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LIVING ON THE EDGE: A COMPARATIVE PHYLOGEOGRAPHIC STUDY OF REFUGIAL AND INSULAR FRAGMENTATION

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LIVING ON THE EDGE: A COMPARATIVE PHYLOGEOGRAPHIC STUDY OF REFUGIAL AND INSULAR FRAGMENTATION

by

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B.S., Biology,
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DISSERTATION

Submitted in Partial Fulfillment of the
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DEDICATION

To my family: For your continued support, encouragement and confidence in me.

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LIVING ON THE EDGE: A COMPARATIVE PHYLOGEOGRAPHIC STUDY OF REFUGIAL AND INSULAR FRAGMENTATION

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Abstract

Pleistocene glacial-interglacial cycles resulted in population isolation that led to inter- and intra- specific genetic divergence in many North American species. The magnitude of isolation also influenced species response to these climatic changes and set the stage for contemporary gene flow. We can refine our understanding of species response to historical climate change by identifying regions of ice-free persistence and refugia during glacial maxima, and geographic locations and genetic dynamics of post-glacial secondary contact. This dissertation examines the role of glacial cover, geographic barriers, habitat fragmentation as a result of changes in sea level, and insularity on the contemporary genetic structure of three widespread, co-distributed, and ecologically distinct small mammals across western North America, with emphasis on the Pacific Northwest. Previous work on long-tailed voles (*Microtus longicaudus*), northwestern deer mice (*Peromyscus keeni*), and dusky shrews (*Sorex monticolus*) was used to formulate hypotheses of geographic distribution of genetic variation, timing of divergence, and regions of glacial persistence. This dissertation uses multilocus genetic data and historical climatic conditions to address these hypotheses. I identify regions of glacial persistence, the effects of historical sea levels on island connectivity, and regions of post-glacial secondary contact of divergent lineages within *M. longicaudus*, *P. keeni* and *S. monticolus*. Additionally, I assess levels of endemism for the islands of Southeast Alaska. The collective findings of this dissertation improve our understanding of effects of historical range fragmentation and insularity on contemporary genetic diversity.

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CHAPTER 1

Introduction

Genetic variability and taxonomic diversity are fundamental components of effective conservation planning. Understanding drivers of evolutionary diversification is important because it better equips ecosystem managers to make preemptive, rather than reactive, decisions. Increased knowledge of past responses of species to vicariant events (e.g., glaciation, orogeny), as well as an understanding of current population dynamics, allow us to investigate how and why genetic variation is partitioned across the landscape (Carstens *et al.* 2013; Soltis *et al.* 1997).

One of the primary drivers of extant boreal diversity was Quaternary (2.6 Ma to present) climatic fluctuation, especially the strong glacial cycles of the Late Pleistocene that have been implicated in the diversification of many North American species (Carstens *et al.* 2005; Godbout *et al.* 2008; Lee-Yaw *et al.* 2007). Repeated glacial and interglacial periods caused isolation due to fragmentation of species, resulting in lineage divergence of allopatric populations (Guralnick 2007; Knowles & Richards 2005; Small *et al.* 2003) and ultimately initiating speciation across a diverse set of organisms (Loehr *et al.* 2006; Mengel 1964; Soltis *et al.* 1997).

The Laurentide and Cordilleran ice sheets (Carrara *et al.* 2007; Dyke & Prest 1987; Roberts 1991) of the Last Glacial Maxima (LGM) covered most of North America with ice free regions to the north (Beringia) and south (Hafner & Sullivan 1995; Marr *et al.* 2008). Additionally, as a result of lower sea levels, exposed continental shelf along the west coast of the ice has been hypothesized to support additional refugia (Burg *et al.*

2005; MacDonald & Cook 1996) including the Alexander Archipelago (AA) of Southeast Alaska (Carrara *et al.* 2007; Mobley 1988). Post-glacial recolonization provided the opportunity for fragmented populations to reestablish geographic contact. The genetic footprints of these species help to clarify biogeographic history (Brunsfeld *et al.* 2001; Hewitt 1996; Riddle 1996).

Other than the few exceptions for extremely wide ranging species (Aubry *et al.* 2009; Fleming & Cook 2002; Godbout *et al.* 2008), most glacial persistence was either in Beringian for high-latitude and Holarctic species (Brunhoff *et al.* 2003) or in the southern portions of the continent (Good & Sullivan 2001). Species with wide geographic ranges provide the opportunity to explore the possibility of persistence in multiple refugia and ice-free regions. Additionally, paleoendemics for British Columbian Haida Gwaii and the AA are proposed (Conroy & Cook 2000; Fleming & Cook 2002) as a result of the existence of coastal refugia (Fladmark 1979). However, this has been a point of contention (Byun *et al.* 1999; Byun *et al.* 1997; Demboski *et al.* 1999). Although these high latitude islands are continental islands, they present unusual colonization and extinction dynamics as a result of glacial cover and recolonization from not only the mainland, but also coastal refugia (Whittaker & Fernández-Palacios 2007).

The major goal of my dissertation is to explore the role of historic climate in shaping genetic diversity and post-glacial dynamics of divergent lineages of three widespread, ecologically distinct, small mammals across both western North America and within the AA. I use a multifaceted approach that utilizes multiple independent loci and incorporates Geographic Information Systems (GIS), hypothesis testing, and statistical phylogeography to address questions related to evolutionary drivers of diversification in

Microtus longicaudus (long-tailed vole) *Peromyscus keeni* (northwest deer mouse), and *Sorex monticolus* (dusky shrew).

Chapter 2 uses multilocus DNA sequences to explore the genetic effects of glacial cover and test previous estimates of divergence among major mitochondrial DNA clades of *M. longicaudus*. Additionally, I explore current levels of gene flow among these lineages across the highly fragmented AA. I focus on the geographic region of Haines, Alaska to evaluate admixture and incomplete lineage sorting between the two northern mtDNA lineages. Lastly, genetic data, genetic diversity, demographic statistics, and species distribution models (SMDs) are used to determine the geographic origin of each cyt *b* clade.

Chapter 3 surveys genetic variation at the northwestern extent of *Peromyscus* in North America with respect to the effects of glacial fragmentation and persistence in multiple refugia. Previous work (Hogan *et al.* 1993; Lucid & Cook 2007; Wike 1998) suggests secondary contact in Yukon and identified cryptic genetic forms. I expand sampling across the geographic range and add independent loci to estimate levels of genetic differentiation and current genetic exchange, and then assess differentiation within the context of climatic niche predictions.

Chapter 4 is a comparative study that focuses on the impacts of historical climate and extent of insularity on current genetic variation across the islands of the Alexander Archipelago. By exploring genetic signatures across three ecologically distinct, co-distributed species, I aim to determine the effects of island size and isolation (MacArthur & Wilson 1967) in a high latitude islands system on genetic diversity (Johnson *et al.* 2000; Lomolino *et al.* 2006). Furthermore, I use SDMs and paleo-shoreline reconstructions to formally test the possibility of glacial coastal refugia. The species-specific Chapters 2 and 3 provide the current genetic landscape necessary to more thoroughly explore contemporary dynamics.

Chapter 5 summarizes the findings of my dissertation, while highlighting important parallels among chapters 2, 3 and 4. I emphasize the conservation and management implications of each chapter and potential ecosystem management challenges for fragmented habitats, like that of the AA. In the face of future climate change, as confounded by anthropogenic land use, it is imperative we provide an understanding of how historic climate change impacted organisms in Northwest North America.

My doctoral dissertation contributes to the fundamental understanding of the need for comprehensive, multi-taxa, multi-technique approach to phylogeography with regard to the influences of historical climate. If we hope to preserve species and communities under future climate change, it is imperative we appreciate the diversity and complexity of species response to past changes.

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CHAPTER 2

Phylogeographic effects of refugia and post-glacial pathways in *Microtus longicaudus*

Abstract

Vicariant barriers as a result of Quaternary climate fluctuations resulted in population isolation and intraspecific divergence in many North American species. Identifying where these populations were isolated, the dynamics of post-glacial recolonization and subsequent contact, and effects of insularity can help us understand the drivers of evolution in northern taxa. Incorporating a multilocus approach under a Bayesian coalescent framework, we explored signatures of divergence and post-glacial colonization within a wide-ranging vole, *Microtus longicaudus* (n=143), to identify glacial refugia, effects of insularity, and dynamics of secondary contact. Through a combination of genetic data and species distribution models, we found that both historical climate and geographic topography influenced contemporary genetic variation in this species. Multiple geographic locations for glacial persistence were identified, including Beringian (Northern), Southeast Alaska (Coastal), and southern continental North American regions. We detected high levels of island endemism and new locations of secondary contact between the Island and Northern clades. Integrative phylogeographic approaches helped identify previously undocumented refugia and intralineage genetic diversity.

Introduction

Population isolation can occur through vicariant events, including but not limited to glaciation and orogeny. Climatic fluctuations of the Quaternary (2.6 million years ago to present) included repeated Pleistocene glacial-interglacial cycles which affected divergence and speciation processes (Carstens *et al.* 2005; Godbout *et al.* 2008; Lee-Yaw *et al.* 2007). During glacial phases, large portions of North America were covered by glaciers, including the most recent Laurentide and Cordilleran ice sheets (Carrara *et al.* 2007; Dyke & Prest 1987; Roberts 1991), resulting in major geographic rearrangements of temperate and arctic species (Lyons 2003). In addition to northern (e.g., Beringia) and southern ice-free areas, there were refugial regions along the coast of British Columbia and in southeastern Alaska (Loehr *et al.* 2006; Pielou 1991; Sawyer *et al*. submitted).

As glaciers receded, deglaciated areas were recolonized by previously isolated populations. Across various taxa, the most common regions of secondary contact of divergent lineages which are postulated to have persisted both south of the ice and in coastal refugia are restricted to regions in southern Canada or the main continent in the United States (Galbreath *et al.* 2009; Good & Sullivan 2001; Nielson *et al.* 2001). Additionally, a few studies have reported contact between lineages in the northern extent of Southeast Alaska near Haines (Conroy & Cook 2000; Demboski & Cook 2001). We hypothesize this northern contact zone reflects post-glacial contact between coastal refugial populations of limited mobility with either a rapidly colonizing southern continental lineage or a northern refugial population that persisted in Beringia.

Vicariant events can lead to changes in demography and allopatric isolation, which impact genetic relationships among postglacial populations (Hewitt 1996; Ibrahim *et al.* 1996; Lessa *et al.* 2003). Refugial populations generally experienced population bottlenecks (Rand 1954; Shafer *et al.* 2010; Stewart *et al.* 2010). Descendent populations in previously glaciated regions show signs of rapid population expansion (Hundertmark *et al.* 2002; Lessa *et al.* 2003; Walker *et al.* 2009) and have reduced levels of genetic variation with little intralineage diversification compared to conspecific lineages that persisted in non-glaciated regions (Hayes & Harrison 1992; Hewitt 2004; Marr *et al.* 2012). However, reconstructing recolonization patterns is complex (Godbout et al. 2008) because of the presence of cryptic refugia (Shafer *et al.* 2010) or phalanx expansion (Hewitt 2000). Also, genetic variation may be higher than expected if there are multiple lineages in a given region, or there is admixture due to secondary contact between lineages expanding from independent refugia into the same region (Fleming & Cook 2002; Marr *et al.* 2008; Petit *et al.* 2003).

The broad range of *M. longicaudus*, spanning 35 degrees of latitude across western North America, provided an excellent opportunity to explore how historic events and insularity shaped endemism and geographic genetic variation across western North America. *Microtus longicaudus* occupies montane and mesic herbaceous habitats (Lomolino *et al.* 1989; Smolen & Keller 1987). Previous work based on variation in a single mitochondrial gene identified a series of geographically discrete lineages with divergence resulting from late Quaternary glacial-interglacial cycling and potential secondary contact in Haines, Alaska (Conroy & Cook 2000). Conroy and Cook (2000) suggested the Island clade experienced recent expansion from a Southeast Alaska refugium with low levels of gene flow among islands. The Northern clade indicated pre-

Last Glacial Maximum (LGM) isolation followed by recent expansion and colonization, while the Central and Southern clades were the result of mid-Pleistocene isolation.

We test previous genetic relationships within *M. longicaudus* (e.g., Conroy & Cook 2000; Spaeth *et al.* 2009) and identify drivers of genetic diversification, timing of divergence, refugial locations, and post-colonization pathways and dynamics by expanding prior sampling and employing a multilocus approach and species distribution models (SDM). We focus on the genetic dynamics of this species at the northern extent of its geographic range because of the complex biogeographical history of the region, potential for contact among divergent lineages within species, and the possibility that populations persisted in previously undetected refugia (Conroy & Cook 2000; Heaton *et al.* 1996; Klein 1965; Sawyer *et al*. submitted).

We explore the multilocus distinction between the mitochondrial Northern and Island clades and relationships among populations across the Alexander Archipelago (AA). We also explore the possibility of gene flow among insular populations and also populations representing divergent lineages. Finally, we refine the extent and location of northern contact zones, including contact in the Haines region of Alaska, as we begin to identify underlying evolutionary processes that have structured this widely distributed species. Conservation design and implementation (Malaney & Cook 2013) can benefit from identifying historical refugia, endemism on islands, and instances of secondary contact within high latitude species, which are crucial to the understanding of contemporary dynamics of gene flow.

Materials and methods

Sampling and laboratory procedures

Most museum specimens used in this work were obtained via fieldwork conducted annually since 1991. Frozen heart or liver tissues from these specimens are archived at the Museum of Southwestern Biology at the University of New Mexico (n=52) and the University of Alaska Museum of the North (n=91). Sampling was expanded from previous studies, now representing 46 general collecting localities spanning the geographic range of *M. longicaudus.* We focused most intensively on northern coastal sampling to explore population structure across the AA and identify potential contact between the Island and Northern clades near Haines Alaska (n=28) (Table 1; Figure 1). Samples represented 11 of the 15 currently recognized subspecies of *M. longicaudus* (Figure 1; Hall 1981). Additional cytochrome *b* gene (cyt *b*) sequences were obtained from GenBank for 67 individuals of *M. longicaudus,* one for each outgroup (*M. pennsylvanicus* and *M. montanus*), as well as a single Rag1 sequence for *M. pennsylvanicus* (Table 1). All sequences were deposited in GenBank (Table 1).

Genomic DNA was extracted using either Omega Bio-Tek (Norcross, GA) E.Z.N.A. tissue extraction kits or standard salt extraction (Fleming & Cook 2002), with final concentrations adjusted to 50ng μl^{-1}. We amplified the complete mitochondrial (mtDNA) cyt *b* (767-1143 bp, n=118) and partial nuclear (nuDNA) gene sequences, including Protein C-est-2 (ETS2, 731 bp, n=71), β-fibrinogen (FGB, 600 bp, n=101), and Recombination Activating Protein 1 (Rag1, 1059 bp, n=83; Table 2). Polymerase chain reaction (PCR) mixtures were 1µl DNA extract, 1 µl of each primer (2mM), 1.5 µl PCR buffer (10x), 1.5 µl $MgCl_2$ (25mM), 1.25 µl of dNTP's (10mM), 1.25 µl of Bovine Serum

Albumen (BSA, 1.5mM), and 0.08 µl of Ampli*Taq* DNA polymerase (Applied Biosystems, Foster City, CA, USA) and was adjusted to a final volume of 15 µl with ddH$_2$O. PCR products were cleaned using ExoSap-IT (Affymetrix, Santa Clara, CA) prior to sequencing at either the High Throughput Genomic Center (Seattle, WA, USA) or using an Applied Biosystems 3110 DNA sequencer (Molecular Biology Facility, UNM) using original PCR primers and BigDye v3.1 (Applied Biosystems) terminator reaction chemistry.

Sequences were visualized and edited in SEQUENCHER v4.2 (GeneCodes Corporation). PHASE v2.1 (Stephens & Scheet 2005; Stephens *et al.* 2001) was used to infer alleles of nuclear heterozygotes. Five runs of 1,000 iterations with different seeds, and a burn-in of 1,000 were conducted and the iterations with the best goodness-of-fit were chosen. Posterior probabilities for nucleotides ≥0.85 were chosen; otherwise each ambiguous site was coded as N and aligned in MEGA v5.2 (Tamura *et al.* 2011) using the MUSCLE algorithm and checked by eye.

Species Distribution Models

We generated SDMs for *M. longicaudus* to identify regions of climate suitability across western North America. Because of relatively small sample sizes for sequence data across the southern continental portion of their range, we were not able to generate clade-specific models. Models included bioclimatic variables obtained from WORLDCLIM (www.worldclim.org, Hijmans *et al.* 2005) at a resolution of 2.5 arc-minutes for current, as well as mid-Holocene (~6ka,) and Last Glacial Maximum (LGM; ~21 ka, http://pmip2.lsce.ipsl.fr/, Braconnot *et al.* 2007), and the last inter-glacial (LIG; ~120 –

140 ka). To avoid over-parameterization of the model, we used ENMTOOLS (Warren *et al.* 2008; Warren *et al.* 2010) to eliminate highly correlated variables (Pearson correlation ≥0.75). Final bioclim variables were selected based on their biological significance for *M. longicaudus*. Locality data were obtained in October 2013 from natural history collections databases (e.g., ARCTOS http://arctos.data-base.uaf.edu and MaNIS http://manisnet.org/; Stein & Wieczorek 2004). To moderate spatial autocorrelation which can lead to over-fitting of the model (Reddy & Davalos 2003), we reduced sample points to 50 km apart by removing intervening samples (Hope *et al.* 2011) which resulted in 149 sample localities.

SDMs were constructed for each time period using MAXENT v3.3.3k (Elith *et al.* 2006; Phillips *et al.* 2006; Phillips & Dudik 2008). Basic assumptions were: no topographic change has occurred, niche conservatism (Wiens & Graham 2005), environmental data adequately predicts species occurrence (Kozak *et al.* 2008; McCormack *et al.* 2010), and sampling records effectively captured the entire niche breadth of the species (Pearson *et al.* 2007). Final runs used bioclim variables 1, 6, 7, 9 and 11 and were performed using cross-validation across 10 runs, with a regularization parameter of 5 (e.g., Hope *et al.* 2011; Warren & Seifert 2011) and 1,000 iterations; all other values were default. Mean and median models were not significantly different from each other, so mean models based on MIROC and CCM models of LGM were averaged in ARCGIS 10.1 (ESRI, Redlands, CA, USA) using the raster calculator. The minimum threshold values for climate suitability were the low median threshold values over all replicates (Pearson *et al.* 2007).

Phylogenetic analyses and estimation of divergence times

Phylogenetic reconstructions using cyt *b* were estimated within Maximum Likelihood (ML) and Bayesian frameworks. The TrN+I+G model of evolution had the lowest AIC value using MODELTEST (Posada & Buckley 2004; Posada & Crandall 1998). ML estimations were performed in MEGA with 1,000 bootstrap replicates. To generate the Bayesian phylogeny and divergence dates for major clades we used BEAST v1.7.5 (Drummond *et al.* 2012) and input files prepared in BEAUTI v1.7.5. A mutation rate of 4% Myr^{-1} was assigned based on previous estimates of 3-5% Myr^{-1} (Brunhoff *et al.* 2003; Conroy & Cook 1999; Hope *et al.* 2013). We applied a coalescent constant size (Kingman 1982) tree prior with a random start tree, using an uncorrelated lognormal relaxed clock for 60 million generations (sampled every 2000). Time to Most Recent Common Ancestor (TMRCA) was determined with a 95% posterior probability distribution in TRACER v1.5 (Rambaut & Drummond 2007). For each tree, convergence statistics were assessed with effective sample size (ESS) values ≥200 in TRACER. Three independent runs were checked for convergence in the trace graphs then combined using LOGCOMBINER v1.7.5, with a 10% burin-in. Tree files were annotated in TREEANNOTATOR v1.7.5, and topologies were visualized in FIGTREE v1.4.0 (Rambaut 2009). Net genetic divergence among major clades was calculated in MEGA.

We used a multilocus approach to explore species relationships (Carstens & Knowles 2007; Edwards *et al.* 2007; Maddison 1997). The species tree was estimated in *BEAST (Heled & Drummond 2010), which uses a Bayesian Markov chain Monte Carlo (MCMC) coalescent approach to coestimate multiple gene trees embedded within the corresponding species tree topology. Because one of our goals was to explore the relationship of major cyt *b* clades, *a priori* groups were based on supported cyt *b* clades. Independent, unlinked loci were partitioned and set to appropriate substitution models (Table 3), calculated in MODELTEST. An uncorrelated lognormal relaxed clock was employed for cyt *b* at a mutation rate of 4% Myr^{-1} and strict clocks were set for estimations of phased nuclear loci based on cyt *b*. The tree priors were set to a Species Tree Yule Process with a piecewise linear and constant root population size model and random start tree. MCMC chain was run for 2 billion iterations, sampling every 2 million. TRACER, LOGCOMBINER and TREEANNOTATOR were used as above.

Migration estimates

We used BAYESASS v3.0.3 (Wilson & Rannala 2003) to determine recent levels of gene flow among populations representing the major cyt *b* clades and across the islands of Southeast Alaska, as well as among northern populations with secondary contact or in close geographic proximity. BAYESASS uses a non-equilibrium, multilocus Bayesian approach to estimate migration rates under a MCMC algorithm. We used phased multilocus data and ran 200 million iterations with a 20 thousand burn-in and sampling every 2 thousand. Mixing parameters of allele frequencies, inbreeding coefficient, and migration rates were adjusted following the program guidelines.

Demographic analyses

To explore signatures of stability and post-glacial expansion through phased multilocus historical demography for each well-supported major cyt *b* clade, we reconstructed Extended Bayesian Skyline Plots (EBSP) and cyt *b* Bayesian skyline plots

(Heled & Drummond 2008) implemented in BEAST. Colorado Plateau and North Pacific Coast, COP and NPC respectively, were omitted due to low sample sizes. Strict molecular clocks for all phased loci and appropriate models of evolution (Table 3) assigned for each of three independent runs per data set included a MCMC chain of 2 billion steps, sampled every 2 million steps. TRACER was used to assess convergence. Significant population size change occurred in EBSPs if zero was excluded from the 95% confidence interval (CI) of the estimate of the number of size-change steps (Lim & Sheldon 2011). To test for recent demographic fluctuation in cyt b major clades for each locus, we calculated a series of population genetic summary statistics (segregating sites (*S*), haplotype diversity (*Hd*), and nucleotide diversity (π)) in DNASP 5.10.1 (Librado & Rozas 2009). Historic demographic change or selection potential were assessed through Tajima's *D* (1989), Fu's *Fs* (1997), and Ramos-Onsin and Rosas' R_2 (Ramos-Onsins & Rozas 2002) with 10 thousand coalescent simulations. Selection potential was assessed through the HKA Test (Hudson *et al.* 1987).

