/A	USA					
Sorex cinereus (east)	NK191366	N/A	USA					
Sorex cinereus (east)	NK191377	N/A	USA					
Sorex cinereus (east)	NK191378	N/A	USA					
Sorex cinereus (east)	NK191663	N/A	USA					
Sorex cinereus (east)	DQ788805	ROM:Mamm:109378	Canada	Nova Scotia, Bon Portage Island	28	43.47	-65.75	DQ788805
Sorex cinereus (east)	DQ788811	ROM:Mamm:109628	Canada	Newfoundland, St. Georges	29	48.37	-58.56	DQ788811
Sorex cinereus (east)	DQ788812	ROM:Mamm:109633	Canada	Newfoundland, St. Georges	29	48.37	-58.56	DQ788812
Sorex cinereus (east)	DQ788815	ROM:Mamm:110067	Canada	Prince Edward Island, Bay View	30	46.47	-63.42	DQ788815
Sorex cinereus (east)	DQ788816	ROM:Mamm:110313	Canada	New Brunswick, Deer Island	31	44.98	-66.98	DQ788816
Sorex cinereus (midwest)	NK34953	MSB:Mamm:125040	USA	Nebraska, S. side of Roundup Lake	32	41.7501	-102.4154	
Sorex cinereus (midwest)	NK154569	MSB:Mamm:140374	USA	Wisconsin, Lookout Farm, Abrahamson Rd.	33	44.4377	-91.5258	
Sorex cinereus (midwest)	NK154570	MSB:Mamm:140375	USA	Wisconsin, Lookout Farm, Abrahamson Rd.	33	44.4377	-91.5258	
Sorex cinereus (midwest)	NK7896	MSB:Mamm:53108	Canada	Manitoba, 5 mi. W Woodbridge	34	49.2125	-96.2625	
Sorex cinereus (midwest)	NK7901	MSB:Mamm:53121	Canada	Manitoba, 1 mi. N, 5 mi. E Marchand	34	49.4583	-96.275	

Sorex cinereus (midwest)	NK7917	MSB:Mamm:53124	Canada	Manitoba, 1 mi. N, 5 mi. E Marchand	34	49.4583	-96.275	
Sorex cinereus (midwest)	NK7943	MSB:Mamm:53213	USA	Minnesota, 0.5 mi. S, 6.5 mi. W Hawley	35	46.8719	-96.4575	AY014941
Sorex cinereus (midwest)	NK7944	MSB:Mamm:53214	USA	Minnesota, 0.5 mi. S, 6.5 mi. W Hawley	35	46.8719	-96.4575	
Sorex cinereus (midwest)	NK63188	MSB:Mamm:73418	USA	Minnesota, Voyageurs National Park, Ash River	36	48d26'	92d	FJ667512
Sorex cinereus (midwest)	NK7932	MSB:Mamm:53136	USA	Minnesota, 1 mi. S, 4 mi. E Bena	37	47.3302	-94.1221	
Sorex cinereus (midwest)	NK7938	MSB:Mamm:53210	USA	Minnesota, 0.5 mi. S, 6.5 mi. W Hawley	35	46.8719	-96.4575	
Sorex cinereus (midwest)	NK191337	N/A	USA		38			
Sorex cinereus (midwest)	NK191345	N/A	USA		39			
Sorex cinereus (midwest)	NK191348	N/A	USA					
Sorex cinereus (midwest)	NK191367	N/A	USA					
Sorex cinereus (midwest)	NK191368	N/A	USA					
Sorex cinereus (midwest)	NK191369	N/A	USA					
Sorex cinereus (midwest)	NK191370	N/A	USA					
Sorex cinereus (midwest)	NK191371	N/A	USA					
Sorex cinereus (midwest)	NK191372	N/A	USA					
Sorex cinereus (midwest)	NK191373	N/A	USA					
Sorex cinereus (midwest)	NK191375	N/A	USA					
Sorex cinereus (midwest)	AF25384	UAM:Mamm:50408	USA	Minesota, Goodhue County	40	44.2014	-92.6461	AY014952
Sorex cinereus (midwest)	DZTM316				41			
Sorex cinereus (southwest)	NK130806	DGR:Mamm:10002148	USA	South Dakota, Blck Hills, Grizzly Campground	42	43.8723	-103.4405	
Sorex cinereus (southwest)	DZTM10	DMNS:Mamm:11007	USA	Colordo, Apishapa Creek	43	37.3411	-105.0006	
Sorex cinereus (southwest)	DZTM11	DMNS:Mamm:11008	USA	Colordo, Apishapa Creek	43	37.3411	-105.0006	
Sorex cinereus (southwest)	MSB110370	MSB:Mamm:110370	USA	Colorado, Fraser Experimental Forest	44	39.84	-105.9	
Sorex cinereus (southwest)	MSB110371	MSB:Mamm:110371	USA	Colorado, Fraser Experimental Forest	44	39.84	-105.9	