Results

Phylogenetic and network analysis

Cyt *b* nucleotide base composition was similar to that previously observed for mammals in general (Irwin *et al.* 1991) and for *M. longicaudus* more specifically (Conroy & Cook 2000; Spaeth *et al.* 2009), with an overall deficit of guanine (13.2%, A 30.7%, C 26.9%, and T 29.1%). We found strong geographic structure within cyt *b* across the geographic range of *M. longicaudus* (Figures 1 - 3). Cutoff values for topological support in the phylogenetic trees were ≥0.7 ML bootstrap support and ≥0.95 Bayesian posterior probability. All phylogenies recovered a Southern clade comprised of two internal lineages (S1: Colorado and Wyoming; S2: New Mexico, Colorado and Arizona), a Central clade (California, Idaho, Montana and Wyoming), and a clade composed of a COP clade (Arizona into Idaho). Also, a northwestern clade consisting of a ML and Bayesian supported NPC clade (British Columbia, Oregon and Washington), Bayesian supported Northern clade (interior Alaska, through Yukon and British Columbia), and Island clade (south-central Alaska, southern Yukon, and Southeast Alaska). Within the AA, Prince of Wales Island representatives appear in both a supported lineage with Tuxekan Island, as well as within the Island clade without further distinction. Mainland Southeast Alaska locations, including Haines and Juneau, have representatives of both the Northern and Island clades. Cyt *b* variation across the range of *M. longicaudus* was not consistent with current subspecies designations (Figure 1).

Both the Northern and Island clades showed substantial internal structure (Figure 2). Haines populations were represented by five supported lineages (four in the Island clade and one in the Northern), as well as four Island clade and five Northern clade individuals without additional lineage support. Net genetic distance (Table 4) between outgroups and major clades within *M. longicaudus* ranged from 8.3% ± 0.7% (Southern to *M. montanus*) to 10.5% ± 0.9% (Southern to *M. pennsylvanicus*). Within *M. longicaudus*, the mean net genetic distance was 2.7% ± 0.4%, with the least divergence between Northern and NPC (0.5% ± 0.1%) and the largest divergence between the S1 clade and Northern, NPC, Island, and Central clades (3.3% ± 0.4%).

The species tree identified a single supported clade consisting of the Island, Northern and NPC cyt *b* clades. No other significant support was detected (Figure 4).

Nuclear gene haplotypes (Figure 5) are either lineage specific or shared across a large number of individuals and are not dependent on geographic proximity, including Haines. This suggests the lack of species tree resolution may be the result of incomplete lineage sorting, rather than hybridization (Toews & Brelsford 2012),but additional methods are needed to accurately distinguish between these two processes. ETS2 has the most structure; however, none of the nuclear genes provided full diagnostic variation.

Genetic diversity, demographic analyses and current levels of gene flow

Nuclear loci had varying amounts of genetic diversity within *M. longicaudus* (Table 3). No selection was detected in the HKA tests for all loci. ETS2 contained one indel of one base, two of two bases, and a single four base indel. FGB contained three single base indels and one seven base indel. Rag1 did not have indels. Outgroup sequences for FGB and *M. montanus* sequences for ETS2 and Rag 1 were not generated.

All Ramos-Onsin and Rozas R_2 values were significant for all loci. Based on degree of genetic variation, significance of expansion statistics (Table 3) and both cyt *b* skyline plots and EBSPs (Figure 6), we inferred population demographic history. Populations that experienced recent expansion generally have low *Hd,* while high *Hd* and π are indicative of stability, and low *Hd* and high π for population bottlenecks. The Island clade is consistent with a founder event that then experienced rapid growth, with high cyt *b Hd* a result of genetic drift in the small populations of the fragmented island system. The Northern clade is also consistent with reduced ancestral population size followed by rapid expansion. The small sample sizes for the NPC and COP clades make inference difficult. The Central clade was historically stable with post-glacial expansion. The

Southern clade represents a glacially stable population that may have experienced a bottleneck at some point in time, although signals of the bottleneck are only present in the cyt *b* data.

The mean of three runs for the Bayesian estimates of migration indicated low levels of gene flow between major cyt *b* clades (Table 5). The Island clade was the most genetically isolated of the major clades. Gene flow (proportion of migrants derived from other populations) among geographically proximate populations of divergent cyt *b* clades was highest from populations in the Northern clade in Haines, and Juneau into Haines for the Island clade (Table 6; Figure 7). Insular populations within the Island clade contained populations that have no more than 0.0187 proportion of migrants between any given island or adjacent mainland pair (Table 7).

Divergence times and alternate models of glacial refugia and postglacial recolonization

Using the average rodent mutation rate, cyt *b* TMRCAs detected for *M. longicaudus* and all clades (except S2) were before the LIG, and for S2 before the LGM. The multilocus estimations also place both *M. longicaudus* and the North/Island clade TMRCAs before the LIG.

SDMs had predictive performances with a mean AUC value of 0.834 (standard deviation 0.04) for the training and test data. The LIG SDM suggests *M. longicaudus* was restricted to coastal or extreme southern locations with an increase in climate suitability for the LGM, allowing northward and eastward movement. By the mid-Holocene, climate conditions were suitable to cover most of the current range of *M. longicaudus*. Because the SDMs are conservative (i.e., limited by a minimum threshold value) with fewer northern continental localities, not all localities currently occupied are predicted in the models (Figure 3).

Discussion

Through the use of multilocus data and SDMs, we explored how historic climatic events structured genetic variation within *M. longicaudus* across western North America and the islands of Southeast Alaska. Typical post-glacial colonization is from southern ice-free regions northward, resulting in classic genetic signatures of expansion. Northern populations are relatively homogenous while southern populations are more variable (Hewitt 2000; Lessa *et al.* 2003; Malaney & Cook 2013). Based on previous studies of *M. longicaudus*, we expected to detect similar genetic signatures across the range of this species, but our results only partially correspond with that expectation in that the northern clades are not genetically homogeneous.

Biogeographic drivers of isolation, glacial refugia and postglacial recolonization

The multilocus estimate for TMRCA of *M. longicaudus* is well before the LIG (Table 9) and comparable to single locus estimates from previous studies (340 ± 70 ka, Conroy & Cook 2000). This estimate predates the fossil record of *M. longicaudus* which includes fossils dated to the Wisconsinan glaciation in Idaho, Wyoming, Colorado and New Mexico (Smolen & Keller 1987) and post-glacial locations in Alberta and British Columbia (Harington 2011b). The absence of a richer fossil record, especially at the northern extent of their range may be a result of poor preservation or difficulty in precise identification of ancient remains (e.g., isolated teeth, Harington 2011a).

Contrary to conclusions drawn by Spaeth *et al.* (2009), we detected cyt *b* intralineage variation and substantial spatial and temporal patterns of genetic differentiation. Also, divergence between major lineages of *M. longicaudus* was likely reinforced through subsequent glacial isolation, as indicated by the SDMs (Figure 3). The southern clades appear stable resulting in deeper genetic structure, while the northern clades have shallow structure due to recent range expansion. This pattern is consistent with persistence and stability of southern clades for greater periods of time, in contrast to the more dynamic history of colonization seen in the northern lineages.

This expanded view of *M. longicaudus* phylogeography largely corroborates previous work based on much more limited geographic and genetic sampling (Conroy & Cook 2000; Spaeth *et al.* 2009), but there are notable discrepancies due to this refined view of how intraspecific variation is partitioned. Spaeth *et al.* (2009) focused on the Greater Yellowstone Ecosystem and identified subfossils from both the Northern and Central clades within Yellowstone (Figure 8) that support the post-glacial presence of *M. longicaudus* south of the ice. “Northern” sampling in Spaeth *et al.* (2009) was limited, however, and could represent COP individuals being genetically associated with their “Northern” clade as result of the sampling scheme, suggested by the wide geographic range of the Northern clade.

Our findings are consistent with previous suggestions that the Island clade persisted in coastal refugia during the LGM, followed by expansion and subsequent isolation on multiple islands (Figure 8). Heaton and Grady (2007) found abundant *M. longicaudus* fossils from On Your Knees Cave on Prince of Wales Island (Figure 8) that radiocarbon date to the middle Wisconsin Interstadial (38 – 25 ka), but fossil evidence disappeared by the LGM due to glacial advance onto this island. *Microtus longicaudus* reappeared in On Your Knees and El Capitan and Bumper caves on Prince of Wales Island by the early Holocene (Heaton *et al.* 2003), which suggests that it re-colonized shortly after the LGM. *Microtus longicaudus* may have re-colonized the islands from as many as three coastal (exposed continental shelf) refugia in the AA (Sawyer *et al.* submitted), rather than from mainland populations. Fossil support for refugial locations in the AA will be difficult to locate, as much of the coast that was exposed during the LGM is now under up to 165 m of water.

SDMs, levels of cyt *b* variation, and multilocus genetic signals suggest that *M. longicaudus* persisted in multiple refugia within the AA. Lack of connectivity between insular populations produced extensive inter-island structure, with populations on 13 of the 19 islands displaying significantly divergent mtDNA. Also, within the AA, *M. longicaudus* is the only vole that ranges across most of the islands, with the exception of Baranof Island. On the mainland it co-occurs with two congeners, *M. oeconomus* (root vole) and *M. pennsylvanicus* (meadow vole). These congeners appear to be spatially associated with the Continental and Beringian clades of *Mustela erminea* (ermine) (Dawson *et al.* 2014; Fleming & Cook 2002; MacDonald & Cook 2007). For *M. longicaudus*, there is no clear association with a single clade of this vole-specialist predator (Verts & Carraway 1998); rather, the island lineage of *M. longicaudus* co-occurs with all three major clades (Continental, Beringian and Island) of ermine.

The Island and Northern clades of *M. longicaudus* appear to have two points of secondary contact (Haines and Juneau) and multiple regions of geographic proximity southward along the mainland coast of Southeast Alaska (Figure 7). These multiple points of contact spread along the coast may lend support for the hypothesis that Island refugial populations followed glacial retreat to recolonize the adjacent mainland through multiple colonization pathways (Figure 8), but more detailed assessment of these mainland sites with increased sampling is needed. A broad region of contact and introgression along the coast may be similar to the broad area of introgression along the coast detected in red-backed voles of the genus *Myodes* (Runck *et al.* 2009). Contrary to previous suggestions that the Northern clade expanded from a single interior route from south of the ice, we conclude that the Northern clade persisted in Beringia and recently expanded southward into previously glaciated regions of southern Alaska, Yukon and northern BC (Figure 8). Although SDMs do not indicate regions north of the ice for Northern populations, the models were conservative and built on relatively limited northern sampling. High levels of intralineage genetic diversity, net genetic distance among other clades, and the restriction of the range of this clade to high latitudes are consistent with persistence in a northern refugium. Other studies on both mammalian and non-mammalian taxa have identified genetic signatures that poin toward the influence of an eastern Beringia refugium during glacial periods (Sawyer *et al.* submitted; Fleming & Cook 2002; Stamford & Taylor 2004).

SDMs also support the persistence of *M. longicaudus* along the coast of Oregon and Washington (NPC clade) during glacial advances. The Central and Southern clades have been effectively isolated and relatively demographically stable since the mid- to late- Pleistocene. Lastly, the COP clade, previously identified from a limited region in northern Arizona, occurs northward into Utah and potentially contacts both the S2 and Central clades.

Contemporary genetic structure and current levels of gene flow

Disentangling signatures of incomplete lineage sorting versus secondary admixture is important to understand the effects of historical climate across contemporary distributions and factors influencing genetic diversification. Recent diversification within *M. longicaudus*, including Haines populations, is reflected in the poorly resolved species tree for populations from northern regions. Future studies could use alternate genetic data to infer if admixture has occurred between ndivergent populations (Qu *et al.* 2012).

Generally, intraspecific cyt *b* net genetic distance is less than 2% while interspecific distances are above 10% in mammals (Bradley & Baker 2001). Values between 2 and 10% warrant further study given the potential for incipient speciation (Hope *et al*. In Press). Low levels of cyt *b* net genetic distance among the Island, Northern, NPC and COP clades fall within the levels of intraspecies variation. The taxonomic status of these clades in relation to the Central and Southern lineages, however, should be clarified. Shallow divergence and levels of genetic differentiation between the Northern clade into Island clade populations near Haines may be explained by the geographic proximity, recent (Holocene) secondary contact, and incomplete lineage sorting of Island and Northern populations. As with net genetic distance, gene flow values between 0.035 and 0.10 warrant further investigation because they are between observed values for inter and intra specific estimates, respectively (e.g. Nakajima *et al.* 2012; Ross *et al.* 2010). The geographic distribution of genetic variation does not correspond to current subspecies designations.

Clear segregation of the Northern, NPC and Island clades from the COP, Central and Southern clades is reflected both the species tree (Figure 4) and recent estimates of migration (Table 5). On the mainland, no detectible levels of admixture are present in the Haines populations but further work using more rapidly evolving loci is needed. Lower levels of gene flow from the Island clade into Haines likely reflect physical barriers to movement (i.e., ocean straits, extant glaciers). Genetic exchange among island populations is limited, likely due to oceanic barriers. Seawater has probably inhibited gene flow among island populations in the AA due to sea level rise during the Holocene (*c*. 14 - 8 ka bathymetric reconstruction, Baichtal & Carlson 2010).

The Haines region has experienced dynamic changes that reflect post-glacial expansion by both Island and Northern clades. Contact or geographic proximity should be further explored along the central and northern coast of Southeast Alaska northward to Haines. Increased sampling and geographic coverage in this study corroborated the previously identified region of secondary contact in Haines (Conroy & Cook 2000) and extended potentially admixed sites southward to at least Juneau.

Conclusions

The dynamic influence of Pleistocene climate variation and glacial cover, as played out over the complex topography of western North America, can be tied to the geographic distribution of genetic variation in *M. longicaudus*. As expected, the mid-Pleistocene onset of diversification is consistent with that observed in other taxa. As with other boreal species, genetic variation and structure is highest in the southern portions of this species range. On the other hand, mtDNA in northern populations also is structured and reflects both persistence in multiple northern refugia (coastal and eastern Beringia) and subsequent isolation on multiple islands of the Alexander Archipelago. Similar refugial regions were recently identified for ermine (Dawson *et al.* 2014).

Phylogeographic breaks generally do not correspond with current subspecies designations (Hall 1981). This is the first study to more intensively examine genetic variation of *M. longicaudus* across the AA (19 islands), as well as extending our view of structure across the entire range of the species using multiple nuclear perspectives. Future sampling in central and southern British Columbia and along the southern periphery of the long-tailed vole's range will expand our view of both diversification and admixture processes. Further incorporation of ancient DNA from fossils could further extend our exploration of genetic variability through time, as observed in areas such as the Greater Yellowstone Ecosystem (Spaeth *et al.* 2009). Identifying the effects of historical climate change on contemporary species sets a powerful stage for predictions for future biotic responses.

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Figures and Tables

Figure 1. Current range and subspecies of *M. longicaudus*. Light gray is the current range, black outlined regions with numbers are the subspecies, and dots are sampling locations colored by major cyt *b* lineages. (a) Entire range, (b) Haines and Southeast Alaska. Subspecies modified from Hall 1981.

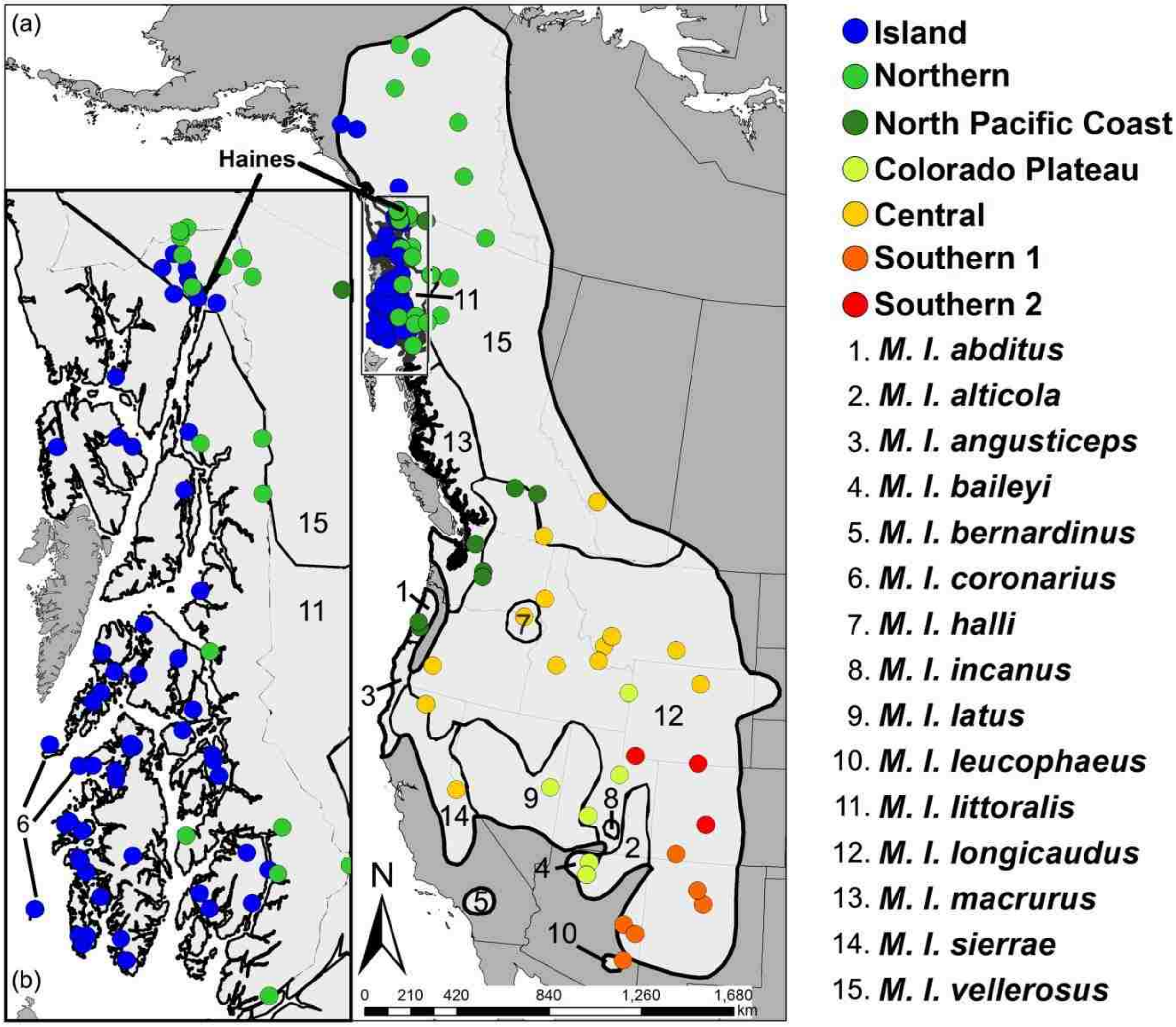


Figure 2. Dated Bayesian cyt*b* trees. Posterior probability ≥0.95 represented with open circles and Maximum Likelihood bootstraps of ≥0.7 with asterisks are shown on branches. Vertical gray bars represent the LIG (left) and LGM (right). Geographic locations for supported intralineage clades are provided. NPC = North Pacific Coast; COP = Colorado Plateau. See Table 8 for abbreviations.

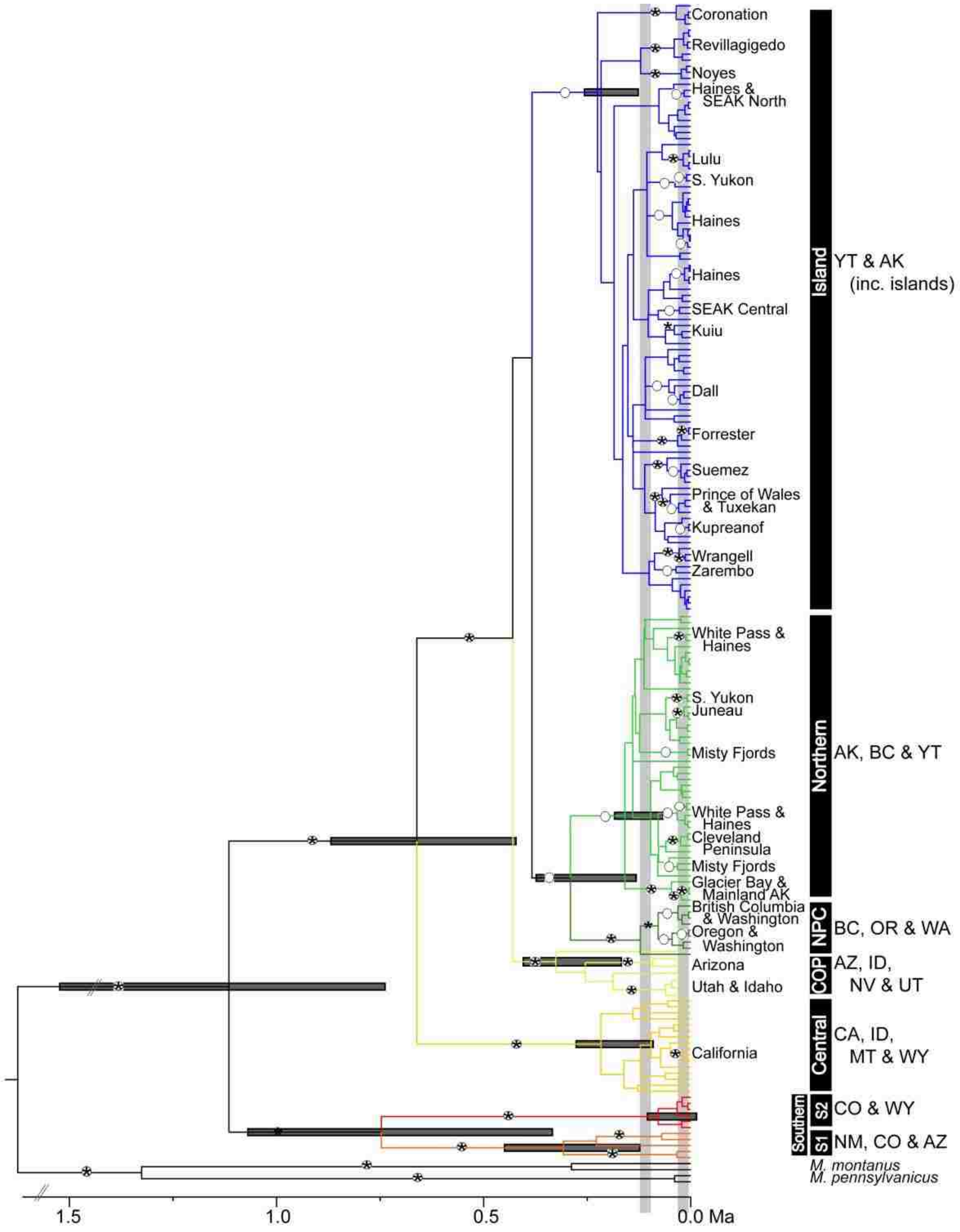


Figure 3. Sampling scheme and SDM output. (a) LIG (~125 ka), (b) LGM (~20 ka), (c) Mid-Holocene (~6 ka), and (d) Current time periods. Sampling localities are major cyt*b* lineage (color: Island=I, Northern=N, NPC=North Pacific Coast, COP=Colorado Plateau, Central=C, and S1 and S2 = Southern). The thick black line in the Current map is the current range for *M. longicaudus*. The solid blue coloring at the LGM is glacial ice cover. SDM climate suitability at each time period is limited by minimum median threshold values over all replicates. Because the SDMs are conservative, not all current localities are predicted in the models.

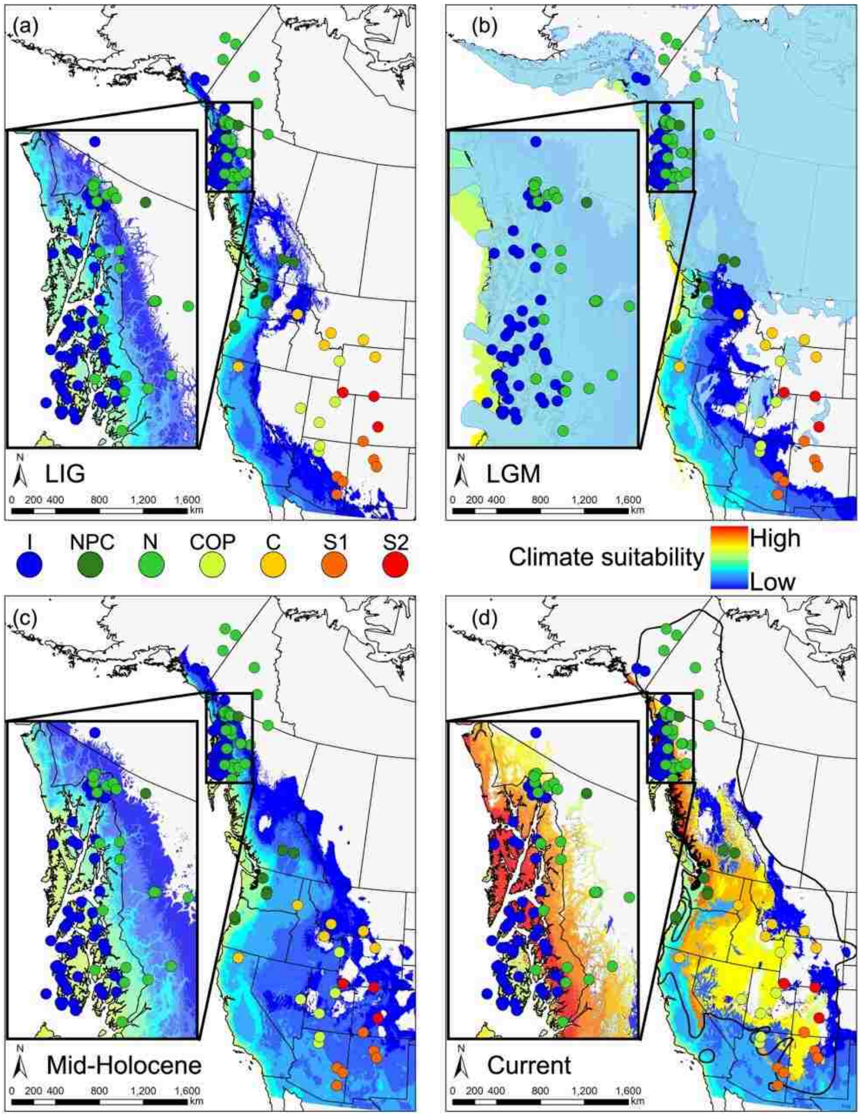


Figure 4. Phased multilocus Bayesian Species Tree. Posterior probabilities of ≥0.95 are represented with open circles on branches of the solid consensus tree. Blue = Island, green = Northern, dark green = NPC, light green = COP, golden = Central, orange = S1, and red = S2. Horizontal gray bars represent divergence date estimates and vertical bars indicate approximate time for the LIG and LGM.

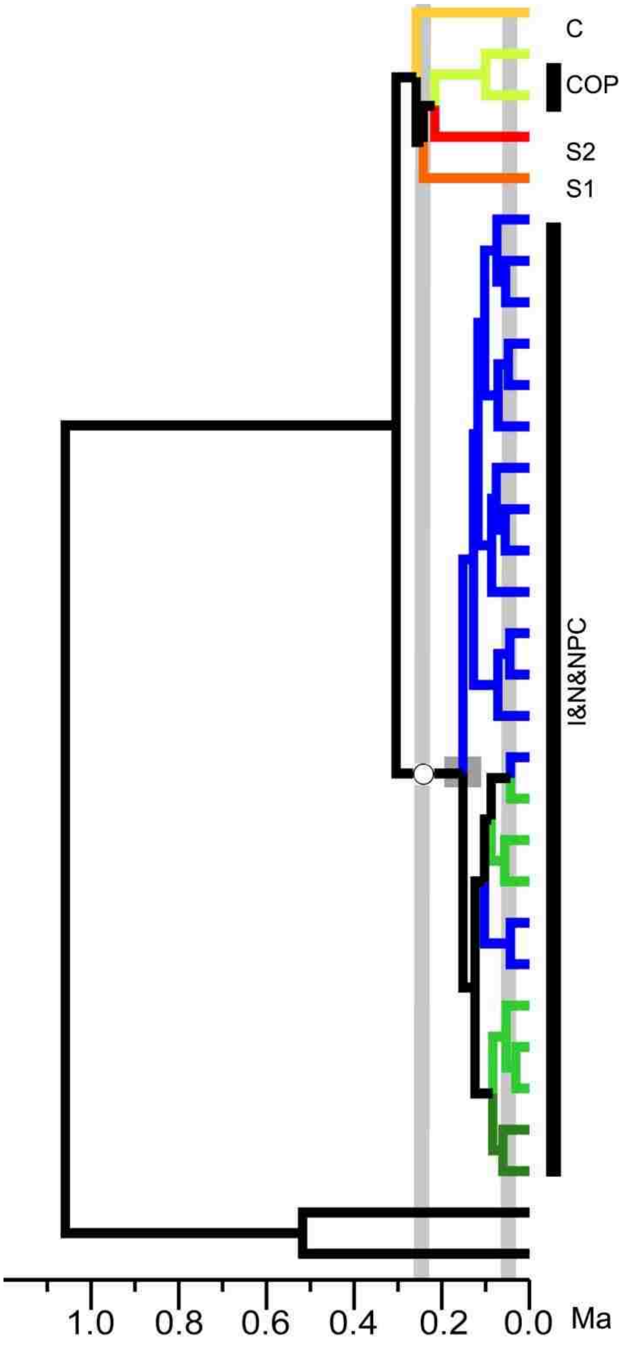


Figure 5. Phased Bayesian gene trees for (a) ETS2, (b) FGB, and (c) Rag1 nuclear loci with posterior probabilities of ≥0.95 represented with open circles on branches of the solid consensus tree. Black dots are Haines individuals. Blue = Island, middle green = Northern, dark green = NPC, light green = COP, gold = Central, orange = S1, and red = S2. Geographic locations (Table 8) for supported intralineage clades are provided.

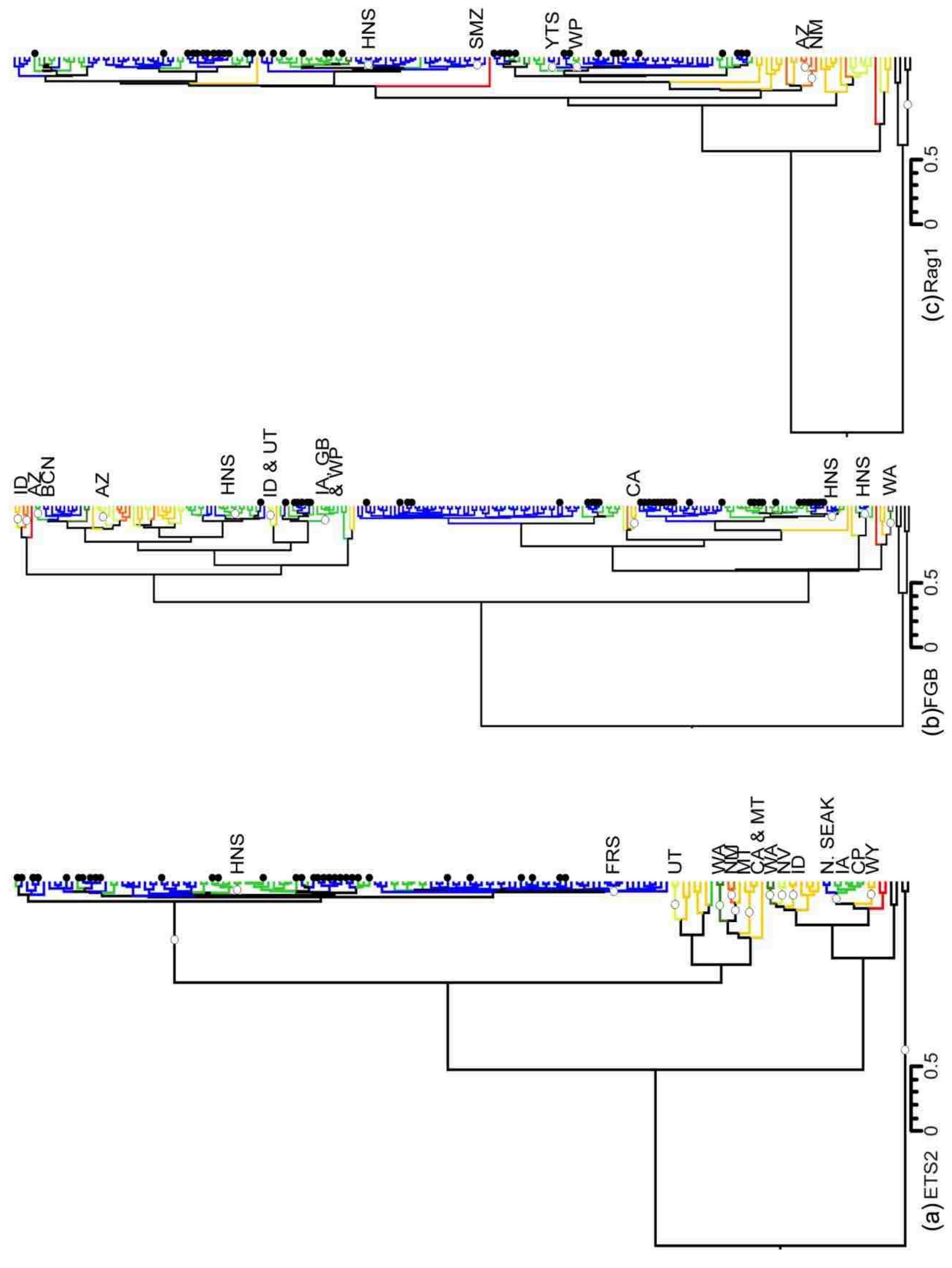
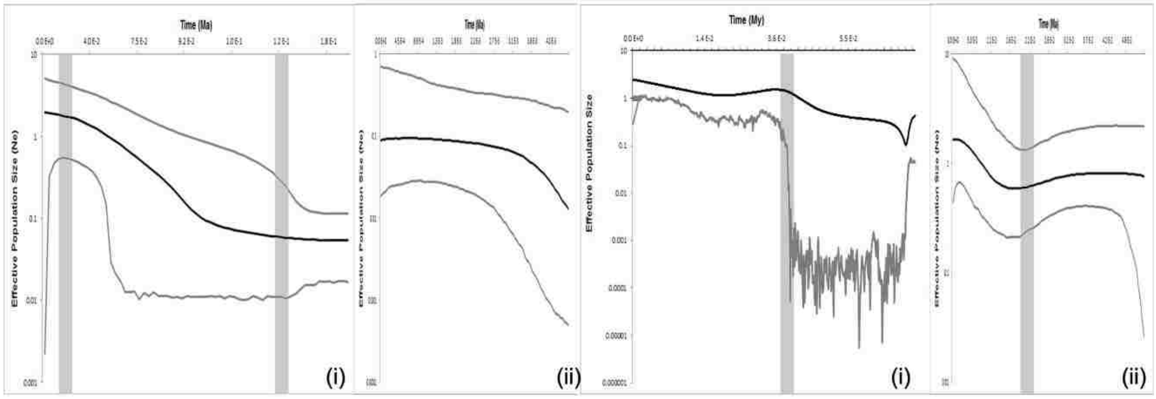

(a) ETS2
0
0.5
HNS
FRS
UT
WA
NM
MT
CA & MT
WA
NV
ID
N. SEAK
IA
CP
WY
(b) FGB
0
0.5
ID
AZ
BCN
AZ
HNS
ID & UT
IA, GB
& WP
CA
HNS
HNS
WA
(c) Rag1
0
0.5
HNS
SMZ
YTS
WP
AZ
NM

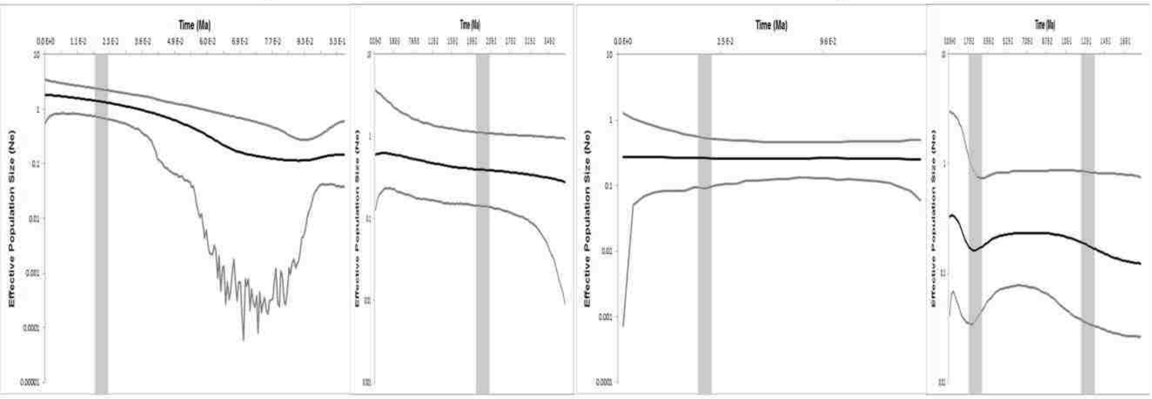
Figure 6. EBSPs (i) and cyt b Bayesian skyline plots (ii) for the major cyt*b* lineage populations: (a) Central, (b) Island, (c) North and (d) South, excluding NPC and COP. EBSP Central line indicates mean change in effective population size through time, with upper and lower lines sowing the 95% posterior density. The x-axis right-to-left from past (TMRCA) to present and is scaled in millions of years and the y-axis is effective population size scaled by generation time. Vertical gray bars indicate the LIG (when applicable, right) and LGM (left) for reference.



(a) *M. longicaudus* - Central

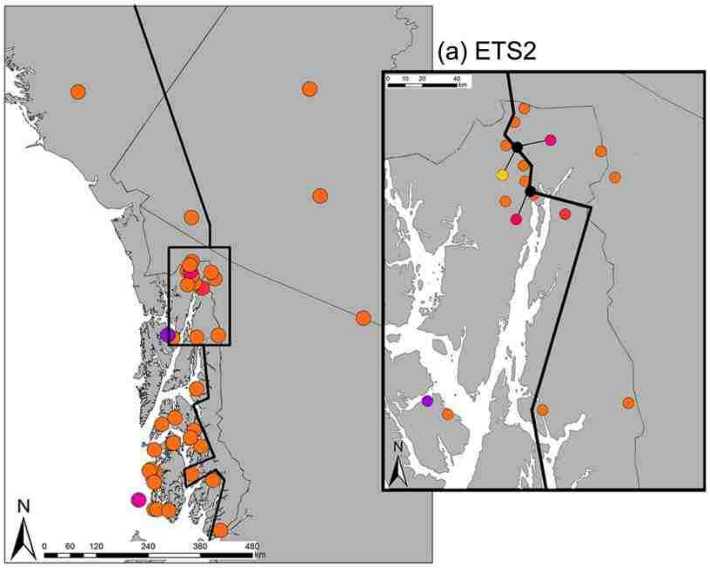
(b) *M. longicaudus* - Island

(c) *M. longicaudus* - North

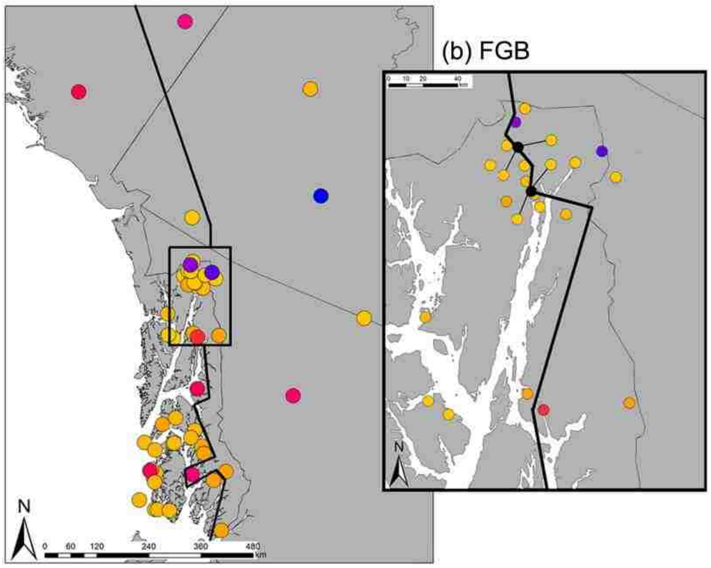


(d) *M. longicaudus* - South

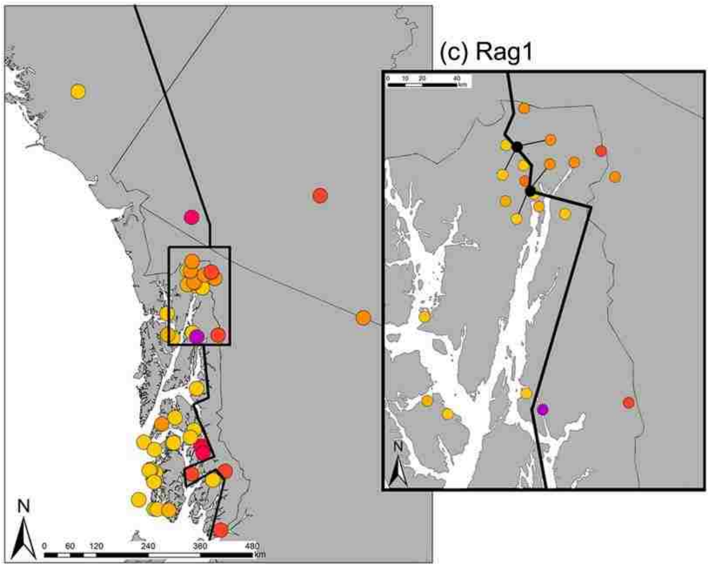
Figure 7. Phased nuclear haplotype distribution in Northern and Island lineages of *M. longicaudus*. (a) ETS2, (b) FGB, and (c) Rag1. Thick black line delimits Island (left) and Northern (right) lineages with sympatry indicated with black sample locations and haplotype variety indicated with adjoining lines. Each color within a locus represents a unique haplotype.



(a) ETS2



(b) FGB



(c) Rag1

Figure 8. Proposed post-glacial colonization routes (arrows) for *M. longicaudus* based on genetic signatures and SDMs. Plus (+) = fossil (SE Alaska)/subfossil (Yellowstone) locations and arrow colors correspond to current cyt *b* lineages: dark green = North Pacific Coast, green = Northern, and blue = Island. Northern and Island lineage refugial locations and post-glacial colonization with locations of secondary contact indicated with the wavy line. Blue line indicates extent of glacial ice at LGM.

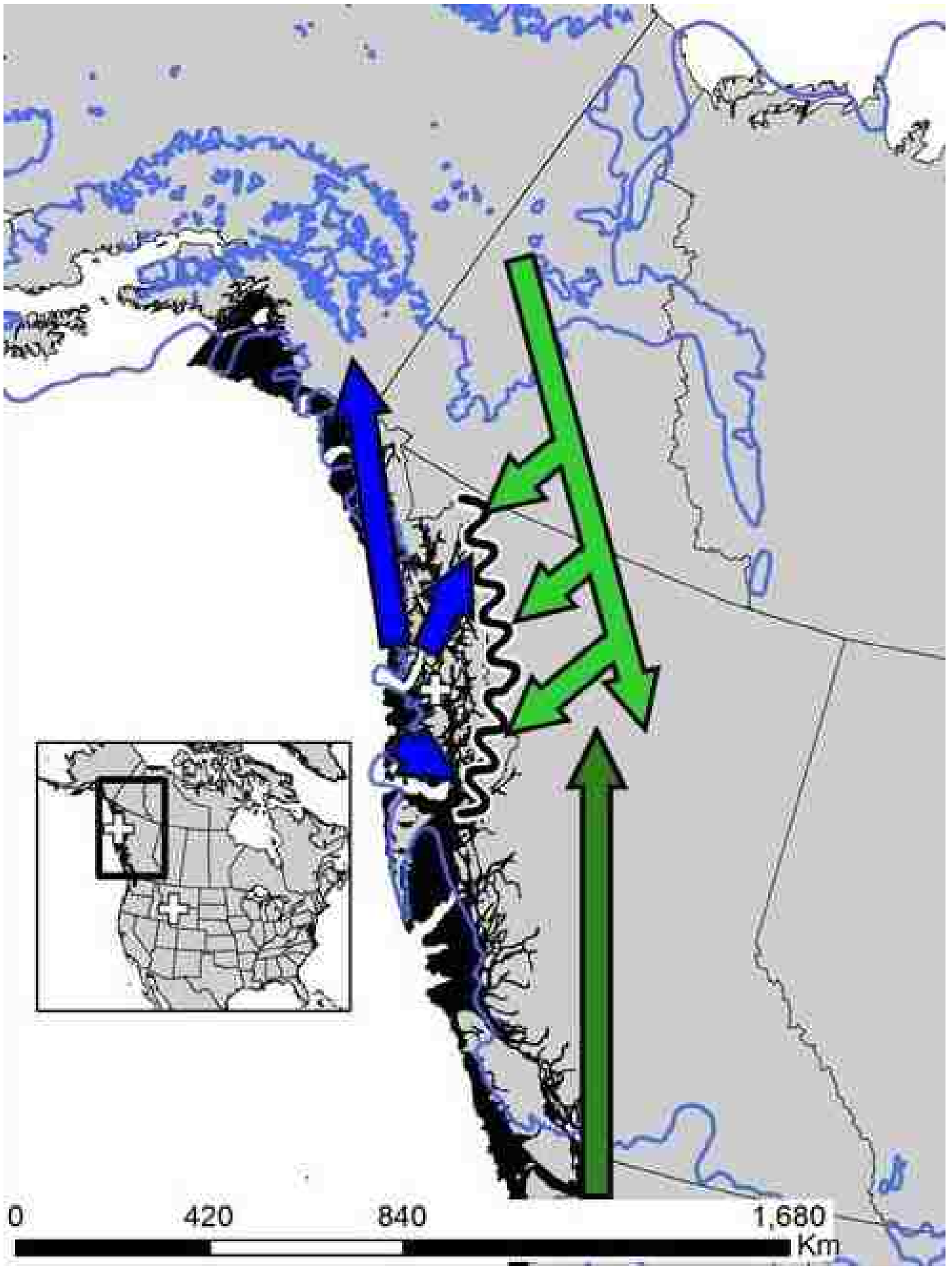


Table 1. Specimens examined. Major cyt*b* lineage C=Central, I=Island, and N=Northern. Museum number acronyms are MSB= Museum of Southwestern Biology; UAM=University of Alaska Museum of the North, Fairbanks. GenBank numbers correspond to cyt*b*, and each allele for ETS2, FGB, and Rag1, respectively, –= not applicable. GenBank in bold were obtained from other studies.