Sorex cinereus (southwest)	MSB110372	MSB:Mamm:110372	USA	Colorado, Fraser Experimental Forest	44	39.84	-105.9
Sorex cinereus (southwest)	MSB110606	MSB:Mamm:110606	USA	Colorado, Rocky Reservoir, NW side of Diamond Peak	45	40.96	-108.9
Sorex cinereus (southwest)	MSB112615	MSB:Mamm:112615	USA	Colorado, 8 mi N Red Feather Lakes along Sheep Creek	46	40.8	-105.59
Sorex cinereus (southwest)	MSB112617	MSB:Mamm:112617	USA	Colorado, 8 mi N Red Feather Lakes along Sheep Creek	46	40.8	-105.59
Sorex cinereus (southwest)	MSB112618	MSB:Mamm:112618	USA	Colorado, 8 mi N Red Feather Lakes along Sheep Creek	46	40.8	-105.59
Sorex cinereus (southwest)	MSB120522	MSB:Mamm:120522	USA	South Dakota, Jewel Cave National Monument	47	43.74	-103.83
Sorex cinereus (southwest)	NK34951	MSB:Mamm:125039	USA	Nebraska, S. side of Roundup Lake	32	41.7501	-102.4154
Sorex cinereus (southwest)	NK34952	MSB:Mamm:125044	USA	Nebraska, S side Crane Lake	32	41.7252	-102.3777
Sorex cinereus (southwest)	NK136589	MSB:Mamm:145905	USA	New Mexico, Stewart Lake	48	35.8298	-105.7241
Sorex cinereus (southwest)	NK156090	MSB:Mamm:154920	USA	Colorado, 4 km. N Lemon Reservoir	48	37.454	-107.6801
Sorex cinereus (southwest)	NK153200	MSB:Mamm:193276	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596
Sorex cinereus (southwest)	NK153304	MSB:Mamm:198343	USA	New Mexico, Santa Fe Mtns., 3.5 km W Elk Mountain	50	35.7713	-105.5931
Sorex cinereus (southwest)	NK1018	MSB:Mamm:41108	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe	51	35.7605	-105.7957
Sorex cinereus (southwest)	NK1001	MSB:Mamm:41109	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe	51	35.7605	-105.7957
Sorex cinereus (southwest)	NK1017	MSB:Mamm:41111	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe	51	35.7605	-105.7957
Sorex cinereus (southwest)	NK1025	MSB:Mamm:41114	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe	51	35.7605	-105.7957
Sorex cinereus (southwest)	NK1020	MSB:Mamm:41117	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe	51	35.7605	-105.7957
Sorex cinereus (southwest)	NK1003	MSB:Mamm:41110	USA	New Mexico, 5 mi. N, 8 mi. E Santa Fe		35.7605	-105.7957
Sorex cinereus (southwest)	NK1037	MSB:Mamm:41158	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357
Sorex cinereus (southwest)	NK1041	MSB:Mamm:41160	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357
Sorex cinereus (southwest)	NK1081	MSB:Mamm:41162	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357
Sorex cinereus (southwest)	NK1039	MSB:Mamm:41164	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357
Sorex cinereus (southwest)	NK1086	MSB:Mamm:41167	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357
Sorex cinereus (southwest)	NK1070	MSB:Mamm:41168	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357

Sorex cinereus (southwest)	NK1077	MSB:Mamm:41169	USA	Colorado, 3.5 mi. S, 1.5 mi. W Ward	52	40.0213	-105.5357	
Sorex cinereus (southwest)	NK808	MSB:Mamm:41237	USA	New Mexico, 4 mi. N Tres Ritos	53	36.1718	-105.4649	
Sorex cinereus (southwest)	NK817	MSB:Mamm:41241	USA	New Mexico, 4 mi. N Tres Ritos	53	36.1718	-105.4649	
Sorex cinereus (southwest)	NK1670	MSB:Mamm:43504	USA	New Mexico, 8 mi. N, 6 mi. E Tres Ritos	54	36.247	-105.4086	
Sorex cinereus (southwest)	NK1675	MSB:Mamm:43509	USA	New Mexico, 8 mi. N, 6 mi. E Tres Ritos	54	36.247	-105.4086	
Sorex cinereus (southwest)	AF395485	N/A	USA	Unknown	55	Unknown	Unknown	AF395485
Sorex cinereus (southwest)	AF395486	N/A	USA	Unknown	55	Unknown	Unknown	AF395486
Sorex cinereus (southwest)	DZTM93	N/A	USA	Colorado	56	36.058	-105.463	
Sorex cinereus (southwest)	DZTM94	N/A	USA	Colorado	56	36.058	-105.463	
Sorex cinereus (southwest)	NK157067	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157068	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157069	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157070	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157071	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157073	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK157074	N/A	USA	New Mexico, Santa Fe Mtns., 1.5 km N. Elk Mountain	50	35.7818	-105.5596	
Sorex cinereus (southwest)	NK34950	MSB:Mamm:125041	USA	Nebraska, NE side of Island Lake	32	41.7447	-102.3824	
Sorex cinereus (west)	NK123278	MSB:Mamm:143101	USA	Alaska, Finger Mountain on Dalton Hwy	57	66.35	-150.46	
Sorex cinereus (west)	NK125271	MSB:Mamm:145344	Canada	Yukon Territory, Rock River Campground	58	66.914	-136.3511	
Sorex cinereus (west)	NK125208	MSB:Mamm:145583	Canada	Yukon Territory, 2 mi. S. Rock River on Hwy. 5	58	66.8862	-136.3383	
Sorex cinereus (west)	NK125209	MSB:Mamm:145584	Canada	Yukon Territory, 2 mi. N Rock River on Hwy. 7	58	66.9487	-136.2345	
Sorex cinereus (west)	NK125217	MSB:Mamm:145610	Canada	Yukon Territory, 0.25 mi. N. Rock River on Hwy 5	58	66.9198	-136.3511	
Sorex cinereus (west)	NK125190	MSB:Mamm:145673	Canada	Yukon Territory, 2 mi. N Rock River on Hwy. 5	58	66.9487	-136.2345	
Sorex cinereus (west)	NK125191	MSB:Mamm:145674	Canada	Yukon Territory, 2 mi. N Rock River on Hwy. 6	58	66.9487	-136.2345	

Sorex cinereus (west)	NK125192	MSB:Mamm:145675	Canada	Yukon Territory, 2 mi. N Rock River on Hwy. 7	58	66.9487	-136.2345
Sorex cinereus (west)	NK156261	MSB:Mamm:155030	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156252	MSB:Mamm:155087	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156240	MSB:Mamm:155139	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156340	MSB:Mamm:155203	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156320	MSB:Mamm:155290	USA	Wyoming, Cora	60	42.95	-110.03
Sorex cinereus (west)	NK156341	MSB:Mamm:155307	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156343	MSB:Mamm:155311	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156344	MSB:Mamm:155312	USA	Wyoming, Squaw Creek, 5 km S., 7.5 km E. Alpine	59	43.121	-110.9255
Sorex cinereus (west)	NK156790	MSB:Mamm:155663	Canada	British Columbia, Stikine River at Glenora	60	57.8368	-131.6765
Sorex cinereus (west)	NK156820	MSB:Mamm:155813	Canada	British Columbia, Stikine River at Hudson Flats	60	57.8203	-131.3983
Sorex cinereus (west)	NK156840	MSB:Mamm:155869	Canada	British Columbia, Stikine River at Glenora	60	57.8368	-131.6765
Sorex cinereus (west)	NK156841	MSB:Mamm:155870	Canada	British Columbia, Stikine River at Glenora	60	57.8368	-131.6765
Sorex cinereus (west)	NK159016	MSB:Mamm:156127	Canada	Alberta, Kananaskis Field Station	61	51.0279	-115.0342
Sorex cinereus (west)	NK159087	MSB:Mamm:156139	Canada	Alberta, Kananaskis Field Station	61	51.0279	-115.0342
Sorex cinereus (west)	NK159089	MSB:Mamm:156211	Canada	Alberta, Kananaskis Field Station	61	51.0279	-115.0342
Sorex cinereus (west)	NK159091	MSB:Mamm:156213	Canada	Alberta, Kananaskis Field Station	61	51.0279	-115.0342
Sorex cinereus (west)	NK154061	MSB:Mamm:156242	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417
Sorex cinereus (west)	NK154062	MSB:Mamm:156243	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417
Sorex cinereus (west)	NK154045	MSB:Mamm:156246	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417
Sorex cinereus (west)	NK154046	MSB:Mamm:156254	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417
Sorex cinereus (west)	NK154047	MSB:Mamm:156255	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417
Sorex cinereus (west)	NK159306	MSB:Mamm:156387	Canada	British Columbia, Nancy Green Summit	62	49.202	-117.8971
Sorex cinereus (west)	NK159489	MSB:Mamm:156441	USA	Montana, Camp Creek, 23 mi. S, 6 mi. W Butte	3	45.6468	-112.6351