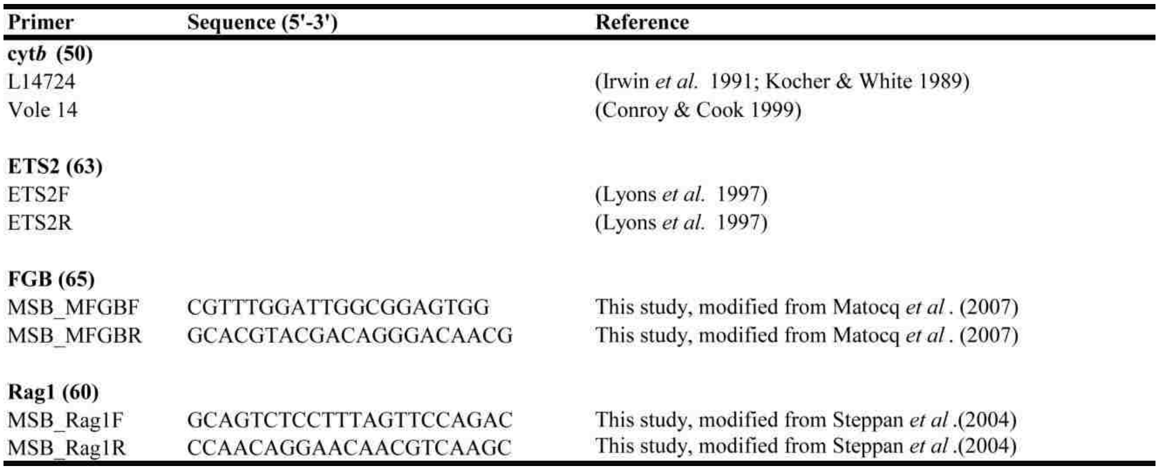
cytb lineage	Specimen Number	Locality	Latitude	Longitude	GenBank Accession Numbers
Central (C)	UAM77991	California	41.409	-122.194	**AF187176**, – / – , – / – , – / –
	UAM77992		41.409	-122.194	**AF187174**, – / – , – / – , – / –
	UAM77993		41.409	-122.194	**AF187175**, – / – , – / – , – / –
	UAM77994		41.409	-122.194	**AF187177**, – / – , – / – , – / –
	MSB227995	Idaho	44.659	-113.216	KF948609,KF948677/KF948678,KF948845/KF948846,KF949027/KF949028
	UAM77997		46.732	-117.000	**AF187173**, – / – , – / – , – / –
	MSB156351	Montana	45.731	-112.676	KF948534, – / – , – / – , – / –
	UAM34299		45.520	-108.820	**AF187172**, – / – , – / – , – / –
	MSB225915	Wyoming	44.226	-107.235	KF948607,KF948673/KF948674,KF948841/KF948842,KF949023/KF949024
Colorado Plateau (COP)	MSB61434	Arizona	35.954	-112.157	**AF187162**, – / – ,KF948853/KF948854, – / –
	MSB61436		35.954	-112.157	**AF187161**, – / – ,KF948855/KF948856, – / –
	MSB61443		36.463	-112.118	**AF187160**, – / – ,KF948857/KF948858,KF949033/KF949034
	MSB143745	Idaho	43.553	-111.243	KF948533, – / – ,KF948785/KF948786, – / –
	MSB227146	Nevada	39.238	-114.689	KF948608,KF948675/KF948676,KF948843/KF948844,KF949025/KF949026
	MSB76827	Utah	38.344	-112.491	KF948610, – / – ,KF948859/KF948860, – / –
	MSB77127		40.186	-111.140	KF948611,KF948683/KF948684,KF948861/KF948862,KF949035/KF949036
Island (I)	UAM30499	Alaska - Glacier Bay	58.450	-135.917	**AF187225**, – / – ,KF948897/KF948898,KF949071/KF949072
	MSB193312	Alaska - Haines	59.218	-135.448	KF948589, – / – ,KF948807/KF948808, – / –
	MSB193325		59.267	-135.603	KF948590, – / – ,KF948809/KF948810,KF948997/KF948998
	MSB193328		59.267	-135.603	KF948591,KF948655/KF948656,KF948811/KF948812,KF948999/KF949000
	MSB193329		59.267	-135.603	KF948592,KF948657/KF948658,KF948813/KF948814,KF949001/KF949002
	MSB193396		59.218	-135.448	KF948593,KF948659/KF948660,KF948815/KF948816,KF949003/KF949004
	MSB193439		59.267	-135.603	KF948594,KF948661/KF948662,KF948817/KF948818,KF949005/KF949006
	MSB193445		59.267	-135.603	KF948595,KF948663/KF948664,KF948819/KF948820,KF949007/KF949008
	MSB193446		59.267	-135.603	KF948596,KF948665/KF948666,KF948821/KF948822,KF949009/KF949010
	MSB193447		59.267	-135.603	KF948597,KF948667/KF948668,KF948823/KF948824,KF949011/KF949012
	MSB193544		59.218	-135.448	KF948552, – / – ,KF948825/KF948826,KF949013/KF949014
	MSB195072		59.267	-135.600	KF948598, – / – ,KF948827/KF948828, – / –
	MSB195212		59.246	-135.175	KF948600, – / – ,KF948831/KF948832,KF949015/KF949016
	MSB195220		59.300	-135.704	KF948601, – / – ,KF948833/KF948834,KF949017/KF949018
	UAM20577		59.433	-135.950	KF948614,KF948689/KF948690,KF948871/KF948872,KF949045/KF949046
	UAM31114		59.575	-136.157	**AF187217**, – / – , – / – , – / –
	UAM52711		59.262	-135.560	KF964341,KF948749/KF948750,KF948947/KF948948,KF949119/KF949120
	UAM64491		59.286	-136.108	KF948576, – / – ,KF948963/KF948964, – / –
	UAM64609		59.415	-136.062	KF948632,KF948763/KF948764,KF948965/KF948966, – / –
	UAM64616		59.415	-136.062	KF948633,KF948765/KF948766,KF948967/KF948968,KF949133/KF949134
	UAM64624		59.366	-135.798	KF948545,KF948767/KF948768,KF948969/KF948970,KF949135/KF949136
	UAM68284		59.163	-135.778	KF948636,KF948773/KF948774,KF948975/KF948976,KF949141/KF949142
	UAM3553	Alaska - interior	61.500	-142.833	**AF187216**, – / – , – / – , – / –
	UAM57777		61.318	-144.235	KF948628,KF948751/KF948752,KF948949/KF948950,KF949121/KF949122
	MSB148983	Alaska - Island	56.642	-133.701	KF948546,KF948647/KF948648,KF948793/KF948794,KF948991/KF948992
	MSB149385		56.668	-134.266	KF948547, – / – , – / – , – / –
	MSB221332		55.488	-133.631	KF948602, – / – , – / – , – / –
	MSB221340		55.488	-133.631	KF948603,KF948669/KF948670,KF948835/KF948836,KF949019/KF949020
	MSB221446		55.469	-133.426	KF948553,KF948671/KF948672,KF948837/KF948838,KF949021/KF949022
	MSB221498		55.469	-133.426	KF948604, – / – , – / – , – / –
	MSB221521		55.469	-133.426	KF948605, – / – , – / – , – / –
	MSB221545		55.469	-133.426	KF948606, – / – ,KF948839/KF948840, – / –
	UAM20507		58.067	-135.233	**AF187211**, – / – ,KF948867/KF948868,KF949041/KF949042
	UAM20611		56.417	-132.833	KF948544, – / – ,KF948873/KF948874,KF949047/KF949048
	UAM20918		56.867	-133.317	**AF187208** , – / – , – / – , – / –
	UAM20919		56.867	-133.317	KF948554, – / – , – / – , – / –
	UAM22912		56.410	-134.033	**AF187224** ,KF948691/KF948692, – / – , – / –
	UAM22913		56.410	-134.033	KF948555, – / – ,KF948875/KF948876,KF949049/KF949050

UAM22918	56.583	-132.833	KF948556,KF948693/KF948694,KF948877/KF948878,KF949051/KF949052
UAM22920	55.918	-134.321	KF964335, – / – , – / – , – / –
UAM22921	55.918	-134.321	**AF187223** , – / – , – / – , – / –
UAM23063	56.350	-132.333	KF948536,KF948695/KF948696,KF948879/KF948880,KF949053/KF949054
UAM23410	55.918	-134.321	**AF187222** , – / – , – / – , – / –
UAM23455	55.502	-131.028	KF964344, – / – , – / – , – / –
UAM23606	55.918	-134.321	**AF187213** ,KF948697/KF948698,KF948883/KF948884,KF949057/KF949058
UAM23659	55.452	-133.660	KF948615, – / – ,KF948885/KF948886,KF949059/KF949060
UAM23726	54.767	-132.183	KF948616, – / – , – / – , – / –
UAM23727	54.767	-132.183	KF948557, – / – , – / – , – / –
UAM23728	54.783	-132.867	**AF187206** ,KF948699/KF948700,KF948887/KF948888,KF949061/KF949062
UAM23804	55.767	-131.017	**AF187212**, – / – , – / – , – / –
UAM23871	56.975	-133.941	**AF187227** , – / – , – / – , – / –
UAM23943	55.817	-131.367	KF964336,KF948703/KF948704,KF948891/KF948892,KF949065/KF949066
UAM23944	55.817	-131.367	KF948617,KF948705/KF948706,KF948893/KF948894,KF949067/KF949068
UAM30504	55.415	-131.696	KF948618, – / – , – / – , – / –
UAM30506	56.150	-133.350	KF948559, – / – , – / – , – / –
UAM30507	56.150	-133.350	KF948560,KF948709/KF948710,KF948899/KF948900,KF949073/KF949074
UAM30508	56.150	-133.350	KF948561,KF948711/KF948712,KF948901/KF948902,KF949075/KF949076
UAM30721	56.150	-133.350	KF948619, – / – , – / – , – / –
UAM31755	55.875	-133.842	KF948542,KF948713/KF948714,KF948903/KF948904,KF949077/KF949078
UAM31784	55.875	-133.842	**AF187218**, – / – , – / – , – / –
UAM31785	55.875	-133.842	KF948537, – / – , – / – , – / –
UAM31786	55.875	-133.842	**AF187214**, – / – , – / – , – / –
UAM31787	55.875	-133.842	KF948543, – / – , – / – , – / –
UAM31788	55.875	-133.842	KF948538,KF948715/KF948716,KF948905/KF948906,KF949079/KF949080
UAM31826	55.100	-132.833	**AF187230**, – / – , – / – , – / –
UAM32929	57.817	-136.150	**AF187205**, – / – , – / – , – / –
UAM32932	57.817	-136.150	KF964338, – / – , – / – , – / –
UAM34288	56.174	-133.369	KF948621, – / – , – / – , – / –
UAM36269	58.079	-135.478	**AF187219**,KF948729/KF948730,KF948921/KF948922,KF949093/KF949094
UAM36579	56.167	-133.317	**AF187215**,KF948731/KF948732,KF948923/KF948924,KF949095/KF949096
UAM41767	55.461	-132.692	**AF187207**, – / – , – / – , – / –
UAM41768	55.283	-133.307	**AF187226**,KF948733/KF948734,KF948925/KF948926,KF949097/KF949098
UAM42372	54.744	-132.771	KF948622, – / – , – / – , – / –
UAM42375	56.417	-132.833	KF948539,KF948735/KF948736,KF948927/KF948928,KF949099/KF949100
UAM42376	56.321	-134.072	KF948565, – / – , – / – , – / –
UAM42377	56.583	-134.000	KF948640, – / – , – / – , – / –
UAM42380	54.821	-133.521	KF948566,KF948737/KF948738,KF948929/KF948930,KF949101/KF949102
UAM42381	54.821	-133.521	**AF187221**,KF948739/KF948740, – / – ,KF949103/KF949104
UAM42385	55.919	-133.685	KF948567, – / – , – / – , – / –
UAM42392	55.267	-133.272	KF948623, – / – , – / – , – / –
UAM42393	55.267	-133.272	KF948568, – / – , – / – , – / –
UAM42429	55.216	-133.138	KF948569, – / – , – / – , – / –
UAM42727	54.821	-133.521	KF948624, – / – , – / – , – / –
UAM42728	54.821	-133.521	KF948581, – / – ,KF948931/KF948932, – / –
UAM43227	55.267	-133.272	KF948582, – / – , – / – , – / –
UAM49638	55.283	-133.307	KF948578,KF948745/KF948746,KF948943/KF948944,KF949115/KF949116
UAM49658	54.807	-132.769	KF948579,KF948747/KF948748,KF948945/KF948946,KF949117/KF949118
UAM49660	54.807	-132.769	KF948627, – / – , – / – , – / –
UAM51686	57.958	-134.307	KF964342, – / – , – / – , – / –
UAM52256	55.950	-133.383	**AF187209**, – / – , – / – , – / –
UAM52262	55.900	-133.333	**AF187220**, – / – , – / – , – / –
UAM62899	56.233	-132.133	KF948540,KF948755/KF948756,KF948953/KF948954,KF949125/KF949126
UAM70243	54.888	-132.366	KF948572,KF948775/KF948776,KF948977/KF948978,KF949143/KF949144

Northern (N)	UAM72153		56.318	-132.286	KF948541, – / – , – / – , – / –
	UAM97289		55.344	-131.498	KF948575, – / – , – / – , – / –
	MSB156999	Alaska - Juneau	58.343	-134.640	KF948550,KF948653/KF948654,KF948803/KF948804,KF948995/KF948996
	UAM74134	Alaska - southeast	57.367	-133.467	KF948573,KF948779/KF948780,KF948981/KF948982,KF949147/KF949148
	UAM74283		57.367	-133.467	KF948638, – / – , – / – , – / –
	UAM74413		57.367	-133.467	KF948639,KF948781/KF948782,KF948983/KF948984,KF949149/KF949150
	UAM34297	Yukon - south	60.400	-137.050	**AF187228** ,KF948725/KF948726,KF948915/KF948916,KF949089/KF949090
	UAM34298		60.400	-137.050	**AF187229**,KF948727/KF948728,KF948917/KF948918,KF949091/KF949092
	UAM34593	Alaska - Glacier Bay	65.228	-144.500	**AF187190**, – / – , – / – , – / –
	UAM34594		65.228	-144.500	**AF187189**, – / – ,KF948919/KF948920, – / –
	MSB195109	Alaska - Haines	59.267	-135.600	KF948599, – / – ,KF948829/KF948830, – / –
	UAM20576		59.433	-135.950	KF948613,KF948687/KF948688,KF948869/KF948870,KF949043/KF949044
	UAM31113		59.575	-136.157	**AF187202**, – / – , – / – , – / –
	UAM48471		59.500	-135.354	KF964340,KF948743/KF948744,KF948939/KF948940,KF949111/KF949112
	UAM64427		59.623	-136.089	KF948630,KF948757/KF948758,KF948955/KF948956,KF949127/KF949128
	UAM64428		59.623	-136.089	KF948570,KF948759/KF948760,KF948957/KF948958,KF949129/KF949130
	UAM64429		59.623	-136.089	KF948631, – / – ,KF948959/KF948960, – / –
	UAM64442		59.623	-136.089	KF948571,KF948761/KF948762,KF948961/KF948962,KF949131/KF949132
	UAM70791		59.540	-136.106	KF948637,KF948777/KF948778,KF948979/KF948980,KF949145/KF949146
	UAM60319	Alaska - interior	65.303	-142.037	KF948629,KF948753/KF948754,KF948951/KF948952,KF949123/KF949124
	UAM65747		63.699	-142.250	KF948634,KF948769/KF948770,KF948971/KF948972,KF949137/KF949138
	UAM32822	Alaska - Juneau	58.183	-133.317	**AF187203**, – / – , – / – , – / –
	UAM34292		58.533	-133.683	KF948563,KF948719/KF948720,KF948909/KF948910,KF949083/KF949084
	UAM34293		58.533	-133.683	KF948564,KF948721/KF948722,KF948911/KF948912,KF949085/KF949086
	UAM34294		58.533	-133.683	KF964337,KF948723/KF948724,KF948913/KF948914,KF949087/KF949088
	UAM75497		58.307	-134.417	KF948574,KF948783/KF948784,KF948985/KF948986,KF949151/KF949152
	UAM23496	Alaska - southeast	56.083	-131.086	**AF187191**, – / – ,KF948881/KF948882,KF949055/KF949056
	UAM23552		56.083	-131.086	KF964339, – / – , – / – , – / –
	UAM23751		55.750	-132.183	**AF187198** , – / – , – / – , – / –
	UAM23752		55.750	-132.183	KF964343,KF948701/KF948702,KF948889/KF948890,KF949063/KF949064
	UAM23883		55.767	-130.883	**AF187199**, – / – , – / – , – / –
	UAM30495		55.750	-132.183	KF948558,KF948707/KF948708,KF948895/KF948896,KF949069/KF949070
	UAM30496		57.008	-132.983	**AF187193**, – / – , – / – , – / –
	UAM30497		57.008	-132.983	**AF187201**, – / – , – / – , – / –
	UAM34284		54.944	-130.334	KF948562,KF948717/KF948718,KF948907/KF948908,KF949081/KF949082
	UAM34285		54.944	-130.334	KF948620, – / – , – / – , – / –
	UAM34286		54.944	-130.334	**AF187194**, – / – , – / – , – / –
	UAM48474		56.027	-130.071	**AF187200**, – / – , – / – , – / –
	UAM76246		55.767	-130.883	**AF187197**, – / – , – / – , – / –
	UAM48463	Alaska - White Pass	59.614	-135.167	**AF187192** , – / – , – / – , – / –
	UAM48465		59.614	-135.167	KF948625,KF948741/KF948742,KF948933/KF948934,KF949105/KF949106
	UAM48466		59.614	-135.167	KF948580, – / – ,KF948935/KF948936,KF949107/KF949108
	UAM48467		59.614	-135.167	KF948626, – / – ,KF948937/KF948938,KF949109/KF949110
	MSB155622	British Columbia	57.837	-131.390	KF948549, – / – , – / – , – / –
	MSB158060		58.045	-129.955	KF948551, – / – ,KF948805/KF948806, – / –
	MSB158239		56.496	-129.425	KF948535, – / – , – / – , – / –
	UAM52714		57.866	-131.284	**AF187204**, – / – , – / – , – / –
	UAM52715		57.855	-131.369	**AF187195**, – / – , – / – , – / –
	UAM68182		59.529	-134.908	KF948635,KF948771/KF948772,KF948973/KF948974,KF949139/KF949140
	MSB144359	Yukon	60.065	-128.619	KF948583,KF948641/KF948642,KF948787/KF948788, – / –
	MSB144391		60.065	-128.619	KF948584,KF948643/KF948644,KF948789/KF948790,KF948987/KF948988
	MSB144481		63.841	-135.461	KF948585,KF948645/KF948646,KF948791/KF948792,KF948989/KF948990
	MSB149145		61.996	-132.609	KF948586, – / – ,KF948795/KF948796, – / –
	MSB149156		61.996	-132.609	KF948587, – / – ,KF948797/KF948798, – / –
North Pacific Coast (NPC)	UAM48484	British Columbia	59.734	-133.667	**AF187196** , – / – ,KF948941/KF948942,KF949113/KF949114

	UAM52717		59.734	-133.667	KF948577, – / – , – / – , – / –
	UAM67039		50.817	-118.967	**AF187184**, – / – , – / – , – / –
	UAM67078		50.817	-120.467	**AF187185**, – / – , – / – , – / –
	UAM69491		50.817	-118.967	**AF187187**, – / – , – / – , – / –
	UAM69492		50.817	-118.967	**AF187188**, – / – , – / – , – / –
	UAM50787	Oregon	44.329	-123.720	**AF187183**, – / – , – / – , – / –
	UAM64165		44.524	-123.861	**AF187182**, – / – , – / – , – / –
	MSB43445	Washington	47.223	-120.993	**AF187180**,KF948679/KF948680,KF948847/KF948848, – / –
	MSB80232		48.200	-121.917	KF948612,KF948685/KF948686,KF948863/KF948864,KF949037/KF949038
	UAM41789		47.000	-120.950	**AF187181**, – / – , – / – , – / –
Southern (S1)	MSB50495	Arizona	34.125	-110.043	**AF187164**, – / – ,KF948849/KF948850,KF949029/KF949030
	MSB53559		33.795	-109.419	**AF187165**, – / – , – / – , – / –
	MSB88783		32.669	-109.881	– , – / – ,KF948865/KF948866,KF949039/KF949040
	MSB155126	Colorado	37.239	-107.759	KF948548, – / – ,KF948801/KF948802, – / –
	MSB43689	New Mexico	35.813	-106.523	**AF187166**, – / – , – / – , – / –
	MSB50701		35.267	-106.199	**AF187163**,KF948681/KF948682,KF948851/KF948852,KF949031/KF949032
Southern (S2)	UAM41634	Colorado	38.529	-106.325	**AF187169**, – / – , – / – , – / –
	UAM43522		38.529	-106.325	**AF187167**, – / – , – / – , – / –
	UAM43523		38.529	-106.325	**AF187170**, – / – , – / – , – / –
	UAM43524		38.529	-106.325	**AF187168**, – / – , – / – , – / –
	MSB155085	Wyoming	41.037	-110.404	KF948588,KF948651/KF948652,KF948799/KF948800,KF948993/KF948994
	UAM69038		41.000	-107.000	**AF187171**, – / – , – / – , – / –
M. montanus	MSB121523				KF948532, – / – , – / – , – / –
M. montanus					**AF119280**, – / – , – / – , – / –
M. pennsylvanicus	MSB110998				KF948531, – / – , – / – , – / –
M. pennsylvanicus	MSB149290				– ,KF948649/KF948650, – / – , – / –
M. pennsylvanicus					**AF119279**, – / – , – / – , – / –
M. pennsylvanicus					– , – / – , – / – ,**AY241463**/ –

Table 2. Primer list and PCR annealing temperatures. Primers used for amplification and sequencing mtDNA Cytochrome B (cyt*b*), and nuclear loci Protein C-est-2 (ETS2), β-fibrinogen (FGB), and Recombination Activating Protein 1 (Rag1) in *M. longicaudus* and outgroup taxa, with annealing temperatures (^{o}C) indicated in parentheses.



Primer	Sequence (5'-3')	Reference
cyt*b* (50)		
L14724		(Irwin *et al.* 1991; Kocher & White 1989)
Vole 14		(Conroy & Cook 1999)
ETS2 (63)		
ETS2F		(Lyons *et al.* 1997)
ETS2R		(Lyons *et al.* 1997)
FGB (65)		
MSB_MFGBF	CGTTTGGATTGGCGGAGTGG	This study, modified from Matocq *et al*. (2007)
MSB_MFGBR	GCACGTACGACAGGGACAACG	This study, modified from Matocq *et al*. (2007)
Rag1 (60)		
MSB_Rag1F	GCAGTCTCCTTTAGTTCCAGAC	This study, modified from Steppan *et al*.(2004)
MSB_Rag1R	CCAACAGGAACAACGTCAAGC	This study, modified from Steppan *et al*.(2004)

Irwin DM, Kocher TD, Wilson AC (1991) Evolution of the Cytochrome *b* gene of mammals. *Journal of Molecular Evolution* **32**, 128-144.

Kocher TD, White TJ (1989*) Evolutionary analysis via PCR* Stockton Press, New York.

Conroy CJ, Cook JA (1999) MtDNA evidence for repeated pulses of speciation within Arvicoline and Murid rodents. *Journal of Mammalian Evolution* **6**, 221-245.

Lyons LA, Laughlin TF, Copeland NG, et al. (1997) Comparative anchor tagged sequences (CATS) for integrative mapping of mammalian genomes. *Nature Genetics* **15**, 47-56.

Matocq MD, Shurtliff QR, Feldman CR (2007) Phylogenetics of the woodrat genus *Neotoma* (Rodentia: Muridae): Implications for the evolution of phenotypic variation in male external genitalia. *Molecular Phylogenetics and Evolution* **42**, 637-652.

Steppan SJ, Adkins RM, Anderson J (2004) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* **53**, 533-553.

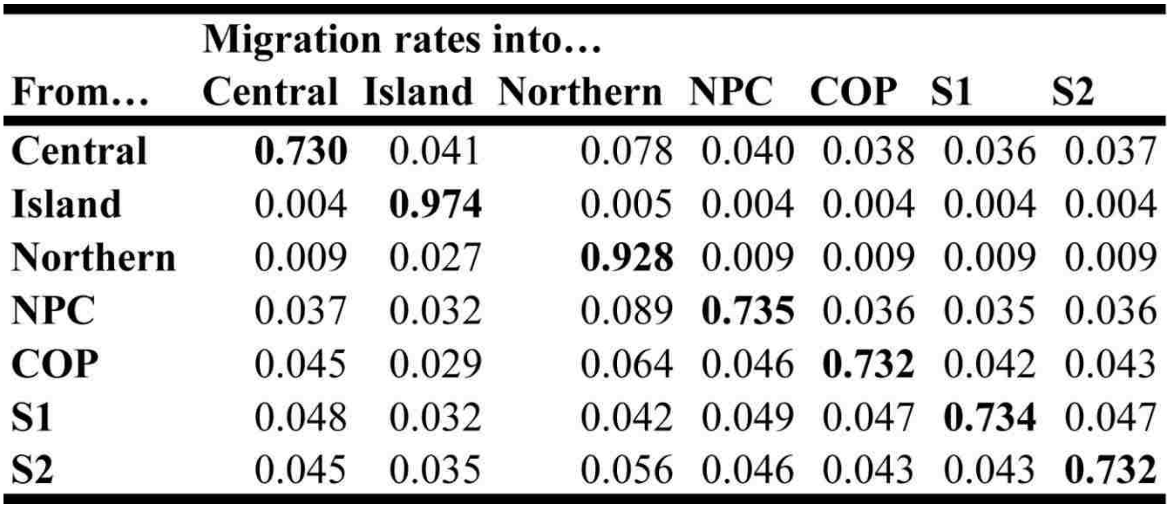
Table 3. Diversity indices, expansion statistics and models of evolution. n = haploid sample size; L = length of sequence; S = variable sites; Eta = #mutations; h = #haplotypes; Hd = haplotype diversity; π = nucleotide diversity; D = Tajima's D; Fs = Fu's FS; r = raggedness index; R2 = Ramos-Onsin's R2; Model = model of evolution as selected by MODELTEST. Bold values are significant at $p<0.05$ ($p<0.02$ for FS).

Group	Gene	n	L	S	h	Hd	Pi	D	Fs (p<.02)	H	R2	Model of Evolution
All Samples	Cytb	196	1143	175	127	0.990	0.01409	**-0.100**	**-0.776**	-0.182	**0.082**	TrN+I+G
	ETS2	80	733	–	–	–	–	–	–	–	–	GTR+I+G
	FGB	110	600	–	–	–	–	–	–	–	–	HKY+G
	Rag1	182	963	–	–	–	–	–	–	–	–	HKY
No Outgroups	Cytb	192	1143	133	123	0.990	0.01137	**-0.075**	**-0.656**	-0.001	**0.082**	
	ETS2	78	733	4	5	0.169	0.00026	**-0.005**	**-0.143**	0.003	**0.097**	
	FGB	108	600	13	13	0.126	0.00024	**-0.005**	**-0.252**	0.002	**0.091**	
	Rag1	89	963	10	11	0.162	0.00020	**-0.028**	**-0.186**	0.002	**0.095**	
Central	Cytb	16	1143	37	14	0.975	0.00761	-0.073	**0.031**	0.051	**0.140**	HKY+I
	ETS2	9	733	3	4	0.654	0.00117	-0.014	0.187	-0.004	**0.167**	GTR+I
	FGB	9	600	17	13	0.928	0.00793	-0.105	**0.055**	0.015	**0.138**	GTR+I
	Rag1	8	963	3	4	0.350	0.00039	**-0.022**	**0.266**	0.000	**0.190**	HKY
Colorado Plateau	Cytb	7	1143	22	7	1.000	0.00877	-0.055	0.503	-0.100	**0.190**	
	ETS2	2	733	12	2	0.667	0.01103	-0.046	0.962	0.081	**0.266**	
	FGB	7	600	8	7	0.879	0.00354	-0.043	0.179	0.000	**0.163**	
	Rag1	3	963	1	2	0.333	0.00035	-0.005	0.324	-0.002	**0.305**	
Island	Cytb	101	1143	70	61	0.983	0.00470	**-0.079**	**-0.319**	0.013	**0.092**	HKY+I+G
	ETS2	43	733	7	4	0.113	0.00044	**-0.024**	-0.039	0.003	0.109	HKY
	FGB	55	600	8	9	0.157	0.00028	**-0.005**	-0.080	0.006	**0.107**	HKY+I
	Rag1	50	963	3	4	0.116	0.00013	**-0.019**	**-0.117**	0.000	**0.110**	TrN
North	Cytb	46	1143	53	29	0.961	0.00395	**-0.094**	**-0.153**	-0.002	**0.108**	HKY+I
	ETS2	20	733	16	8	0.501	0.00043	-0.073	-0.087	-0.006	**0.113**	HKY+I
	FGB	29	600	5	7	0.728	0.00192	-0.053	-0.016	0.002	**0.109**	GTR+I
	Rag1	22	963	3	4	0.452	0.00052	-0.018	0.090	-0.002	**0.130**	HKY
North Pacific Coast	Cytb	11	1143	16	8	0.945	0.00511	-0.063	0.169	-0.019	**0.163**	
	ETS2	2	733	11	3	0.833	0.00989	-0.025	0.911	0.048	**0.268**	
	FGB	3	600	11	4	0.867	0.01002	-0.046	0.493	-0.008	**0.213**	
	Rag1	2	963	0	1	0.000	0.00000	–	–	–	–	
South	Cytb	11	1143	36	9	0.945	0.01378	-0.090	0.330	0.009	**0.156**	HKY+I
	ETS2	2	733	17	3	0.833	0.01551	-0.050	1.161	-0.009	**0.257**	HKY
	FGB	5	600	7	7	0.867	0.00501	-0.056	0.192	0.004	**0.179**	HKY+I
	Rag1	4	963	4	5	0.893	0.00156	-0.030	0.289	-0.012	**0.221**	HKY

Table 4. Between group net genetic distance. The number of base differences per site from estimation of net average between groups of sequences are shown. Standard error estimate(s) is above the diagonal. All ambiguous positions were removed for each sequence pair. Evolutionary analyses were conducted in MEGA5.

	Central	Colorado Plateau	Island	North Pacific Coast	Northern	Southern	*M. pennsylvanicus*	*M. montanus*
Central		0.40%	0.40%	0.40%	0.40%	0.40%	0.80%	0.70%
Colorado Plateau	2.30%		1.10%	0.80%	0.30%	0.40%	0.80%	0.70%
Island	2.50%	0.20%		0.30%	0.30%	0.40%	0.80%	0.70%
North Pacific Coast	2.30%	0.20%	1.10%		0.10%	0.40%	0.80%	0.80%
Northern	2.60%	1.10%	1.10%	0.50%		0.50%	0.80%	0.70%
Southern	3.30%	2.90%	3.30%	3.30%	3.30%		9.90%	7.70%
M. pennsylvanicus	10.20%	9.80%	10.00%	10.10%	10.00%	0.80%		0.60%
M. montanus	8.70%	8.40%	8.50%	9.00%	8.80%	0.70%	4.70%	

Table 5. Major cyt*b* lineage Bayesian migration estimates determined in BAYESASS. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows).



	Migration rates into…						
From…	**Central**	**Island**	**Northern**	**NPC**	**COP**	**S1**	**S2**
Central	**0.730**	0.041	0.078	0.040	0.038	0.036	0.037
Island	0.004	**0.974**	0.005	0.004	0.004	0.004	0.004
Northern	0.009	0.027	**0.928**	0.009	0.009	0.009	0.009
NPC	0.037	0.032	0.089	**0.735**	0.036	0.035	0.036
COP	0.045	0.029	0.064	0.046	**0.732**	0.042	0.043
S1	0.048	0.032	0.042	0.049	0.047	**0.734**	0.047
S2	0.045	0.035	0.056	0.046	0.043	0.043	**0.732**

Table 6. Island and Northern cyt*b* lineage populations near the geographic regions of contact (Haines and Juneau, Alaska). Bayesian migration estimates determined in BAYESASS. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows).

	Migration rates into…					
From…	**I-interior AK**	**I-Glacier Bay**	**I-Haines**	**I-Juneau**	**I-SE AK**	**I-Yukon**
I-interior AK	**0.682**	0.014	0.025	0.014	0.014	0.014
I-Glacier Bay	0.015	**0.682**	0.026	0.015	0.014	0.015
I-Haines	0.008	0.008	**0.830**	0.008	0.008	0.008
I-Juneau	0.014	0.015	0.027	**0.682**	0.014	0.014
I-SE AK	0.013	0.013	0.046	0.013	**0.680**	0.013
I-Yukon	0.014	0.014	0.035	0.014	0.014	**0.681**
N-interior AK	0.014	0.014	0.029	0.014	0.014	0.014
N-Glacier Bay	0.014	0.014	0.018	0.014	0.014	0.014
N-Haines	0.012	0.012	0.074	0.012	0.011	0.012
N-Juneau	0.013	0.013	0.063	0.013	0.013	0.013
N-SE AK	0.010	0.010	0.030	0.010	0.010	0.010
N-Yukon	0.013	0.013	0.049	0.013	0.013	0.013

Migration rates into…						
N-interior AK	**N-Glacier Bay**	**N-Haines**	**N-Juneau**	**N-SE AK**	**N-Yukon**	**From…**
0.014	0.014	0.014	0.014	0.022	0.014	**I-interior AK**
0.015	0.015	0.015	0.015	0.015	0.015	**I-Glacier Bay**
0.008	0.008	0.008	0.008	0.009	0.008	**I-Haines**
0.014	0.015	0.015	0.015	0.016	0.015	**I-Juneau**
0.013	0.013	0.013	0.013	0.023	0.013	**I-SE AK**
0.014	0.014	0.014	0.014	0.017	0.014	**I-Yukon**
0.681	0.014	0.015	0.014	0.020	0.014	**N-interior AK**
0.014	**0.682**	0.015	0.014	0.025	0.015	**N-Glacier Bay**
0.011	0.012	**0.681**	0.011	0.026	0.012	**N-Haines**
0.013	0.013	0.013	**0.680**	0.019	0.013	**N-Juneau**
0.010	0.010	0.010	0.010	**0.770**	0.011	**N-SE AK**
0.013	0.013	0.013	0.013	0.022	**0.680**	**N-Yukon**

Table 7. Bayesian migration estimates for Southeast Alaska populations determined in BAYESASS for *M. longicaudus*. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows). Location abbreviations are in Table 11 and I = Island and N = Northern lineages.

	Migration rates into…																			
From…	**I_CGF**	**I_CRN**	**I_DAL**	**I_FST**	**I_KRF**	**I_KSC**	**I_KUI**	**I_LUL**	**I_MIT**	**I_MLGB**	**I_MLHNS**	**I_MLJNO**	**I_MLS**	**I_MLSEC**	**I_MLSEN**	**I_NYS**	**I_ORI**	**I_POW**	**I_REV**	**I_SMZ**
I_CGF	**0.6773**	0.0094	0.0092	0.0093	0.0094	0.0094	0.0092	0.0091	0.0089	0.0089	0.0106	0.0089	0.0090	0.0090	0.0088	0.0093	0.0089	0.0096	0.0097	0.0092
I_CRN	0.0092	**0.6779**	0.0093	0.0094	0.0094	0.0094	0.0091	0.0091	0.0089	0.0088	0.0106	0.0089	0.0089	0.0090	0.0088	0.0093	0.0089	0.0096	0.0100	0.0091
I_DAL	0.0093	0.0096	**0.6769**	0.0095	0.0094	0.0095	0.0091	0.0091	0.0089	0.0087	0.0111	0.0089	0.0088	0.0089	0.0088	0.0094	0.0089	0.0098	0.0102	0.0090
I_FST	0.0092	0.0096	0.0093	**0.6772**	0.0094	0.0094	0.0092	0.0092	0.0089	0.0090	0.0103	0.0090	0.0089	0.0091	0.0088	0.0093	0.0090	0.0097	0.0099	0.0092
I_KRF	0.0093	0.0094	0.0092	0.0092	**0.6774**	0.0094	0.0091	0.0092	0.0089	0.0089	0.0103	0.0090	0.0090	0.0090	0.0089	0.0094	0.0090	0.0097	0.0098	0.0092
I_KSC	0.0093	0.0096	0.0091	0.0094	0.0095	**0.6774**	0.0091	0.0091	0.0089	0.0088	0.0110	0.0089	0.0088	0.0089	0.0088	0.0094	0.0088	0.0099	0.0101	0.0091
I_KUI	0.0093	0.0094	0.0093	0.0093	0.0095	0.0094	**0.6770**	0.0091	0.0089	0.0089	0.0101	0.0090	0.0089	0.0091	0.0089	0.0094	0.0090	0.0095	0.0098	0.0092
I_LUL	0.0093	0.0095	0.0092	0.0094	0.0095	0.0094	0.0092	**0.6767**	0.0090	0.0089	0.0104	0.0090	0.0089	0.0091	0.0089	0.0093	0.0089	0.0096	0.0098	0.0092
I_MIT	0.0092	0.0093	0.0092	0.0093	0.0093	0.0094	0.0092	0.0092	**0.6761**	0.0091	0.0100	0.0092	0.0091	0.0092	0.0091	0.0093	0.0091	0.0095	0.0095	0.0092
I_MLGB	0.0092	0.0093	0.0093	0.0094	0.0093	0.0093	0.0092	0.0092	0.0092	**0.6761**	0.0097	0.0091	0.0092	0.0092	0.0092	0.0093	0.0091	0.0094	0.0096	0.0092
I_MLHNS	0.0095	0.0097	0.0090	0.0095	0.0095	0.0095	0.0088	0.0090	0.0087	0.0086	**0.6821**	0.0087	0.0086	0.0088	0.0084	0.0094	0.0085	0.0100	0.0107	0.0090
I_MLJNO	0.0092	0.0094	0.0092	0.0093	0.0093	0.0093	0.0092	0.0092	0.0091	0.0092	0.0100	**0.6760**	0.0091	0.0092	0.0091	0.0093	0.0091	0.0094	0.0096	0.0092
I_MLS	0.0093	0.0094	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0091	0.0092	0.0095	0.0092	**0.6761**	0.0092	0.0092	0.0093	0.0092	0.0093	0.0095	0.0092
I_MLSEC	0.0092	0.0094	0.0092	0.0095	0.0094	0.0095	0.0091	0.0092	0.0090	0.0090	0.0102	0.0090	0.0090	**0.6763**	0.0089	0.0093	0.0090	0.0095	0.0099	0.0092
I_MLSEN	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0094	0.0092	0.0092	0.0092	**0.6762**	0.0092	0.0092	0.0093	0.0093	0.0093
I_NYS	0.0093	0.0094	0.0092	0.0093	0.0094	0.0095	0.0092	0.0092	0.0090	0.0090	0.0104	0.0090	0.0090	0.0091	0.0089	**0.6767**	0.0090	0.0096	0.0097	0.0092
I_ORI	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0093	0.0092	0.0092	0.0092	0.0092	0.0093	**0.6762**	0.0093	0.0093	0.0093
I_POW	0.0093	0.0096	0.0092	0.0095	0.0095	0.0094	0.0091	0.0091	0.0087	0.0087	0.0113	0.0088	0.0087	0.0090	0.0087	0.0093	0.0087	**0.6783**	0.0102	0.0090
I_REV	0.0094	0.0096	0.0091	0.0095	0.0094	0.0094	0.0090	0.0091	0.0087	0.0088	0.0107	0.0087	0.0088	0.0090	0.0086	0.0093	0.0087	0.0095	**0.6799**	0.0091
I_SMZ	0.0093	0.0095	0.0093	0.0094	0.0094	0.0095	0.0091	0.0091	0.0089	0.0088	0.0108	0.0089	0.0088	0.0090	0.0088	0.0093	0.0089	0.0098	0.0101	**0.6768**
I_SWN	0.0092	0.0093	0.0092	0.0092	0.0093	0.0093	0.0093	0.0093	0.0093	0.0092	0.0094	0.0092	0.0092	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0093
I_TXN	0.0092	0.0093	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0092	0.0092	0.0092	0.0092	0.0092	0.0092	0.0093	0.0093	0.0092
I_WRG	0.0093	0.0094	0.0092	0.0093	0.0093	0.0094	0.0093	0.0092	0.0091	0.0091	0.0097	0.0090	0.0090	0.0091	0.0090	0.0093	0.0091	0.0094	0.0097	0.0092
I_WRN	0.0093	0.0096	0.0091	0.0094	0.0095	0.0094	0.0090	0.0090	0.0087	0.0087	0.0113	0.0088	0.0087	0.0089	0.0086	0.0093	0.0087	0.0099	0.0102	0.0090
I_YTS	0.0093	0.0094	0.0092	0.0093	0.0093	0.0094	0.0092	0.0092	0.0091	0.0091	0.0100	0.0091	0.0091	0.0091	0.0090	0.0093	0.0091	0.0095	0.0096	0.0092
I_ZRB	0.0092	0.0094	0.0093	0.0094	0.0094	0.0093	0.0091	0.0092	0.0091	0.0090	0.0101	0.0091	0.0091	0.0091	0.0091	0.0093	0.0091	0.0095	0.0097	0.0092
N_MLCP	0.0094	0.0093	0.0093	0.0092	0.0094	0.0094	0.0092	0.0092	0.0090	0.0090	0.0096	0.0090	0.0090	0.0091	0.0090	0.0093	0.0091	0.0095	0.0096	0.0092
N_MLGB	0.0093	0.0093	0.0092	0.0093	0.0093	0.0093	0.0092	0.0092	0.0091	0.0091	0.0093	0.0092	0.0092	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0092
N_MLHNS	0.0092	0.0092	0.0093	0.0092	0.0093	0.0092	0.0093	0.0093	0.0092	0.0093	0.0093	0.0092	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0093	0.0093
N_MLJNO	0.0093	0.0095	0.0093	0.0096	0.0096	0.0095	0.0090	0.0091	0.0088	0.0087	0.0115	0.0087	0.0087	0.0089	0.0086	0.0094	0.0086	0.0099	0.0109	0.0089
N_MLMFD	0.0092	0.0095	0.0093	0.0092	0.0095	0.0096	0.0092	0.0091	0.0088	0.0087	0.0103	0.0088	0.0088	0.0089	0.0087	0.0093	0.0088	0.0096	0.0100	0.0090
N_MLSEC	0.0092	0.0093	0.0093	0.0092	0.0093	0.0093	0.0093	0.0092	0.0092	0.0091	0.0095	0.0092	0.0091	0.0091	0.0092	0.0093	0.0092	0.0094	0.0094	0.0092
N_MLSES	0.0093	0.0093	0.0092	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0093	0.0092	0.0092	0.0093	0.0093	0.0093
N_MLTYR	0.0093	0.0093	0.0092	0.0093	0.0094	0.0093	0.0092	0.0092	0.0092	0.0092	0.0100	0.0091	0.0091	0.0092	0.0091	0.0093	0.0091	0.0094	0.0095	0.0092
N_MLWP	0.0093	0.0095	0.0092	0.0092	0.0094	0.0095	0.0092	0.0092	0.0090	0.0089	0.0101	0.0090	0.0090	0.0091	0.0090	0.0093	0.0090	0.0095	0.0098	0.0092
N_YTC	0.0092	0.0093	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0091	0.0091	0.0098	0.0091	0.0091	0.0091	0.0091	0.0093	0.0091	0.0094	0.0096	0.0092