Sorex cinereus (west)	NK154063	MSB:Mamm:156505	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417	
Sorex cinereus (west)	NK154059	MSB:Mamm:156583	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417	
Sorex cinereus (west)	NK159334	MSB:Mamm:156594	Canada	British Columbia, Bluberry Creek	62	49.258	-117.9395	
Sorex cinereus (west)	NK154048	MSB:Mamm:156601	USA	Montana, Price Creek, 9 mi. E. of Monida	2	44.5659	-112.1417	
Sorex cinereus (west)	NK195343	MSB:Mamm:225114	USA	Idaho, Clear Creek, 6 mi. N, 2 mi. E Lowman	63	44.1675	-115.5633	
Sorex cinereus (west)	NK195347	MSB:Mamm:225125	USA	Idaho, Clear Creek, 6 mi. N, 2 mi. E Lowman	63	44.1675	-115.5633	
Sorex cinereus (west)	AY014944	N/A	USA	Alaska, Fairbanks	64	64.85	-147.72	AY014944
Sorex cinereus (west)	NK196651	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196654	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196657	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196659	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196669	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196677	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196684	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196685	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196686	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196688	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196690	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196691	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196692	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196695	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196704	N/A	USA	Idaho, Lemhi Co.	6	44.935	-113.5528	
Sorex cinereus (west)	NK196709	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196713	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	

Sorex cinereus (west)	NK196714	N/A	USA	Idaho, Lemhi Co.	6	44.9508	-113.6134	
Sorex cinereus (west)	NK196728	N/A	USA	Idaho, Lemhi Co.	7	44.9759	-113.516	
Sorex cinereus (west)	NK196736	N/A	USA	Idaho, Lemhi Co.	7	44.9759	-113.516	
Sorex cinereus (west)	NK196737	N/A	USA	Idaho, Lemhi Co.	7	44.9759	-113.516	
Sorex cinereus (west)	NK196747	N/A	USA	Idaho, Lemhi Co.	6	44.9516	-113.6154	
Sorex cinereus (west)	NK196750	N/A	USA	Idaho, Lemhi Co.	6	44.9516	-113.6154	
Sorex cinereus (west)	NK196751	N/A	USA	Idaho, Lemhi Co.	6	44.9516	-113.6154	
Sorex cinereus (west)	NK196753	N/A	USA	Idaho, Lemhi Co.	6	44.9516	-113.6154	
Sorex cinereus (west)	NK196756	N/A	USA	Idaho, Lemhi Co.	6	44.9509	-113.6134	
Sorex cinereus (west)	NK196762	N/A	USA	Idaho, Lemhi Co.	65	44.6762	-113.6172	
Sorex cinereus (west)	NK196775	N/A	USA	Idaho, Lemhi Co.	7	44.9701	-113.6018	
Sorex cinereus (west)	NK196778	N/A	USA	Idaho, Lemhi Co.	7	44.9701	-113.6018	
Sorex cinereus (west)	NK196779	N/A	USA	Idaho, Lemhi Co.	7	44.9701	-113.6018	
Sorex cinereus (west)	NK196780	N/A	USA	Idaho, Lemhi Co.	7	44.9701	-113.6018	
Sorex cinereus (west)	DQ788814	ROM:Mamm:109706	Canada	Alberta, Gost River	61	51.31	-115.19	DQ788814
Sorex cinereus (west)	DQ788813	ROM:Mamm:110124	Canada	Alberta, Kananaskis	61	50.79	-114.8	DQ788813
Sorex cinereus (west)	AF2687	UAM:Mamm:20754	USA	Alaska, Earl West Marsh	66	56.2667	-132.1333	
Sorex cinereus (west)	AF1028	UAM:Mamm:22096	USA	Alaska, Little Cr., Downstream Red Dog Rd.	67	67.8833	-163.1667	
Sorex cinereus (west)	AF2785	UAM:Mamm:22986	USA	Alaska, Trout Lake	66	56.35	-132.3333	
Sorex cinereus (west)	AF5127	UAM:Mamm:23047	USA	Alaska, Chandalar Shelf	68	68.0667	-149.5833	AY014942
Sorex cinereus (west)	AF4587	UAM:Mamm:23660	USA	Alaska, Haines	69	59.15	-135.35	AY014950
Sorex cinereus (west)	AF4732	UAM:Mamm:23765	USA	Alaska, Cleveland Peninsula, Union Bay	70	55.75	-132.1833	AY014947
Sorex cinereus (west)	AF4300	UAM:Mamm:24030	USA	Alaska, Misty Fiords, 2 km. NW Willard Inlet	71	54.8167	-130.65	AY014949
Sorex cinereus (west)	AF7378	UAM:Mamm:33126	USA	Alaska, Grayling Creek Shelter	72	66.1292	-165.1292	