Migration rates into…																
I_SWN	**I_TXN**	**I_WRG**	**I_WRN**	**I_YTS**	**I_ZRB**	**N_MLCP**	**N_MLGB**	**N_MLHNS**	**N_MLJNO**	**N_MLMFD**	**N_MLSEC**	**N_MLSES**	**N_MLTYR**	**N_MLWP**	**N_YTC**	**From…**
0.0090	0.0089	0.0091	0.0099	0.0089	0.0091	0.0092	0.0090	0.0090	0.0093	0.0098	0.0091	0.0090	0.0090	0.0096	0.0089	**I_CGF**
0.0090	0.0089	0.0091	0.0099	0.0088	0.0090	0.0090	0.0090	0.0090	0.0095	0.0098	0.0090	0.0088	0.0089	0.0095	0.0089	**I_CRN**
0.0089	0.0089	0.0090	0.0101	0.0088	0.0090	0.0091	0.0089	0.0089	0.0097	0.0098	0.0089	0.0088	0.0089	0.0096	0.0088	**I_DAL**
0.0090	0.0090	0.0091	0.0099	0.0089	0.0090	0.0091	0.0090	0.0090	0.0095	0.0097	0.0089	0.0090	0.0090	0.0096	0.0089	**I_FST**
0.0090	0.0090	0.0091	0.0098	0.0089	0.0090	0.0091	0.0090	0.0090	0.0095	0.0098	0.0091	0.0090	0.0089	0.0095	0.0088	**I_KRF**
0.0089	0.0089	0.0089	0.0101	0.0088	0.0091	0.0091	0.0089	0.0089	0.0095	0.0098	0.0089	0.0088	0.0090	0.0097	0.0088	**I_KSC**
0.0090	0.0090	0.0091	0.0098	0.0089	0.0090	0.0093	0.0091	0.0091	0.0093	0.0099	0.0090	0.0090	0.0089	0.0097	0.0089	**I_KUI**
0.0091	0.0089	0.0091	0.0099	0.0089	0.0092	0.0091	0.0090	0.0090	0.0094	0.0098	0.0090	0.0090	0.0090	0.0096	0.0089	**I_LUL**
0.0092	0.0092	0.0092	0.0096	0.0091	0.0091	0.0092	0.0091	0.0091	0.0095	0.0094	0.0091	0.0091	0.0092	0.0094	0.0092	**I_MIT**
0.0092	0.0091	0.0092	0.0095	0.0091	0.0092	0.0092	0.0091	0.0091	0.0095	0.0094	0.0092	0.0091	0.0092	0.0093	0.0091	**I_MLGB**
0.0088	0.0085	0.0089	0.0105	0.0084	0.0089	0.0087	0.0086	0.0085	0.0100	0.0100	0.0085	0.0086	0.0089	0.0097	0.0085	**I_MLHNS**
0.0092	0.0091	0.0092	0.0095	0.0090	0.0092	0.0092	0.0091	0.0091	0.0095	0.0095	0.0091	0.0091	0.0092	0.0094	0.0091	**I_MLJNO**
0.0092	0.0092	0.0092	0.0094	0.0092	0.0092	0.0092	0.0092	0.0092	0.0092	0.0094	0.0092	0.0092	0.0092	0.0093	0.0092	**I_MLS**
0.0090	0.0090	0.0091	0.0099	0.0089	0.0092	0.0091	0.0090	0.0090	0.0096	0.0097	0.0090	0.0089	0.0091	0.0096	0.0091	**I_MLSEC**
0.0092	0.0093	0.0093	0.0093	0.0092	0.0092	0.0093	0.0092	0.0093	0.0092	0.0094	0.0092	0.0093	0.0093	0.0093	0.0092	**I_MLSEN**
0.0090	0.0090	0.0091	0.0098	0.0090	0.0091	0.0092	0.0090	0.0091	0.0094	0.0096	0.0090	0.0089	0.0091	0.0095	0.0090	**I_NYS**
0.0092	0.0092	0.0093	0.0093	0.0092	0.0093	0.0093	0.0092	0.0092	0.0092	0.0094	0.0092	0.0093	0.0091	0.0093	0.0093	**I_ORI**
0.0089	0.0087	0.0090	0.0103	0.0087	0.0090	0.0091	0.0088	0.0088	0.0098	0.0100	0.0088	0.0088	0.0089	0.0096	0.0087	**I_POW**
0.0088	0.0087	0.0090	0.0101	0.0086	0.0090	0.0091	0.0089	0.0087	0.0099	0.0102	0.0087	0.0088	0.0088	0.0098	0.0087	**I_REV**
0.0089	0.0089	0.0090	0.0101	0.0088	0.0090	0.0090	0.0089	0.0090	0.0096	0.0098	0.0089	0.0089	0.0090	0.0096	0.0089	**I_SMZ**
0.6762	0.0092	0.0092	0.0093	0.0092	0.0092	0.0092	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0092	0.0093	0.0092	**I_SWN**
0.0092	**0.6762**	0.0092	0.0093	0.0092	0.0093	0.0093	0.0092	0.0093	0.0093	0.0093	0.0093	0.0092	0.0092	0.0093	0.0092	**I_TXN**
0.0090	0.0091	**0.6765**	0.0097	0.0090	0.0092	0.0092	0.0091	0.0092	0.0094	0.0097	0.0091	0.0091	0.0091	0.0095	0.0091	**I_WRG**
0.0089	0.0087	0.0089	**0.6797**	0.0087	0.0089	0.0089	0.0088	0.0089	0.0097	0.0099	0.0087	0.0087	0.0088	0.0096	0.0087	**I_WRN**
0.0091	0.0091	0.0092	0.0096	**0.6761**	0.0091	0.0092	0.0091	0.0091	0.0094	0.0095	0.0091	0.0091	0.0091	0.0094	0.0091	**I_YTS**
0.0091	0.0091	0.0092	0.0096	0.0090	**0.6762**	0.0091	0.0091	0.0091	0.0095	0.0095	0.0091	0.0091	0.0091	0.0095	0.0090	**I_ZRB**
0.0091	0.0091	0.0091	0.0096	0.0091	0.0091	**0.6771**	0.0092	0.0091	0.0093	0.0098	0.0091	0.0090	0.0090	0.0096	0.0090	**N_MLCP**
0.0092	0.0091	0.0092	0.0093	0.0092	0.0092	0.0093	**0.6765**	0.0093	0.0093	0.0094	0.0093	0.0092	0.0092	0.0093	0.0092	**N_MLGB**
0.0092	0.0092	0.0093	0.0093	0.0092	0.0093	0.0093	0.0092	**0.6762**	0.0092	0.0093	0.0092	0.0092	0.0092	0.0093	0.0092	**N_MLHNS**
0.0088	0.0087	0.0090	0.0104	0.0086	0.0090	0.0090	0.0087	0.0085	**0.6781**	0.0102	0.0086	0.0087	0.0089	0.0098	0.0087	**N_MLJNO**
0.0089	0.0088	0.0089	0.0101	0.0087	0.0090	0.0091	0.0090	0.0089	0.0095	**0.6797**	0.0089	0.0088	0.0088	0.0099	0.0087	**N_MLMFD**
0.0092	0.0092	0.0092	0.0094	0.0092	0.0092	0.0093	0.0092	0.0092	0.0092	0.0095	**0.6764**	0.0092	0.0092	0.0093	0.0092	**N_MLSEC**
0.0092	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0092	0.0092	0.0093	0.0093	0.0092	**0.6762**	0.0092	0.0093	0.0092	**N_MLSES**
0.0092	0.0091	0.0092	0.0096	0.0091	0.0092	0.0092	0.0091	0.0092	0.0094	0.0094	0.0091	0.0091	**0.6761**	0.0093	0.0091	**N_MLTYR**
0.0091	0.0090	0.0091	0.0099	0.0089	0.0091	0.0092	0.0090	0.0090	0.0093	0.0099	0.0090	0.0090	0.0090	**0.6772**	0.0089	**N_MLWP**
0.0091	0.0091	0.0092	0.0095	0.0091	0.0092	0.0092	0.0092	0.0091	0.0094	0.0095	0.0092	0.0091	0.0092	0.0094	**0.6761**	**N_YTC**

Table 8. Locality abbreviations. Standard state and province abbreviations apply for unlisted locations.

Region	Location
Alaskan Islands	Chichagof (CGF)
	Coronation (CRN)
	Dall (DAL)
	Forrester (FRS)
	Kosciusko (KSC)
	Kuiu (KUI)
	Kupreanof (KRF)
	Lulu (LUL)
	Mitkof (MIT)
	Noyes (NYS)
	Orr (ORI)
	Prince of Wales (POW)
	Revillagigedo (REV)
	Suemez (SMZ)
	Sukkwan (SWN)
	Tuxekan (TXN)
	Warren (WRN)
	Wrangell (WRG)
	Zarembo (ZRB)
mainland	British Columbia (BC)
	Mainland Southeast Alaska (MLSE)
	Northern mainalnd Southeast (MLSEN)
	Cleveland Peninsula (CP/MLCP)
	Foggy Bay (FB/MLFB)
	Glacier Bay (GB/MLGB)
	Haines (HNS/MLHNS)
	Interior Alaska (IAK/MLS)
	Juneau (JNO/MLJNO)
	Klukwan (KLU/MLKLU)
	Misty Fjords (MFD/MLMFD)
	Southeast Central (SEC AK/MLSEC)
	Southeast North (SEN AK/MLSEN)
	Southeast South (SES AK/MLSES)
	Skagway (SKW/MLSKW)
	Taiya River (TYR/MLTYR)
	White Pass (WP/MLWP)
	British Columbia - Central (BCC)
	British Columbia - North (BCN)
	British Columbia - South (BCS)
	Washington (WA)
	Yukon Territory - Central (YTC)
	Yukon Territory - South (YTS)

Table 9. Cyt *b* and phased multilocus divergence date estimates.

	cyt*b*			multilocus		
Lineage	**95% HPD lower**	**mean**	**95% HPD upper**	**95% HPD lower**	**mean**	**95% HPD upper**
M.longicaudus	775,600	1,115,100	1,561,100	220,800	296,400	402,200
Southern	371,700	727,600	1,106,900			
S1	160,800	307,900	487,200			
S2	23,737	78,589	142,200			
Central/North/Island	459,600	661,200	906,300			
Central	128,500	217,000	314,400			
Colorado Plateau	171,400	294,300	420,500			
North/Island	306,400	435,400	581,900	124,200	150,000	188,000
North Pacific Coast	169,500	294,200	169,500			
North	105,000	159,000	221,600			
Island	164,600	225,100	294,200			

CHAPTER 3

Deer mice at high-latitudes: genetic consequences of refugia and insularity in response to historical climate change

ABSTRACT

Aim We surveyed genetic data for the northern geographic extent of deer mice (genus *Peromyscus*) to identify lineage diversification as a result of occupancy in uncommon, multiple ice-free regions, and rapid post-glacial colonization.

Location North America, with a focus on northwestern North America (British Columbia, Alaska, and Yukon).

Methods We used sequences from one mitochondrial and three nuclear loci from 390 deer mouse specimens, including *P. maniculatus, P. keeni,* and *Peromyscus* sp. nov. (Yukon), to assess species limits, population structure, and demographic change as a result of historical climate change. Historical migration estimates and phylogenetic gene tree and species tree estimates used a Bayesian approach. Species distribution models were built to explore niche overlap of major clades.

Results Divergence among the three clades began prior to the last interglacial. Both the cyt *b* and multilocus species trees strongly support *P. keeni* and *Peromyscus* sp. nov. (Yukon) as independent from *P. maniculatus*; however, *P. maniculatus* likely represents multiple species. Substantial substructure was observed for *P. keeni* and *P. maniculatus*. Northern clades differ in potential distributions.

Main conclusions Northwestern species of deer mice persisted in at least three ice-free regions (Beringia, Southeast Alaska and southern continent) throughout the Pleistocene glacial cycles. In Southeast Alaska, there is limited gene flow among island populations of *P. keeni*. Taxonomic revisions are needed for *P. maniculatus.* No sympatric locations were identified, but are likely to be detected with additional sampling in regions of close proximity.

INTRODUCTION

Vicariant events that result in genetic differentiation are a major focus in phylogeographic studies. Pleistocene (2.5 Ma – 11.7 ka) vicariant events seem to have initiated speciation in a diversity of northwestern North American animals and plants, including North American warblers (Parulidae, Mengel, 1964), mountain sheep (*Ovis* sp., Loehr *et al.*, 2006), grasshoppers (*Melanoplus*, Carstens & Knowles, 2007a), and plants (angiosperms and a fern, Soltis *et al.*, 1997). For many northern organisms, glacial-interglacial cycles drove instances of landscape fragmentation and population isolation, often followed by secondary contact. Those events left distinct genetic signatures of stability for populations that persisted in ice-free regions and expansion for populations descendent from postglacial colonizers (Hewitt, 1996; Lessa *et al.*, 2003).

During glacial periods, most western North America species persisted in ice-free regions either north in Beringia or south of the ice (Rand, 1954; Jorgensen *et al.*, 2003; Eddingsaas *et al.*, 2004). Glacial refugia along the northwestern coast of North America, the result of lower sea levels and exposed continental shelf, have also been proposed (Fladmark, 1979; Hewitt, 1996; Fleming & Cook, 2002), but remain the subject of extensive debate (Cook & MacDonald, 2013). Generally, only widespread species such as the red fox (*Vulpes vulpes*, Aubry *et al.*, 2009), alpine groundsel (*Packera pauciflora*, Bain & Golden, 2005), and ermine (*Mustela erminea*, Fleming & Cook, 2002)], persisted in both southern and northern ice-free regions. Most species were limited to proximate regions (e.g., Southern and southern Northwest Coast, Beringia and northern Northwest Coast). Identifying the constituent species and characterizing the communities that persisted in glacial refugia provides a basis for understanding the temporal and spatial dynamics of biotic response to climate change (Soltis *et al.*, 1997; Carstens *et al.*, 2013) and for the development of effective conservation strategies (Cook *et al.*, 2006).

The genetic footprints of populations can provide insight into the late Pleistocene history of isolation, expansion, and in some cases, secondary contact (e.g., Lucid & Cook, 2007; Weksler *et al.*, 2010). Common regions of secondary contact in western North America are in areas between and along the Coastal and Rocky mountain ranges (Remington, 1968; Swenson & Howard, 2005). To date, only a handful of studies identify regions where multiple lineages contact in northwestern North America. Arctic grayling (*Thymallus* sp.), for example, persisted in two ice-free regions in Beringia, resulting in three distinct mtDNA lineages from Northern Beringia, Southern Beringia, and Yukon (Stamford & Taylor, 2004). Alpine groundsel (*Packera pauciflora*, Bain & Golden, 2005), spruce beetles (*Dendroctonus rufipennis*, Maroja *et al.*, 2007), and shrews (*Sorex cinereus* complex, Hope *et al.*, 2012) persisted in both Beringia and on the continent south of the ice, while lake trout (*Salvelinus namaycush*, Wilson & Hebert, 1998), ermine (*Mustela erminea*, Fleming & Cook, 2002), lodgepole pine (*Pinus contorta*, Godbout *et al.*, 2008), and the long-tailed vole (*Microtus longicaudus*, Sawyer and Cook *submitted*), endured glacial periods in ice-free areas in Beringia, southern continent (south of the ice) and coastal refugia. Additionally, based on a previously identified clade restricted to Yukon, deer mice are hypothesized to have persisted south of the Cordilleran and Laurentide ice, in Pacific coastal refugia and potentially in Beringia (Wike, 1998; Lucid & Cook, 2007).

Deer mice of the genus *Peromyscus* (Cricetidae, Neotominae) are among North America’s most species-rich, widespread, and well-studied terrestrial small mammals.

The taxonomic and phylogeographic history of *Peromyscus* in the Pacific Northwest was first addressed with recognition of *P. keeni* (as *P. sitkensis*, Merriam, 1897) as distinct from *P. maniculatus* by Cowan (1935). Since then, various genetic approaches (Hogan *et al.*, 1997; Dragoo *et al.*, 2006; Gering *et al.*, 2009) and analysis of phallic and bacular morphology (Sullivan *et al.*, 1990) confirmed the separation of *P. maniculatus* (Wagner, 1845) from *P. keeni* (Rhoads, 1894) or identified areas of sympatry (Gunn & Greenbaum, 1986; Hogan *et al.*, 1993; Zheng *et al.*, 2003). Across the broad, continental distribution of *P. maniculatus* , considerable variation in morphological characters exists and is likely related to wide habitat variation ranging from scrublands to deserts, forests, and swamps (Hall, 1981; Carleton, 1989; Hogan *et al.*, 1993). Six well-supported mtDNA lineages were identified throughout this range (Dragoo *et al.*, 2006; Kalkvik *et al.*, 2012): clade 1) Pacific Northwest and Rocky Mountain States, 2) Plains States, 3) West Coast, 4) southern New Mexico and Mexico, 5) northeast United States and eastern Canada, and 6) northeast and north-central United Sates and south-central Canada. Patterns of phylogeographic structure are consistent with those uncovered in other mammals that experienced Pleistocene range fluctuations in North America (Brant & Orti, 2003; Runck & Cook, 2005), but high levels of mitochondrial differentiation call into question the validity of *P. maniculatus* as a single species (Dragoo *et al.*, 2006).

Relative to *P. maniculatus, P. keeni* occurs within 200 km of the Pacific Coast, from northern Washington to southern Yukon, and is found on large islands in British Columbia (Vancouver Island, Haida Gwaii) and the Alexander Archipelago (AA) of Southeast Alaska. *Peromyscus keeni* prefers open canopy forests from coastal lowlands through high-elevation and alpine forest. Where their distributions overlap, *P. keeni* can be found at higher elevations (Hall, 1981; Hogan *et al.*, 1993). Studies suggest that *P. keeni* survived the Pleistocene in coastal refugia in either British Columbia or Southeast Alaska (Zheng *et al.*, 2003; Lucid & Cook, 2004; Walker, 2005).

The northwestern extent of the ranges of both *P. maniculatus* and *P. keeni* is in Yukon (Hall, 1981; Hogan *et al.*, 1993; Wike, 1998). Analyses of DNA restriction fragment length polymorphisms and sequences suggest the presence of a previously unidentified species in Yukon (*Peromyscus* sp. nov.), with comparable divergence times with either *P. maniculatus* or *P. keeni* that pre-date the Wisconsinan glaciation (Wike, 1998; Lucid & Cook, 2007). The dynamics, both within and among *P. keeni*, *P. maniculatus* and *Peromyscus* sp. nov., allow us to study the impact of Pleistocene range fragmentation into multiple refugia and potential post-glacial secondary contact of these divergent clades.

We explore the effects of Pleistocene glacial-interglacial cycles on speciation and lineage diversification for the *P. maniculatus* complex at the northern extent of their range. We hypothesize signatures of three regions of glacial persistence will be present: far-eastern Beringia for *Peromyscus* sp. nov. (Wike, 1998); Pacific Northwest Coast (e.g., British Columbia, Southeast Alaska) for *P. keeni* (Zheng *et al.*, 2003; Lucid & Cook, 2004); and southern continent for *P. maniculatus* (Zheng *et al.*, 2003; Yang & Kenagy, 2009). Occupation in all of these ice-free regions during the LGM would represent an uncommon pattern of glacial persistence, subsequent diversification, and location of secondary contact when compared to other glacial relics (Cook *et al.*, 2001; Cook *et al.*, 2006; Shafer *et al.*, 2010). We also evaluate strength of genetic divergence as a result of isolation on levels of contemporary gene flow and genetic differentiation both within and among clades. Lastly, we evaluate differences in niche requirements among *Peromyscus* sp. nov., *P. keeni* and *P. maniculatus* for signs of differentiation in climatic requirements in response to historical climate and regions of glacial persistence.

MATERIALS AND METHODS

Sampling and DNA sequencing

A total of 390 specimens representing 69 localities and all six clades identified in previous work on *P. maniculatus* (Dragoo *et al.*, 2006; Kalkvik *et al.*, 2012) were analyzed. These spanned the geographic range of *P. maniculatus*, *P. keeni*, with focused sampling in Yukon and Southeast Alaska (Table 1 and Fig. 1). Most specimens were collected over 25 years of fieldwork and deposited at either the University of Alaska Museum of the North (n=235) or the Museum of Southwestern Biology at the University of New Mexico (n=140). The University of Washington Burke Museum (n=8) and Gwaii Haanas National Park Reserve and Haida Heritage Site (n=7) also provided material. Of these, 71 specimens of *P. keeni* were used only for clade specific assessments of migration analyses. Seven of eight subspecies of *P. keeni* and 17 of 27 subspecies of *P. maniculatus* are represented. In additional to sequences generated, we obtained one *P. keeni*, 54 *P. maniculatus*, and *P. leucopus* (outgroup) cyt *b* sequence, and for β-fibrinogen (FGB) and interphotoreceptor retinoid-binding protein (IRBP) for *P. melanotis* from GenBank (outgroup; Table 1). Lastly, for migration estimates within *P. keeni*, additional shorter cyt *b* sequences (479 bp; n=220) from across the geographic range of *P. keeni* were downloaded from GenBank (Zheng *et al.*, 2003; Lucid & Cook, 2004).

Using either Omega Bio-Tek (Norcross, GA) E.Z.N.A. kits or through standard salt methods, we extracted total genomic DNA to a final concentration of 50ng µl^{-1}. The complete mitochondrial (mtDNA) cytochrome *b* gene (cyt *b*, 1143 bp, n=204) was amplified using primers L14734 (Ohdachi *et al.*, 2001) and CytBRev (Anderson & Yates, 2000). The following partial nuclear genes (nuDNA) were also sequenced (Table 2): FGB (587 bp, n=169), IRBP (459 bp, n=160), and zona pellucida 3 (ZP3, 314 bp, n=176). Polymerase chain reaction (PCR) experiments used 1µl DNA extract, 1 µl of each primer (2mM), 1.5 µl PCR buffer (10x), 1.5 µl $MgCl_2$ (25mM), 1.25 µl of dNTP's (10mM), 1.25 µl of Bovine Serum Albumen (BSA, 1.5mM), and 0.08 µl of Ampli*Taq* DNA polymerase (Applied Biosystems, Foster City, CA, USA) and adjusted to a final volume of 15 µl with ddH_2O. PCR products were cleaned using ExoSap-IT (Affymetrix, Santa Clara, CA). We used original PCR primers for automated sequencing at either the High Throughput Genomic Center (Seattle, WA, USA) or using an Applied Biosystems 3110 DNA sequencer (Molecular Biology Facility, UNM) with BigDye v3.1 (Applied Biosystems) chemistry.

Alleles of heterozygotes were inferred using five independently seeded runs of 1000 iterations with an initial burn-in of 1000 implemented in PHASE v2.1 (Stephens *et al.*, 2001; Stephens & Scheet, 2005). The iterations with the best goodness-of-fit were chosen. Posterior probabilities for nucleotides ≥0.85 were chosen, otherwise ambiguous sites were coded as N. Only phased sequences were used for analysis. Sequences were edited in SEQUENCHER v4.2 (GeneCodes Corporation), aligned in MEGA v5.2 (Tamura *et al.*, 2011) using the MUSCLE algorithm and checked by eye.

Inferences of population history

Extended Bayesian skyline plots (EBSP, Heled & Drummond, 2008) and Bayesian skyline plots were implemented in BEAST to explore multilocus and cyt *b* historical demography, respectively, for each major cyt *b* clade. Loci were unlinked and partitioned to their respective substitution models (Table 3), as determined using MODELTEST (Posada & Crandall, 1998). All loci were set to strict molecular clocks and rates for phased nuclear loci were estimated based on cyt *b* with a rate of 4% Myr^{-1} (rodent rate of 6-10% Myr^{-1}, Brunhoff *et al.*, 2003; Hope *et al.*, 2013). Three independent runs per data set included Markov chain Monte Carlo (MCMC) chains of 2 billion steps, sampled every 2 million. We used TRACER v1.5 (Rambaut & Drummond, 2007) to assess convergence. Significant population size change occurred if zero was excluded from the 95% confidence interval (CI) of the estimate of the number of size-change steps (Lim & Sheldon, 2011).

To test for recent demographic fluctuation, we used DNASP 5.10.1 (Librado & Rozas, 2009) to calculate standard diversity indices for the major cyt *b* clades for each phased locus, including segregating sites (S), haplotype diversity (Hd), and nucleotide diversity (π). Additionally, we calculated Tajima's D (1989), Fu's F*s* (1997), and R_2 (Ramos-Onsins & Rozas, 2002) with 10 thousand coalescent simulations to assess historic demographic change or selection. Selection potential was also assessed through an HKA Test (Hudson *et al.*, 1987). Cyt *b* net genetic distance among major clades was calculated in MEGA.

Phylogenetic analyses and timing of divergence

Phylogenetic relationships of *Peromyscus* in Yukon were initially evaluated for cyt *b* using Maximum Likelihood (ML) and Bayesian frameworks. Models of evolution (Table 3) were inferred in MODELTEST (Posada & Crandall, 1998; Posada & Buckley, 2004) and ML calculations with 1000 bootstrap replicates were achieved in MEGA. Divergence dates for major clades and a Bayesian phylogeny were simultaneously estimated using BEAST v1.7.5 (Drummond *et al.*, 2012) with input files prepared in BEAUTI v1.7.5. Settings for three independent runs were 2 billion generations, sampled every 2 million generations and using an uncorrelated lognormal relaxed clock. Tree priors were a speciation Yule Process (Yule, 1925; Gernhard, 2008) using a random start tree. Time to Most Recent Common Ancestor (TMRCA) was determined with a 95% posterior probability distribution in TRACER v1.5. Runs with trace convergence and acceptable effective sample size (ESS; minimum of 200) were combined using LOGCOMBINER v1.7.5, with a 10% burn-in and annotated in TREEANNOTATOR v1.7.5. Topologies were visualized in FIGTREE v1.4.0 (Rambaut, 2009).

A multi-locus approach to phylogenetics provides independent signals that contribute to the discovery of species' relationships (Maddison, 1997; Carstens & Knowles, 2007b; Edwards *et al.*, 2007). Using a coalescent Bayesian MCMC method implemented in BEAST, *BEAST (Heled & Drummond, 2010) co-estimates species trees and contained gene trees. *A priori* groups were based on supported cyt *b* lineages and data were partitioned by independent, unlinked loci using an uncorrelated, lognormal relaxed clocks for cyt *b* at a rate of 4% Myr^{-1} while estimated nuclear loci used strict molecular clocks. Models of evolution (Table 3) were determined using MODELTEST.

Two billion iterations, sampled every 200 thousand were performed using a random start tree under a species tree: Yule process tree prior, with a piecewise linear and constant root population size model. TRACER, LOGCOMBINER and TREEANNOTATOR were used as above.

Migration estimates

We estimated recent migration and gene flow among Yukon and surrounding populations of *Peromyscus*, as well as Southeast Alaska populations of *P. keeni* using BAYESASS v3.0.3 (Wilson & Rannala, 2003). BAYESASS uses a non-equilibrium, multilocus Bayesian approach to estimate recent migration rates, under a MCMC algorithm. We ran 200 million iterations with a 20 thousand burn-in sampling every 2000. Mixing parameters of allele frequencies, inbreeding coefficient and migration rates were adjusted following the program guidelines. Additionally, to help identify the location of coastal refugia, we added 220 previously published cyt *b* for *P. keeni* across their entire distribution, trimmed our sequences to match the minimal length (479 bp), and partitioned the data into three different population pairs. Models 1 and 2 are consistent with Zheng et al. (2003). The three models were: 1) Southern coastal refugium: Washington versus the remaining range, 2) either Southern or Northern coastal island refugium: Southern (southern British Columbia, Vancouver Island and Washington) versus Northern (northern British Columbia, Yukon and Alaska), and 3) Southeast Alaska coastal refugium: Southeast Alaska islands versus all mainland populations.

Ecological differentiation

The three major clades surveyed here (*P. keeni*, *P. maniculatus* and *Peromyscus* sp. nov.) are found in close proximity, which could lead to potential ecological differentiation. To assess the degree of differentiation with respect to climatic requirements, we generated Species Distribution Models (SDMs) for *P. keeni*, *P. maniculatus* West and *Peromyscus* sp. nov. for both western North America and areas north of central British Columbia. Nineteen bioclimatic variables for current conditions were obtained from WORLDCLIM (www.worldclim.org, Hijmans *et al.*, 2005) at a resolution of 2.5 arc-minutes. To avoid over-parameterization of the model, we used ENMTOOLS v.1.4.3 (Warren *et al.*, 2008; Warren *et al.*, 2010) to eliminate highly correlated variables (Pearson correlation coefficient ≥0.75), with final selection based on variables most biologically relevant to *Peromyscus*. Species localities were determined with cyt *b* sequences rather than museum point localities because of potential mis-identification among the three clades. All non-repetitive sampling localities for *Peromyscus* sp. nov. (n=14), *P. keeni* (n=74) and *P. maniculatus* (n=47) were used.

SDMs were constructed using MAXENT v3.3.3k (Elith *et al.*, 2006; Phillips *et al.*, 2006; Phillips & Dudik, 2008) under the following assumptions: no topographic change, niche conservatism (Wiens & Graham, 2005), environmental data adequately predicts species occurrence (Kozak *et al.*, 2008; McCormack *et al.*, 2010), and sampling records effectively capture the niche breadth of the species (Pearson *et al.*, 2007). Final runs used bioclim variables 1, 6, 7, 9 and 11 and were performed using cross-validation across 10 runs, with a regularization parameter (Hope *et al.*, 2011; Warren & Seifert, 2011) of 1 for *Peromyscus* sp. nov. and 5 for *P. keeni* and *P. maniculatus* with 1000 iterations, all other values were left as default. Minimum threshold values were the low median threshold values over all replicates (Pearson *et al.*, 2007). Using ENMTOOLS we conducted a comparison of niche similarity, by calculating Schoener's D (Schoener, 1968), the *I* statistic (Warren *et al.*, 2008), and relative rank (RR; Warren & Seifert, 2011) between clades. Highly similar ranges have values approaching 1.0, while no range similarity is 0.

RESULTS

Sampling

Nucleotide base variation was as expected for mammals for the 260 cyt *b* sequences analyzed (Irwin *et al.*, 1991) and consistent with previous studies of *Peromyscus* (Zheng *et al.*, 2003; Lucid & Cook, 2004; Dragoo *et al.*, 2006) with an overall guanine deficit (13.0%, A 32.1%, C 26.5% and T 28.4%). Varying levels of nucleotide composition were observed across all loci (Table 3). FGB and IRBP had no indels, whereas Zp3 had one indel of eight base pairs and one of a single base position. Evidence of selection for all loci was not detected as indicated by non-significant HKA.

Phylogenetic analyses and timing of divergence:

The cyt *b* phylogenetic reconstruction was largely consistent with previously observed relationships (Dragoo *et al.*, 2006; Lucid & Cook, 2007; Kalkvik *et al.*, 2012). *Peromyscus maniculatus* was composed of four major clades (Western, Eastern, Southern, and Southwest, previously clades 1 & 2, 5 & 6, 4, and 3, respectively), but lacking reciprocal monophyly with respect to other species of *Peromyscus* (Fig. 1 and Fig. 2). We considered posterior probabilities ≥0.95 and bootstrap values ≥0.7 to be significant support. We detected support for a Southern clade (previously clade 4) from southern New Mexico and Mexico, a Southwest clade (previously clade 3) from Baja California, California and Nevada, an Eastern clade (previously clades 5 & 6) ranging from the Plains states to the East Coast and northward into Canada but with three additional subclades (East - a, previously 5; East - b, previously 5 & 6; East - c, previously 6), and a Western clade (previously clade 1) that also includes a Plains states subclade (previously clade 2) that extends northward to central Yukon. Additionally, the Western clade contains a lineage for northern British Columbia and southern Yukon. Both *P. keeni* (Washington up through Yukon) and *Peromyscus* sp. nov. (Yukon only) were supported. Most of the divergence date estimates (TMRCA) for each of these major clades occurred between 128.9 and 221.5 ka (Table 4).

The species tree reconstruction (Fig. 3) yielded support for *P. keeni*, *Peromyscus* sp. nov., a clade consisting of *P. keeni* and *Peromyscus* sp. nov., and the British Columbia/Yukon clade within *P. maniculatus* West. All other cyt *b* clades remained unresolved. Multilocus estimates of divergence times for these supported clades are estimated at between 34 and 90 ka (Table 4). Furthermore, cyt *b* clades generally are detected across each nuclear locus, but evidence of incomplete lineage sorting and recent diversification is reflected in the short branches in nuclear trees (Fig. 4).

Inferences of population history

A combination of expansion statistics, genetic variation (Table 3), Bayesian skyline plots and EBSPs (Fig. 5) were used to assess whether populations representing major cyt *b* clades experienced stable conditions historically and whether there are detectable signs of expansion. High *Hd* and *π* indicate stability, low *Hd* and high *π* for population bottlenecks, and low *Hd* and *π* for recently expanded populations. Inferences for all *P. maniculatus* East lineages, and the Southwest and Southern clades were difficult due to low sample sizes. *Peromyscus maniculatus* West was initially stable, but experienced demographic expansion. *Peromyscus keeni* experienced demographic expansion. The high *Hd* for cyt *b* could be a result of the fragmented distribution with limited connectivity across the islands of the AA coupled with the smaller effective population size for mitochondrial loci. *Peromyscus* sp. nov. contained mixed signals across loci, but skyline plots suggest this clade experienced recent expansion. Net genetic distance (Table 5) based on cyt *b* ranges from 0.5% ± 3.6% between *P. keeni* and *P. maniculatus* Southwest to 4.8% ± 0.6% between *Peromyscus* sp. nov. and *P. maniculatus* East - c, in addition to the 9.20 - 14% (± 0.8 – 1%) between this complex and the outgroups of *P. leucopus* and *P. melanotis*.

Migration estimates

The Bayesian estimates of recent migration (mean across three runs) between Yukon and northern British Columbian populations indicate *Peromyscus* sp. nov. has the highest proportion of immigrants from Yukon *P. keeni* at 0.0959, and only 0.0098 from *P. maniculatus* West from Yukon (Table 6). *Peromyscus keeni* in Yukon has a proportion of 0.0116 migrant genes from *Peromyscus* sp. nov. and 0.008 from *P. maniculatus* West from Yukon, and Yukon *P. maniculatus* West has 0.0239 immigrant genes from Yukon *P. keeni* and 0.013 from *Peromyscus* sp. nov. *Peromyscus keeni* gene flow valuations revealed no greater than a 0.0185 proportion of genes donated from any given island or adjacent mainland population pairwise comparison (Table 7). For tests of refugial locations, there is only slightly higher migration from islands of the AA onto the mainland, with minimal proportions in either direction (0.0049 and 0.0019, respectively). Much greater differences in gene flow were detected in the other two models, with a clear north to south migration (Table 8).

Ecological differentiation

Predictive performance for SDMs was determined through the use of ≥0.75 AUC values of model performance. Highest climate suitability (Fig. 6) for *Peromyscus* sp. nov. occurs in higher latitudes, along the West Coast for *P. keeni*, and non-montane regions across the West for *P. maniculatus*. Greatest potential range overlap is between *Peromyscus* sp. nov. and *P. maniculatus* West with average overlap of 0.836. Least overlap is between *Peromyscus* sp. nov. and *P. keeni* with average overlap of 0.498 (Table 9).

DISCUSSION

Pleistocene climatic fluctuations influenced diversification in many North American species. Wide ranging species that were subsequently segregated into refugial populations may reflect increased phylogeographic structure. For *Peromyscus* of northwestern North America, late Pleistocene glacial cycling heavily influenced demography and diversification. Gene tree analysis of cyt *b* sequences identified four clades of *P. maniculatus* (West, East, South and Southwest); yet these clades lack reciprocal monophyly in both the cyt *b* and species trees. Support for distinctive *P. keeni* and *Peromyscus* sp. nov. was recovered in both the cyt *b* and multilocus species trees with divergence initiated prior to the LGM.

Effects of glacial persistence and migration on genetic and ecological differentiation

Three major geographic regions were detected for glacial persistence within the *Peromyscus* complex: 1) Southern for *P. maniculatus*, 2) Coastal for *P. keeni*, and 3) Northern/Beringia for *Peromyscus* sp. nov. All *P. maniculatus* lineages show signs of stable populations during the LGM, with the addition of post-glacial expansion in the Western clade. *Peromyscus* sp. nov., although now occupying a limited range, apparently persisted in eastern Beringia during the confluence of the Laurentide and Cordilleran ice sheets in central Yukon and subsequently expanded southward into southern Yukon. Fossil *Peromyscus* from Thistle Creek at the southern end of the Klondike Gold Fields in Yukon date to the LIG (Fig. 1; G.D. Zazula, pers. comm.; Storer, 2003). We predict that *Peromyscus* fossils dating to the LGM will be found in other regions in Yukon and east-central Alaska that remained ice- free.

Contemporary SDMs identify northern regions as optimal environmental conditions for *Peromyscus* sp. nov., coastal regions for *P. keeni* and non-montane continental areas for *P. maniculatus* West. High niche overlap may be influenced by methods based on raw output models that include areas of low suitability, combined with limited sampling for *Peromyscus* sp. nov. and very broad sampling for *P. maniculatus* West.

Although other species (e.g., *Microtus longicaudus* and *Sorex monticolus*)show sympatry between divergent mtDNA lineages near Haines and Juneau, Alaska, (Conroy

& Cook, 2000; Demboski & Cook, 2001; Sawyer and Cook *submitted*; Sawyer et al. *submitted*), *Peromyscus* clades are geographically proximal east of the Coast Range (Fig. 1 and 8). No localities in Yukon have been identified yet with more than a single species of *Peromyscus* (Fig. 7). We would expect to find sympatry in Yukon between Kluane National Park and Reserve and Whitehorse, with *Peromyscus* sp. nov. to the north, *P. keeni* to the south and southwest, and *P. maniculatus* to the west and southwest. *Peromyscus keeni* and *P. maniculatus* are both found east of the Coast Mountains in British Columbia, and also overlap in Washington (Fig. 1), as previously detected (Zheng *et al.*, 2003).

Our ability to detect refugia is essential component of rigorous study of biotic diversity at high latitudes (Ashcroft, 2010; Stewart *et al.*, 2010; Dawson *et al.*, 2014). *Peromyscus keeni* occupied coastal refugia throughout glacial cycles, but now ranges from Washington, northward through southern Yukon. We agree with Lucid and Cook (2004) that the high levels of differentiation of *P. keeni* populations of the AA are a result of *P. keeni* occupying coastal refugia in the AA during the LGM followed by isolation and differentiation on individual islands. Peromyscine fossils found in karst systems, specifically Devil's Canopy and On Your Knees Caves, by Heaton and Grady (2003; 2007) suggest this region was recolonized in the early Holocene before higher sea levels fragmented the islands. However, the lack of genetic diversity throughout the southern portion (i.e., Washington, southern British Columbia) of the range of *P. keeni*, combined with greater structure in the North (i.e., AA) may be a result of either coastal refugia or faster rates of genetic drift due to the fragmented landscape. The mtDNA tree places Vancouver Island and Washington specimens basal to most populations of the AA;

however, Washington individuals are sister to the "ABC" (Admiralty, Baranof and Chichagof) and Haida Gwaii island clades, while other Washington individuals are found with the main AA group.

By expanding sampling to include previously published sequences, we were able to explore direction of colonization across the entire range of *P. keeni*. Zheng et al. (2003) concluded that *P. keeni* persisted in southern coastal refugia near Vancouver Island; however, their northern sampling was limited. In this study, there is substantial support for southward colonization from north coastal refugia. Lack of gene flow from the AA populations onto the mainland reflects oceanic barriers to movement, as the low levels of interisland exchange also suggest. Given the highly structured mtDNA tree, divergence dates, fossil evidence and directionality tests of colonization, we conclude that *P. keeni* persisted in coastal refugia in Southeast Alaska, and perhaps Haida Gwaii, throughout the Pleistocene glacial cycles.

Hibbard (1968) noted that fossil records for *Peromyscus* are scant and suggests the *P. maniculatus* group represents a late Pleistocene radiation. The contact of southern (*P. maniculatus*), coastal (*P. keeni*) and northern (*Peromyscus* sp. nov.) refugial populations in south central Yukon is unusual for North American mammals, especially for a species group with such a broad geographic range (e.g., Swenson & Howard, 2005; Shafer *et al.*, 2010). Within Yukon, higher estimates of gene flow are also likely the result of historical exchange rather than contemporary gene flow, given the support for distinct clades in the multilocus analysis, with higher estimates between *P. keeni* and *Peromyscus* sp. nov. the result of historic proximity and timing of secondary contact for post-glacial colonizers. However, our data suggest there is not enough gene flow between these two species to prohibit differentiation. Our estimates of gene flow fall between the interspecific (0.035) and intraspecific (0.10) ranges (Table 6), thus warrant further investigations regarding the validity of species level designation (e.g., Ross *et al.*, 2010; Nakajima *et al.*, 2012).

CONCLUSIONS

Cryptic species and glacial refugia often elude detection, but spatially extensive sampling and use of phylogenetic coalescent analysis, multilocus sequence data, and environmental modeling, can provide signatures of diversification that provide insight into refugial locations and dynamics that are the result of historic climate change and glaciation. Our analyses provided perspectives on the evolution of northern *Peromyscus*. Glacial-interglacial cycling over the past 300 ka played a role in the diversification of three distinctive clades of *Peromyscus* in Yukon. These clades are the result of long-term separation in three ice-free regions: far-eastern Beringia (*Peromyscus* sp. nov.), coasts of Southeast Alaska and possibly Haida Gwaii (*P. keeni*), and southern continental (*P. maniculatus*). We detected geographic proximity, but no contact among these species in south central Yukon. More intensive sampling and assessment of deer mice from southern Yukon and northern British Columbia will refine the geographic range of this new *Peromyscus*, potential sympatry with *P. keeni* or *P. maniculatus*, and the degree of differentiation from *P. keeni* and *P. maniculatus*. We suggest that coastal refugia for *P. keeni* existed near Southeast Alaska, and Haida Gwaii, as proposed by Lucid and Cook (2004), but not Vancouver Island as proposed by Zheng *et al.* (2003). Further work should focus on refining the number of coastal refugia, their location (northern AA, southern AA or Haida Gwaii), and their contribution to extant diversity. The clade that is sister to most other *P. keeni* in our analyses included individuals from Haida Gwaii (Fig. 2). Lack of reciprocal monophyly, support for multiple lineages, and diversification within each clade of *P. maniculatus*, suggest multiple regions of incipient diversification distributed across the United States south of the glacial extent, but a clear picture of structure in *P. maniculatus* will require much more extensive sampling of geography and genes. *Peromyscus* sp. nov. has a limited distribution, *P. keeni* is primarily restricted to the fragmented islands of the Alexander Archipelago, and diversity within *P. maniculatus* warrants further study. Lastly, we concur with previous work that suggested the endemic northern clade of *Peromyscus* is a distinct species and worthy of formal taxonomic recognition under the evolutionary and genealogical concordance species concepts.

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Tables and Figures

Figure 1. Sampling scheme for *Peromyscus*. The thick yellow line is the current range for *P. maniculatus* and the blue line is *P. keeni*. The solid blue coloring is the LGM glacial ice cover. (a) Sampling localities are shown by both major cyt*b* lineage (see key for colors, numbers in parenthesis indicate previously designated lineage numbers from Dragoo et al. 2006), (b) Yukon sampling, and (c) *P. keeni* sampling with near-by *P. maniculatus* West. Pluses indicate known pre-LGM fossil localities. The map is projected in North America Albers Equal Area Conic.