Sorex cinereus (west)	AF7380	UAM:Mamm:33127	USA	Alaska, Seward Pen, Grayling Creek Shelter	72	66.1292	-165.1292	AY014943
Sorex cinereus (west)	AF15804	UAM:Mamm:34511	USA	Alaska, Anita Bay	66	56.1833	-132.45	
Sorex cinereus (west)	AF12700	UAM:Mamm:35396	Canada	British Columbia, Nash River Valley	73	55.3319	-128.9653	
Sorex cinereus (west)	AF12701	UAM:Mamm:35397	Canada	British Columbia, Nash River Valley	73	55.3319	-128.9653	
Sorex cinereus (west)	AF14892	UAM:Mamm:36762	USA	Montana, Carbon County	74	45.52	-108.82	AY014948
Sorex cinereus (west)	AF24304	UAM:Mamm:47276	USA	Alaska, Kanuti National Wildlife Refuge	75	66.3195	-151.7913	AY014951
Sorex cinereus (west)	AF12688	UAM:Mamm:52330	Canada	British Columbia, Nash River Valley	76	55.3319	-128.9653	
Sorex cinereus (west)	AF12694	UAM:Mamm:52331	Canada	British Columbia, Nash River Valley	76	55.3319	-128.9653	
Sorex cinereus (west)	AF46378	UAM:Mamm:55636	USA	Alaska, Serpentine Hot Springs	72	65.8525	-164.6959	
Sorex cinereus (west)	AF46218	UAM:Mamm:55856	USA	Alaska, W bank Rabbit Creek	77	67.5155	-163.5864	
Sorex cinereus (west)	AF46217	UAM:Mamm:55945	USA	Alaska, E bank Rabbit Creek	77	67.5152	-163.5834	
Sorex cinereus (west)	AF46233	UAM:Mamm:55954	USA	Alaska, E bank Rabbit Creek	77	67.5152	-163.5834	
Sorex cinereus (west)	AF48575	UAM:Mamm:56469	USA	Alaska, Aniralik Lake	78	68.2097	-159.8314	
Sorex cinereus (west)	AF34313	UAM:Mamm:73775	USA	Alaska, Salt Lake Bay	79	57.95	-135.6333	
Sorex cinereus (west)	AF36106	UAM:Mamm:75251	USA	Alaska, confluence of Fox River and Lil Creek	80	64.7792	-163.7944	
Sorex cinereus (west)	AF7436	UAM:Mamm:76416	USA	Alaska, Seward Pen, Grayling Creek Shelter	72	66.1292	-165.1292	AY014945
Sorex cinereus (west)	AF36131	UAM:Mamm:76984	USA	Alaska, confluence of Fox River and Lil Creek	80	64.7792	-163.7944	
Sorex cinereus (west)	AF44714	UAM:Mamm:77186	Canada	Northwest Territories, Fort Liard	81	60.39	-117.29	
Sorex cinereus (west)	AF45234	UAM:Mamm:78012	USA	Alaska, Kiki Creek	82	63.7261	-149.055	
Sorex cinereus (west)	AF59024	UAM:Mamm:79394	USA	Alaska, SE side Walker Lake	83	67.1008	-154.2709	
Sorex cinereus (west)	AF58964	UAM:Mamm:79563	USA	Alaska, SE side Walker Lake	83	67.1008	-154.2709	
Sorex cinereus (west)	AF58580	UAM:Mamm:79575	USA	Alaska, S side Takahula Lake	83	67.3457	-153.6451	
Sorex cinereus (west)	AF58634	UAM:Mamm:81776	USA	Alaska, SE side Takahula Lake	83	67.35	-153.6451	
Sorex cinereus (west)	AF58503	UAM:Mamm:82015	USA	Alaska, E side of Lake Isiak	84	67.7193	-156.1382	

Sorex cinereus (west)	IF10766	UAM:Mamm:83455	USA	Alaska, Baird Mountains	85	67.6022	-159.7897	
Sorex cinereus (west)	AF1571	UAM:Mamm:89373	USA	Alaska, Alaska Peninsula, N side of surprise lake	86	56.935	-158.1083	AY014946
Sorex cinereus (west)	IF10899	UAM:Mamm:93330	USA	Alaska, Waring Mountains	87	67.0144	-158.4972	
Sorex cinereus (west)	IF10796	UAM:Mamm:93333	USA	Alaska, Baird Mountains, headwaters Akillik River	88	67.4824	-158.2472	
Sorex cinereus (west)	IF10798	UAM:Mamm:93336	USA	Alaska, Baird Mountains, headwaters Akillik River	88	67.4824	-158.2472	
Sorex cinereus (west)	IF10787	UAM:Mamm:93388	USA	Alaska, Baird Mountains, headwaters Akillik River	88	67.4824	-158.2472	
Sorex cinereus (west)	IF10757	UAM:Mamm:93402	USA	Alaska, Baird Mountains	88	67.6022	-159.7897	
Sorex cinereus (west)	IF10838	UAM:Mamm:93412	USA	Alaska, Waring Mountains	87	67.0144	-158.4972	
Sorex cinereus (west)	IF10768	UAM:Mamm:93438	USA	Alaska, Baird Mountains	88	67.6022	-159.7897	
Sorex cinereus (west)	IF10832	UAM:Mamm:93456	USA	Alaska, Waring Mountains	87	67.0144	-158.4972	
Sorex cinereus (west)	IF10805	UAM:Mamm:93458	USA	Alaska, Baird Mountains, headwaters Akillik River	88	67.4824	-158.2472	
Sorex cinereus (west)	IF10816	UAM:Mamm:93468	USA	Alaska, Baird Mountains, headwaters Akillik River	88	67.4824	-158.2472	
Sorex cinereus (west)	IF10829	UAM:Mamm:93478	USA	Alaska, Waring Mountains	87	67.0144	-158.4972	
Sorex cinereus (west)	IF10733	UAM:Mamm:94544	USA	Alaska, Baird Mountains	88	67.6047	-159.7982	
Sorex cinereus (west)	UWBM39644	UWBM:Mamm:39644	USA	Alaska, Glennallen	89	62.1	-145.62	EU088304
Sorex cinereus (west)	UWBM39645	UWBM:Mamm:39645	USA	Alaska, Glennallen	89	62.1	-145.62	EU088305
Sorex emarginatus	KU54346	KUM:Mamm:54346	Mexico	Durango, Las Adjuntas	90	23.6592	-105.575	
Sorex fumeus	NK7778	MSB:Mamm:53147	USA	Pennsylvania, 2.75 mi. S, 1 mi. W Rector	N/A	40.1568	-79.2578	
Sorex haydeni	AJ000458	DZT:Mamm:420	Canada	Alberta, Okotoks	91	50.7255	-113.9706	AJ000458
Sorex haydeni	AJ000459	DZT:Mamm:421	Canada	Alberta, Okotoks	91	50.7255	-113.9706	AJ000459
Sorex haydeni	NK7942	MSB:Mamm:53212	USA	Minnesota, Clay County	92	46.858	-96.457	AY014938
Sorex haydeni	DQ788827	ROM:Mamm:109790	Canada	Alberta, Okotoks	91	50.7255	-113.9706	DQ788827
Sorex haydeni	DQ788828	ROM:Mamm:109821	Canada	Alberta, Okotoks	91	50.7255	-113.9706	DQ788828
Sorex haydeni	AF23162	UAM:Mamm:50345	USA	South Dakota, Bluestem Game Production Area	93	43.67	-98.14	AY014939

Sorex haydeni	AF23163	UAM:Mamm:50346	USA	Minnesota, Davison County	94	43.67	-98.14	AY014940
Sorex haydeni	FW9477				95			
Sorex haydeni	FW9478				96			
Sorex haydeni	FW9479							
Sorex haydeni	FW9480							
Sorex jacksoni	UAM21508	UAM:Mamm:21508	USA	St. Lawrence Island, W end Koozata Lagoon (S. Kangee)	97	63.4333	-171.1	
Sorex jacksoni	UAM21510	UAM:Mamm:21510	USA	St. Lawrence Island, W end Koozata Lagoon (S. Kangee)	97	63.4333	-171.1	
Sorex jacksoni	AY014922	UAM:Mamm:21518	USA	Alaska, St. Lawrence Island	97	63.43	-170.32	AY014922
Sorex jacksoni	AY014923	UAM:Mamm:21520	USA	Alaska, St. Lawrence Island	97	63.43	-170.32	AY014923
Sorex jacksoni	AY014924	UAM:Mamm:21521	USA	Alaska, St. Lawrence Island	97	63.43	-170.32	AY014924
Sorex jacksoni	AY014925	UAM:Mamm:21522	USA	Alaska, St. Lawrence Island	97	63.43	-170.32	AY014925
Sorex jacksoni	AY014926	UAM:Mamm:21526	USA	Alaska, St. Lawrence Island	97	63.43	-170.32	AY014926
Sorex leucogaster	UAM43110	UAM:Mamm:43110	Russia	Sakhalinskaya Oblast, Paramushir Island	98	50.19	155.62	
Sorex longirostris	NK7699	MSB:Mamm:53220	USA	Florida, 1 mi. S, 4 mi. W Iamonia	99	30.6554	-84.2316	
Sorex longirostris	NK7700	MSB:Mamm:53221	USA	Florida, 1 mi. S, 4 mi. W Iamonia	99	30.6554	-84.2316	
Sorex longirostris	NK7722	MSB:Mamm:53222	USA	Florida, 1 mi. S, 4 mi. W Iamonia	99	30.6554	-84.2316	
Sorex longirostris	NK7741	MSB:Mamm:53224	USA	Virginia, 1/2 mi. S, 7.5 mi. W Whaleyville	100	36.5809	-76.8199	
Sorex longirostris	NK7724	MSB:Mamm:53225	USA	Virginia, 1/2 mi. S, 7.5 mi. W Whaleyville	100	36.5809	-76.8199	
Sorex longirostris	NK7723	MSB:Mamm:53227	USA	Virginia, 8 mi. W Whaleyville	100	36.5862	-76.8339	
Sorex longirostris	PKK 4724	N/A	USA	Tennessee, Shelby Co., E.J. Meeman Biological St.	101	35.329	-90.071	
Sorex longirostris	PKK4849	N/A	USA	Tennessee, Parry County NE Alvin Creek, Hwy 100	102	35.95	-87.137	
Sorex longirostris	PKK4894	N/A	USA	Tennessee, Parry County NE Alvin Creek, Hwy 101	102	35.95	-87.137	
Sorex longirostris	NDM3113		USA	Virginia, Mecklenburg County	103	36.68	-78.38	AY014953
Sorex longirostris	PKK4847		USA	Tennessee, Perry County, NE Alvin Creek, Hwy 100	102	35.95	-87.137	AY014954

Sorex lyelli	MVZ216121	MVZ:Mamm:216121	USA	California, Bohler Creek	104	37.9003	-119.1298	
Sorex lyelli	MVZ217162	MVZ:Mamm:217162	USA	California, upper Kerrick Meadow, Yosemite National Park	105	38.1221	-119.4816	
Sorex milleri	CNMA26549	CNMA:Mamm:26549	Mexico	Nuevo Leon, Cerro Potosi	106	24.86	-100.25	
Sorex milleri	KU67281	KUM:Mamm:67281	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex milleri	KU67283	KUM:Mamm:67283	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex milleri	KU67284	KUM:Mamm:67284	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex milleri	KU67290	KUM:Mamm:67290	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex milleri	KU67296	KUM:Mamm:67296	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex milleri	KU67299	KUM:Mamm:67299	Mexico	Coahuila, San Antonio de las Alazanas	107	25.2722	-100.371	
Sorex monticolus	DZTM9	DMNS:Mamm:11006	USA	Colordo, Apishapa Creek	N/A	37.3411	-105.0006	
Sorex monticolus	NK125392	MSB:Mamm:145441	USA	Alaska, Palmer Creek Road	N/A	60.8312	-149.5359	
Sorex monticolus	NK154042	MSB:Mamm:156241	USA	Montana, Price Creek, 9 mi. E. of Monida	N/A	44.5659	-112.1417	
Sorex nanus	CAR 1438	N/A	USA	New Mexico, Sandoval County	N/A	35.8814	-106.3771	
Sorex nanus	DZTM24				N/A			
Sorex portenkoi	AF7467	UAM:Mamm:33259	Russia	Chukotka, Vsadnik Bay	108	64.38	-173.3	AY014921
Sorex portenkoi	IF7561	UAM:Mamm:83828	Russia	Chukotka, Ulhum River	108	64.4167	-172.5333	
Sorex portenkoi	IF7570	UAM:Mamm:83837	Russia	Chukotka, Ulhum River	108	64.4167	-172.5333	
Sorex portenkoi	IF7573	UAM:Mamm:83840	Russia	Chukotka, Ulhum River	108	64.4167	-172.5333	
Sorex portenkoi	IF7584	UAM:Mamm:83851	Russia	Chukotka, Ulhum River	108	64.4167	-172.5333	
Sorex portenkoi	IF7585	UAM:Mamm:83852	Russia	Chukotka, Ulhum River	108	64.4167	-172.5333	
Sorex portenkoi	IF5222	UAM:Mamm:84282	Russia	Chukotka, 2km SSE confluence Volchya River and Liman Sea	109	64.8164	177.5456	
Sorex portenkoi	IF5228	UAM:Mamm:84286	Russia	Chukotka, 2km SSE confluence Volchya River and Liman Sea	109	64.8164	177.5456	
Sorex portenkoi	IF5243	UAM:Mamm:84290	Russia	Chukotka, 2km SSE confluence Volchya River and Liman Sea	109	64.8164	177.5456	
Sorex portenkoi	IF5187	UAM:Mamm:84327	Russia	Chukotka, 3 km SSE confluence Volchya River and Liman Sea	109	64.8056	177.5542	

Sorex portenkoi	IF5187	UAM:Mamm:84327	Russia	Chukotka, 2km SSE confluence Volchya River and Liman Sea	109	64.8164	177.5456	
Sorex preblei	NK656	MSB:Mamm:40717	USA	Oregon, Harney County, 28 mi. S, 5 mi. E Burns	110	43.1808	-118.9534	AY014937
Sorex preblei	NK652	MSB:Mamm:40718	USA	Oregon, Harney County, 28 mi. S, 5 mi. E Burns	110	43.1808	-118.9534	AY014936
Sorex preblei	DQ086479	MVZ:Mamm:206292	USA	California, Lassen Volcanic National Park	111	40.4775	-121.4319	DQ086479
Sorex preblei	FW3861	N/A	USA	Oregon, Harney County	110	42.7	-118.5	
Sorex preblei	RBCM19015	RBCM:Mamm:19015	Canada	British Columbia	112	50.3198	-119.2692	
Sorex preblei	RBCM19993	RBCM:Mamm:19993	Canada	British Columbia	112			
Sorex preblei	RBCM20005	RBCM:Mamm:20005	Canada	British Columbia	112			
Sorex preblei	JEB1104	UWBM:Mamm:78306	USA	Washington, Douglas County	113	47.57	-120.02	EU088306
Sorex pribilofensis	IF10051	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	IF10052	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	IF10053	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	IF10054	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	IF10055	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	IF10056	N/A	USA	Alaska, St. Paul Island	114	57.18	-170.25	
Sorex pribilofensis	AY014931	UAM:Mamm:22593	USA	Alaska, St. Paul Island	114	57.18	-170.25	AY014931
Sorex pribilofensis	AY014932	UAM:Mamm:22594	USA	Alaska, St. Paul Island	114	57.18	-170.25	AY014932
Sorex pribilofensis	AY014933	UAM:Mamm:22596	USA	Alaska, St. Paul Island	114	57.18	-170.25	AY014933
Sorex rohweri	JEB79	UWBM	USA	Washington	N/A			
Sorex rohweri	JR1545	UWBM	USA	Washington	N/A			
Sorex trowbridgii	NK73088	MSB:Mamm:83485	USA	Washington, Naval Submarine Base, Bangor	N/A	47.7191	-122.7185	
Sorex ugyunak	NK123279	MSB:Mamm:143102	USA	Alaska, Finger Mountain on Dalton Hwy	115	66.35	-150.46	
Sorex ugyunak	NK125515	MSB:Mamm:143121	USA	Alaska, Lake Galbraith Campground	116	68.45	-149.47	
Sorex ugyunak	AF7390	UAM:Mamm:33128	USA	Alaska, Seward Pen, Grayling Creek Shelter	117	66.1292	-165.1292	AY014928

Sorex ugyunak	AF7431	UAM:Mamm:33139	USA	Alaska, Seward Pen, Grayling Creek Shelter	117	66.1292	-165.1292	AY014930
Sorex ugyunak	AF7213	UAM:Mamm:34141	USA	Alaska, Lake Galbraith	116	68.4928	-149.4925	AY014929
Sorex ugyunak	AF11764	UAM:Mamm:36761	USA	Alaska, Point Barrow	118	71.35	-156.6	AY014927
Sorex ugyunak	AF7374	UAM:Mamm:46994	USA	Alaska, Kougarok Airfield, mi. 83.2 Taylor Highway	119	65.425	-164.6433	
Sorex ugyunak	AF46295	UAM:Mamm:55565	USA	Alaska, Kuzitrin Lake	120	65.3894	-163.2645	
Sorex ugyunak	AF46229	UAM:Mamm:55850	USA	Alaska, W bank Rabbit Creek	121	67.5155	-163.5864	
Sorex ugyunak	AF46208	UAM:Mamm:56121	USA	Alaska, W bank of Situkuyok River	121	67.2046	-163.1624	
Sorex ugyunak	AF48342	UAM:Mamm:56384	USA	Alaska, Kaluich Creek Upland	122	67.6639	-158.1906	
Sorex ugyunak	AF48601	UAM:Mamm:56475	USA	Alaska, Aniralik Lake	123	68.2097	-159.8314	
Sorex ugyunak	AF61835	UAM:Mamm:78479	USA	Alaska, Fortress Mountain	124	68.5809	-152.9476	
Sorex ugyunak	AF58479	UAM:Mamm:81918	USA	Alaska, N of Lake Isiak	125	67.7274	-156.1588	
Sorex ugyunak	AF58502	UAM:Mamm:82014	USA	Alaska, E side of Lake Isiak	125	67.7193	-156.1382	
Sorex ugyunak	AF58507	UAM:Mamm:82017	USA	Alaska, N of Lake Isiak	125	67.7274	-156.1588	
Sorex ugyunak	AF58513	UAM:Mamm:82018	USA	Alaska, N of Lake Isiak	125	67.7274	-156.1588	
Sorex ugyunak	AF58528	UAM:Mamm:82020	USA	Alaska, E side of Lake Isiak	125	67.7193	-156.1382	
Sorex ugyunak	AF58324	UAM:Mamm:82073	USA	Alaska, N side of Lake Tulilik	126	68.1168	-154.1202	
Sorex ugyunak	AF58247	UAM:Mamm:82135	USA	Alaska, N side of Lake Tulilik	126	68.1168	-154.1202	
Sorex ugyunak	AF58385	UAM:Mamm:82243	USA	Alaska, N side of Lake Tulilik	126	68.1168	-154.1202	
Sorex ugyunak	AF58421	UAM:Mamm:82247	USA	Alaska, N side of Lake Tulilik	126	68.1168	-154.1202	
Sorex ugyunak	UWBM39815	UWBM:Mamm:39815	USA	Alaska, Barrow	118	71.28	-156.79	EU088307
Sorex vagrans	NK7990	MSB:Mamm:53248	USA	California, 14 mi. N, 2.5 mi. W Bridgeport	N/A	38.4749	-119.2606	

Fig. S1A. Independent Cyt b genealogy used to infer species tree relationships. Specimen numbers are coincident with the Appendix.

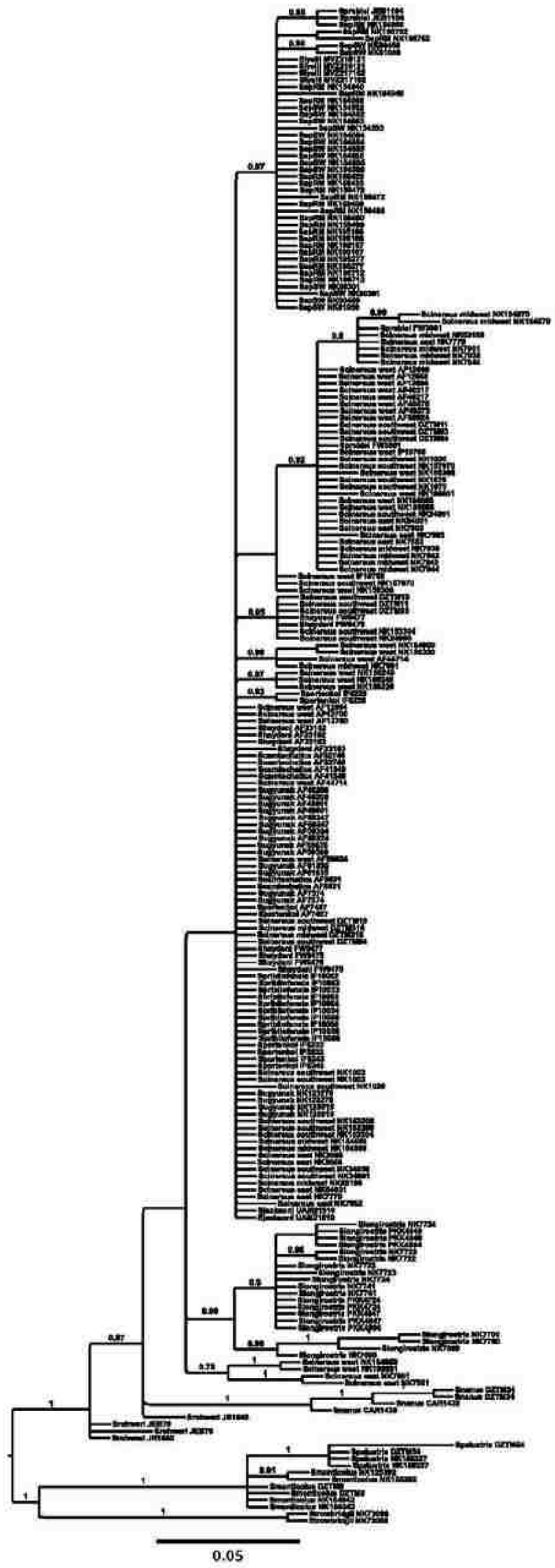

Fig. S1B. Independent ApoB nuclear genealogy used to infer species tree relationships. Specimen numbers are coincident with the Appendix.

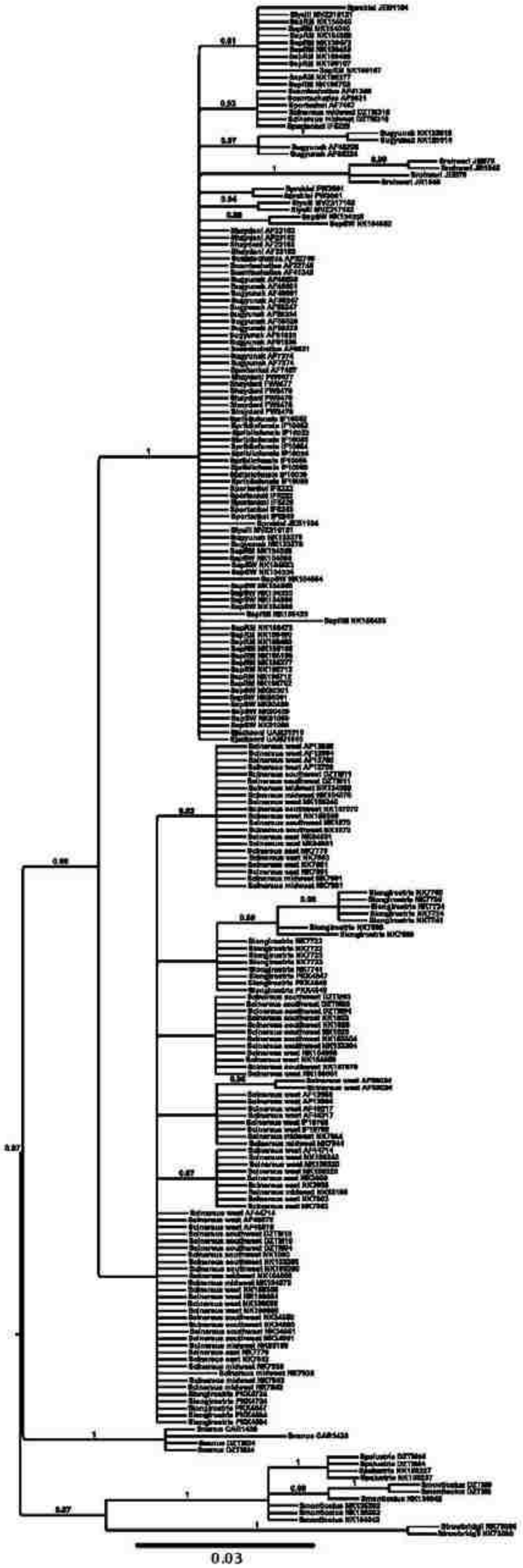

Fig. S1C. Independent BRCA1 nuclear genealogy used to infer species tree relationships. Specimen numbers are coincident with the Appendix.

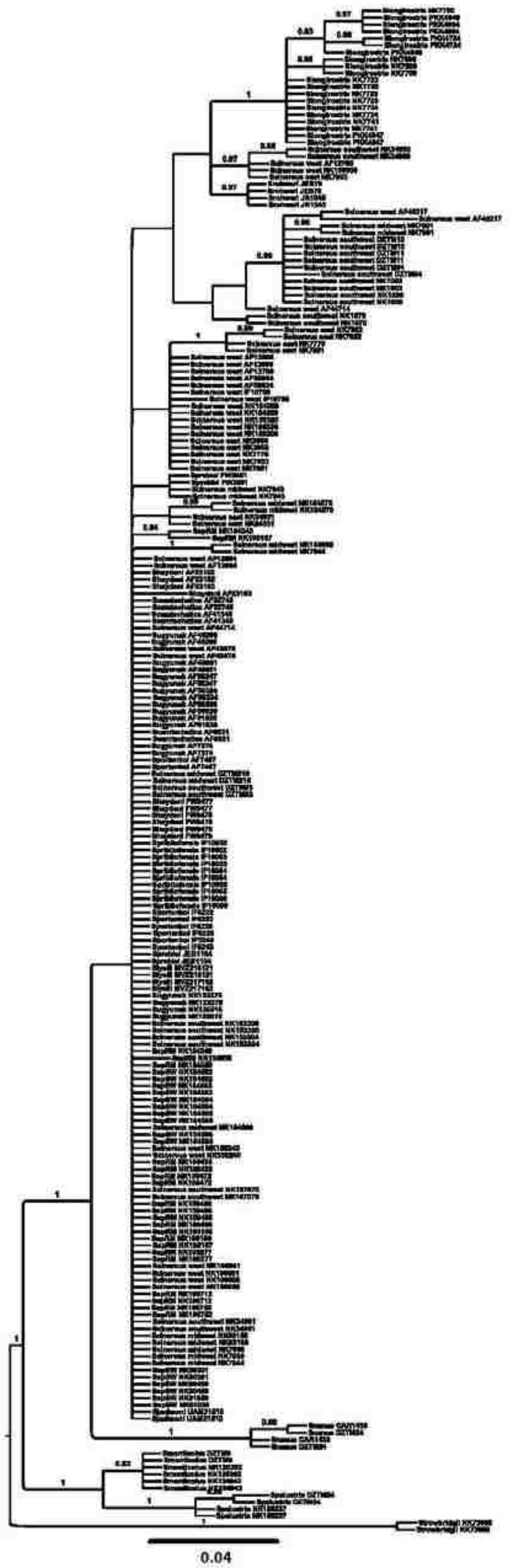

Fig. S1D. Independent IFN1 nuclear genealogy used to infer species tree relationships. Specimen numbers are coincident with the Appendix.

Fig. S1E. Independent MYH2 nuclear genealogy used to infer species tree relationships. Specimen numbers are coincident with the Appendix.

CONCLUSIONS

In this dissertation, I presented four independent but complimentary studies that highlight some of the theory and methodologies currently employed to investigate the evolutionary and ecological responses of organisms to a changing environment. Shrews (genus *Sorex*) are an excellent group for molecular phylogenetic and phylogeographic investigations as they are a pervasive and diverse mammalian component of most northern hemisphere ecosystems. Shrews are small and have high metabolic rates and rapid turnover that jointly may translate to relatively fast evolution for mammals. Although small, they are often abundant and can respond dramatically to environmental change. However, population demographics have revealed variable strategies both within and among species that exhibit rapid movement and population size change, or alternatively persistence and stability, collectively reflecting highly variable ecological associations and life histories.

In the first chapter previous taxonomy reflecting two distinct species divided at the Bering Strait was not supported suggesting instead that transcontinental movement from Siberia into North America was as recent as the latest glacial maximum and population isolation within a single species was due to subsequent climate warming and sea level change. Genetic evidence from an extremely broad distribution illustrated multiple biogeographic regions associated with differentiation and in particular a significant phylogeographic break within Europe, all reflecting a history of southward population contraction and isolation in multiple refugia during glacial cold phases.

An investigation of *Sorex tundrensis* in the second chapter was performed to provide a further line of evidence for patterns revealed by *S. minutissimus*, both species with a closely overlapping and Holarctic current distribution. The results of this second study however revealed a different evolutionary response to climate change, indicating persistence instead of movement in response to change although localized population size change was evident through time. Explicit hypothesis testing revealed a comparatively deeper timeframe for inter-population divergence within *S. tundrensis* discordant with a cyclical glacial periodicity. As revealed by habitat affinities to riparian and river floodplain corridors, isolated populations likely persisted independent of prevailing environmental change. A variable response among different species highlights community turnover through time. In addition, *S. tundrensis* displayed distinct population structure within Beringia providing evidence that this broad area potentially constitutes multiple sub-refugia.

With the addition of multiple other small mammal taxa in the third chapter, it was again evident within a comparative framework that Beringia constituted a highly heterogeneous area through time and species could respond differently to climate change depending on their ecological affinities. Certain species including *S. tundrensis* persisted within Beringia for extended periods in multiple discrete areas. Other species including *S. minutissimus* expanded rapidly through Beringia as favorable climate allowed, but were only recently split across the Bering Strait. Finally other Arctic (cold- and xeric-adapted) species such as the lemmings likely persisted in associated tundra areas of Beringia and may have benefited from glacial phases during the Pleistocene. The results strongly indicate that diversification across Beringia has been ongoing over multiple glacial episodes and that speciation within a Pleistocene timeframe has been possible through repeated cyclical allopatry and extended isolation through this variable landscape.

The final chapter, again in a comparative sense, focused on multiple species within the *cinereus* complex of shrews but instead of being largely co-distributed, these species form a patchwork of parapatric or allopatric distributions through Beringia and most of North America. Distinct separation between the species despite relatively shallow genetic divergence reflects ecological differences that are coincident with phylogenetic relationships revealed here through a multi-locus assessment of the evolutionary history of this group. Early sorting into very generally mesic- versus xeric-adapted species resulted in an out of phase response to environmental change, all again associated with a Pleistocene climate regime. Diversification within this group reflects a rapid contemporary radiation and dynamic spatial evolution to occupy a vast current distribution. The scenario of differentiation through time presented here represents an impressive sequence of events even when only considering the influence of climate and geography and should be considered a valuable template for the consequences of environmental change shaping diversity and distribution through this broad study area.

With respect to our current climate crisis, it is valuable to notice how species will respond variably to a changing environment. While some species will benefit from climate warming through population expansion, others will experience population contraction. In both instances this may be accompanied by significant range shifts and isolation/reconnection dynamics. Zones of contact through the history of diversification of a given group can lead to periodic introgression and can significantly influence differentiation among populations or incipient species (and our interpretation of relationships). Yet other species have diverged largely independently of major environmental fluctuations. A firm knowledge of how species will respond to a realized set of environmental conditions can be obtained from analyzing the genetic signatures of past variability. A comparative assessment over multiple taxa, with thorough geographic coverage obtained from rigorous field sampling, will help us predict how future changes may affect communities in any given region. Ultimately conservation of the various components of biodiversity will rely on a firm understanding of the dynamics of environmental and community change.