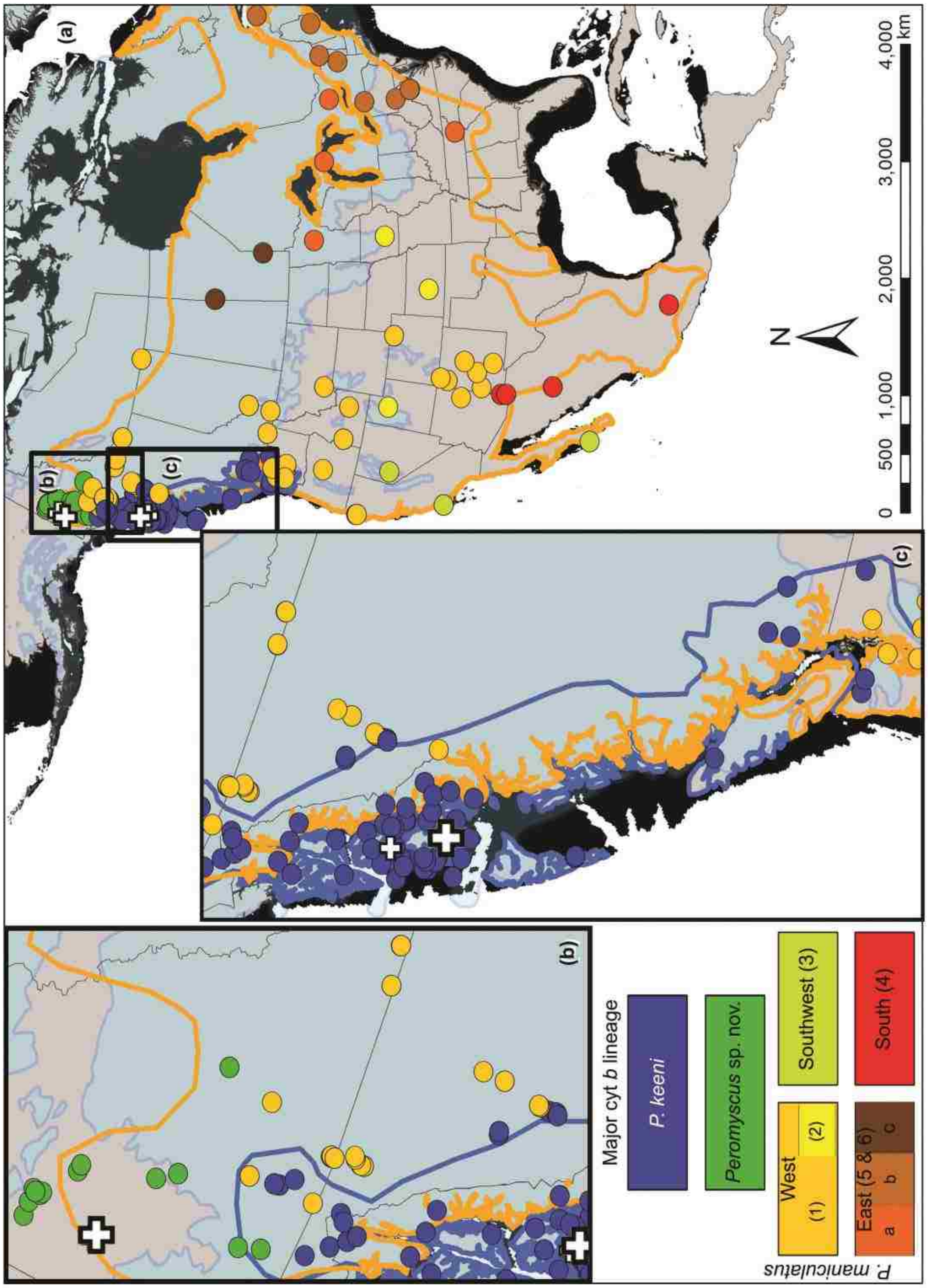
(a)
(b)
(c)
N
0
500
1,000
2,000
3,000
4,000
km
Major cyt b lineage
P. keeni
Peromyscus sp. nov.
P. maniculatus
West
(1)
(2)
Southwest (3)
East (5 & 6)
a
b
c
South (4)

Figure 2. Dated Bayesian cyt *b* trees. Posterior probability ≥0.95 represented with open circles and Maximum Likelihood bootstraps of ≥0.7 with asterisks are shown on branches. Numbers in parentheses indicate previously designated lineage numbers (Dragoo et al. 2006). Horizontal gray bars indicate divergence dates (95% HPD) and vertical gray bars represent the LIG (left) and LGM (right). Geographic location for supported intra-lineage clades are immediately right of taxon tips (see table 1 for abbreviations). Outgroups = *P. melanotis* and *P. leucopus*.

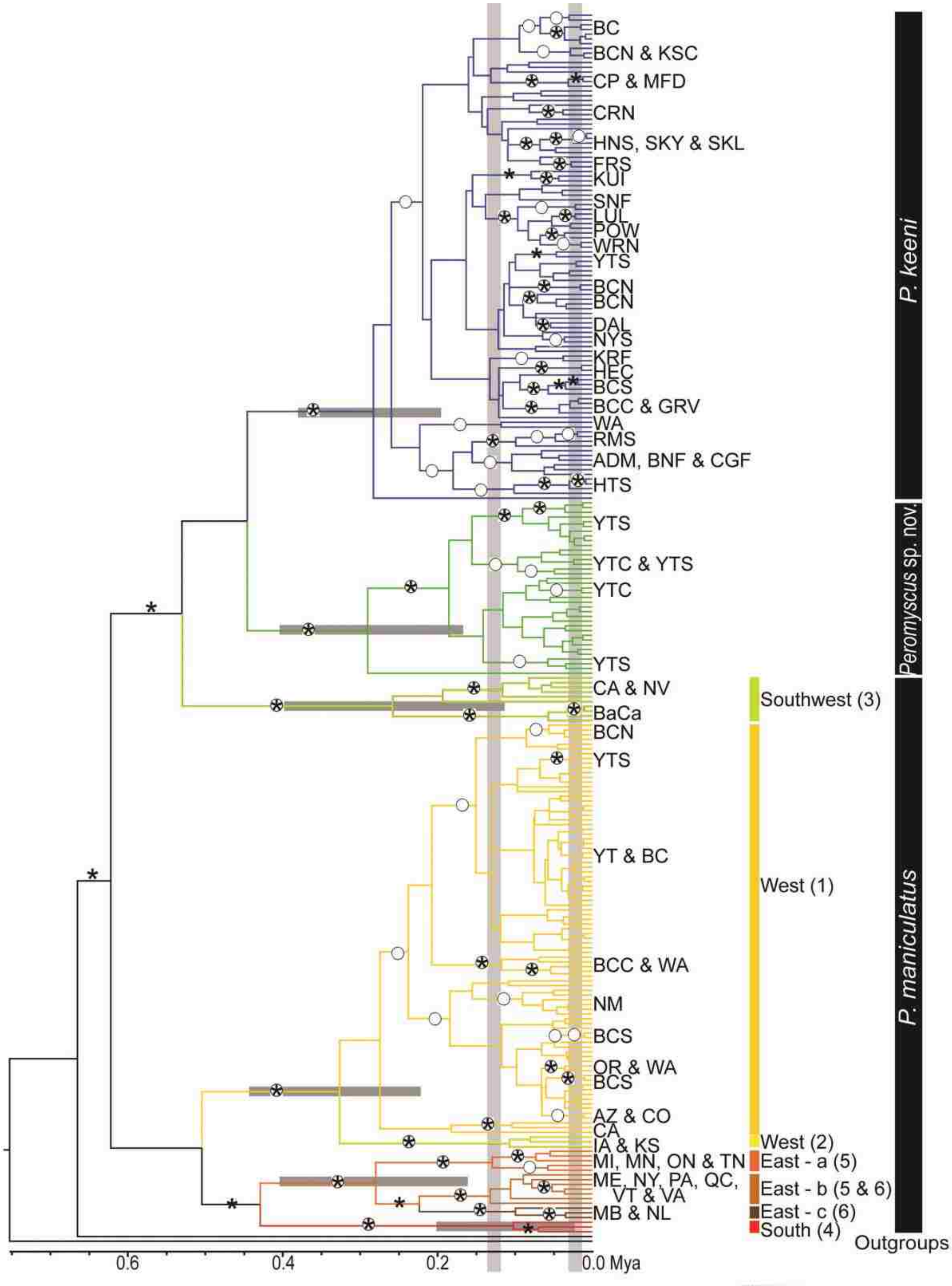
BC
BCN & KSC
CP & MFD
CRN
HNS, SKY & SKL
FRS
KUI
SNF
LUL
POW
WRN
YTS
BCN
BCN
DAL
NYS
KRF
HEC
BCS
BCC & GRV
WA
RMS
ADM, BNF & CGF
HTS
YTS
YTC & YTS
YTC
YTS
CA & NV
BaCa
BCN
YTS
YT & BC
BCC & WA
NM
BCS
OR & WA
BCS
AZ & CO
CA
IA & KS
MI, MN, ON & TN
ME, NY, PA, QC,
VT & VA
MB & NL
0.6
0.4
0.2
0.0 Mya
P. keeni
Peromyscus sp. nov.
P. maniculatus
Southwest (3)
West (1)
West (2)
East - a (5)
East - b (5 & 6)
East - c (6)
South (4)
Outgroups

Figure 3. Multilocus Bayesian Species Tree. Posterior probabilities of ≥0.95 are represented with open circles on branches of the solid consensus tree. Black = outgroups (*P. melanotis* and *P. leucopus*). Horizontal gray bars represent divergence date estimates and vertical bars indicate approximate time for the LIG and LGM.

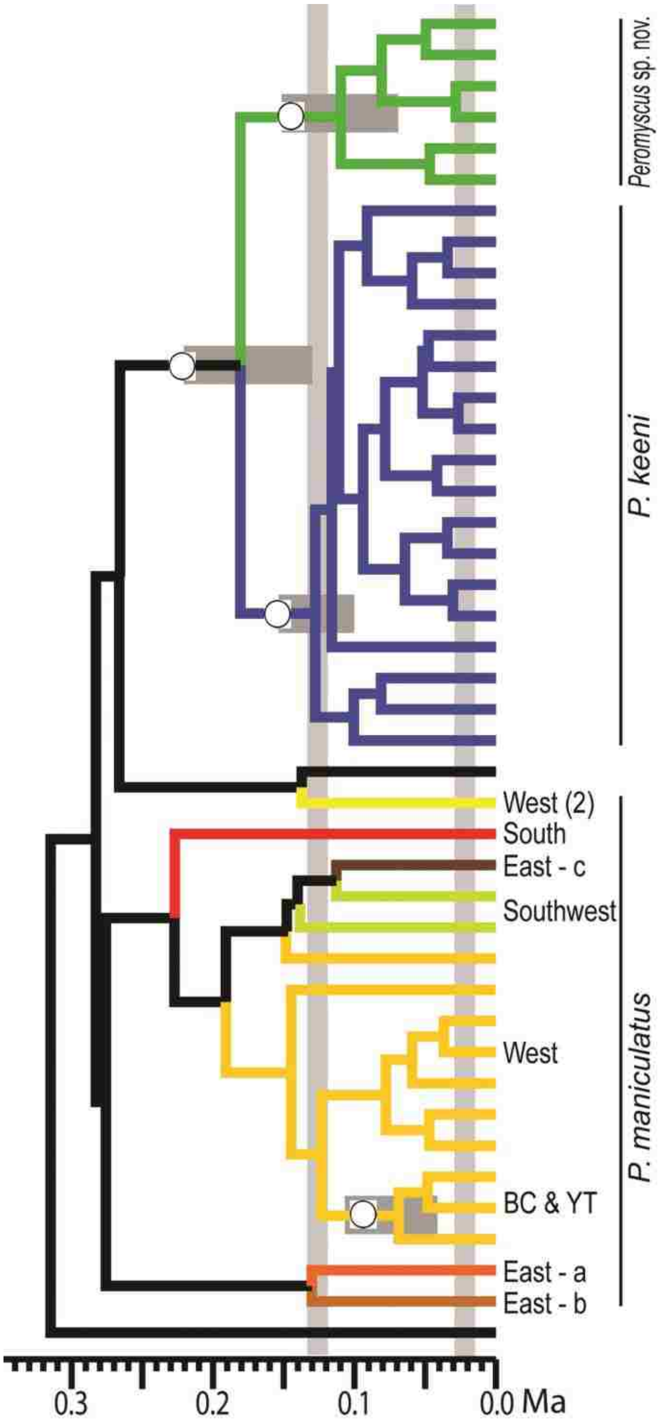

Figure 4. Bayesian gene trees for *Peromyscus* FGB, IRBP and Zp3 nuclear loci with posterior probabilities of ≥0.95 represented with open circles. Yukon samples are indicated with black dots. Geographic locations (see table 1 for abbreviations) for supported intra-lineage clades are provided. Blue = *P. keeni*, green = *Peromyscus* sp. nov., yellow-green = *P. maniculatus* Southwest, golden = *P. maniculatus* West, orange = *P. maniculatus* East - a, light brown = *P. maniculatus* East - b, dark brown = *P. maniculatus* East - c, red = *P. maniculatus* South, and black = outgroups (*P. melanotis* and *P. leucopus*).

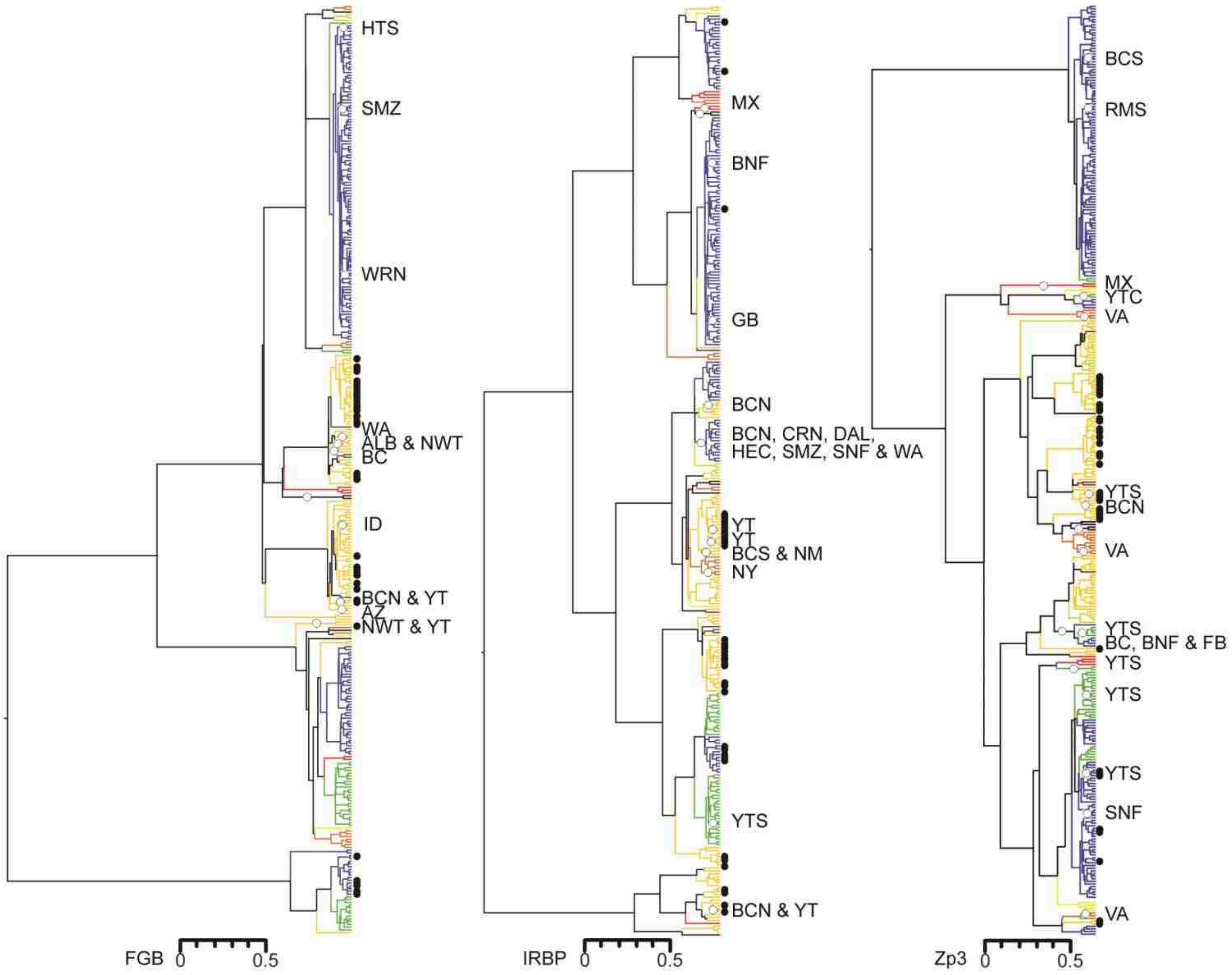
HTS
SMZ
WRN
WA
ALB & NWT
BC
ID
BCN & YT
AZ
NWT & YT
FGB
0
0.5
MX
BNF
GB
BCN
BCN, CRN, DAL,
HEC, SMZ, SNF & WA
YT
YT
BCS & NM
NY
YTS
BCN & YT
IRBP
0
0.5
BCS
RMS
MX
YTC
VA
YTS
BCN
VA
YTS
BC, BNF & FB
YTS
YTS
YTS
SNF
VA
Zp3
0
0.5

Figure 5. EBSPs (i) and cyt *b* skyline (ii) plots for *Peromyscus* sp. nov., *P. keeni*, and *P. maniculatus* West. Central line indicates mean change in effective population size through time, with upper and lower lines sowing the 95% posterior density. The x-axis is read right-to-left from past (TMRCA) to present and is scaled in millions of years and the y-axis is the effective population size scaled by generation time. Vertical gray bars indicate the LGM for reference.

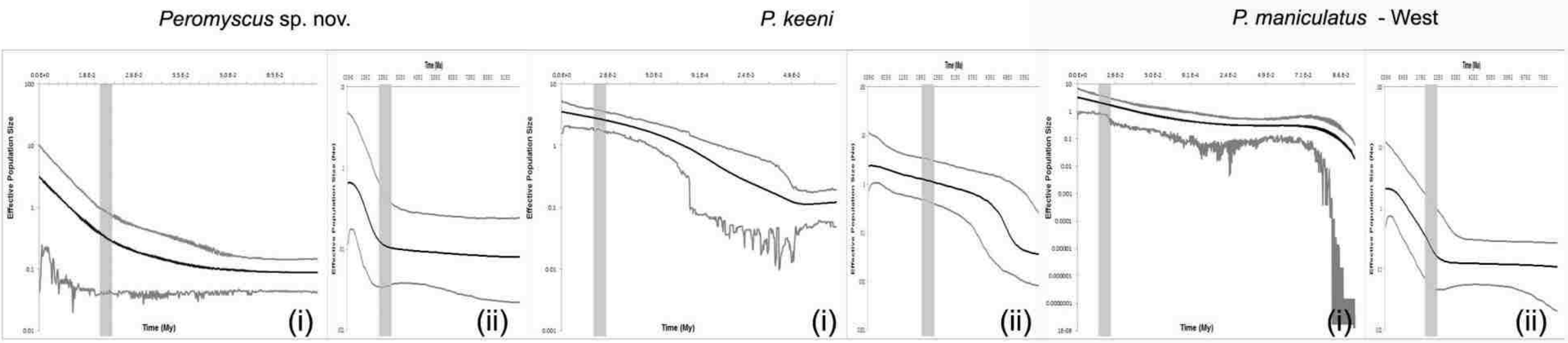
Peromyscus sp. nov.
P. keeni
P. maniculatus - West
Effective Population Size
Effective Population Size (Ne)
Time (My)
Time (Ma)
(i)
(ii)
(i)
(ii)
(i)
(ii)

Figure 6. SDM habitat suitability for (a) *Peromyscus* sp. nov., (b) *P. keeni*, and (c) *P. maniculatus* - West with low habitat suitability at the minimum median threshold values over all replicates.

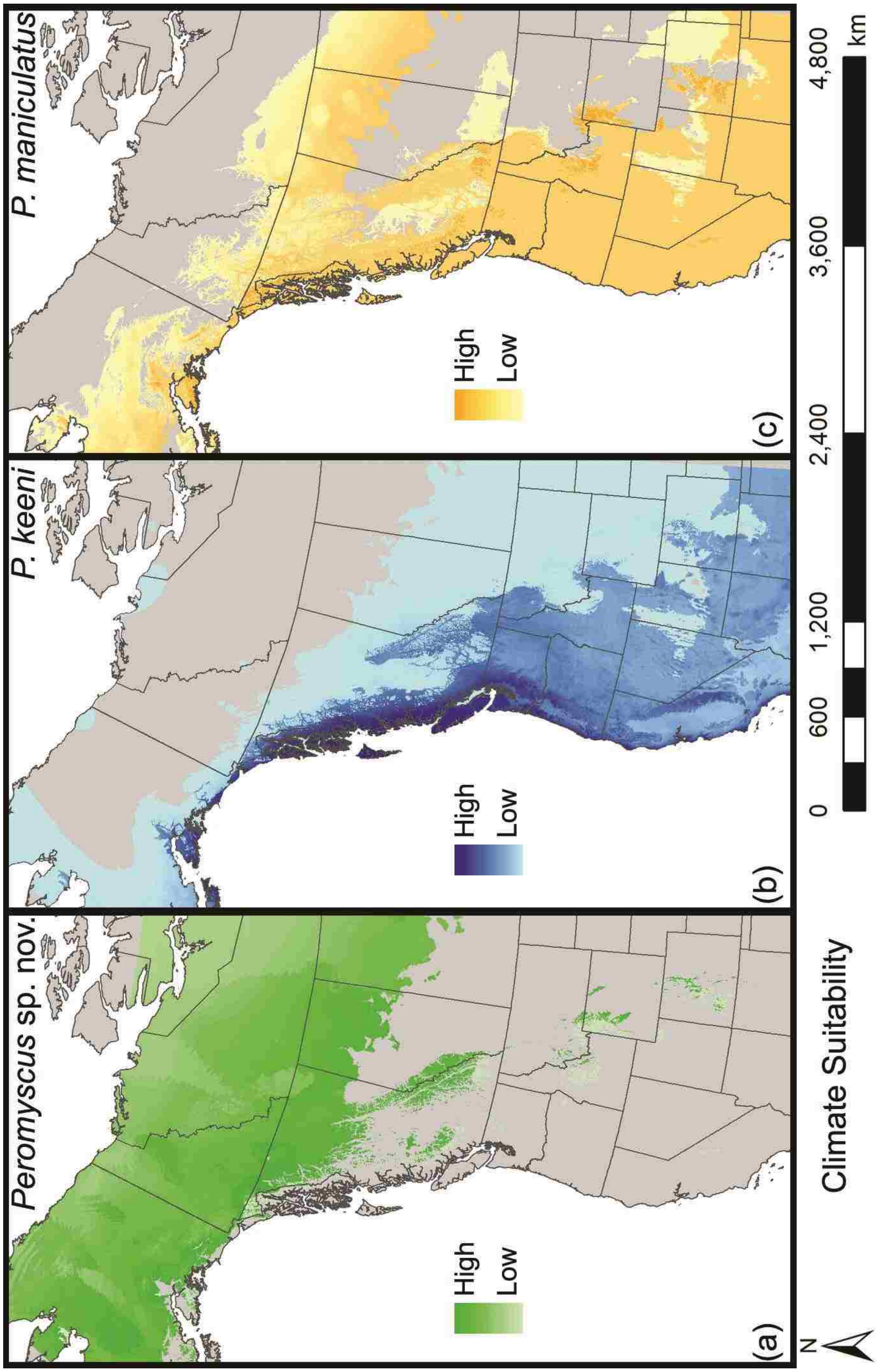

Figure 7. Yukon, Southeast Alaska and British Columbian *Peromyscus*. The arrow indicates an area of sympatry and the box representing a region of close proximity among major lineages. Black lines are major roads, circles are sampling localities: green = *Peromyscus* sp. nov., blue = *P. keeni*, and yellow = *P. maniculatus*.

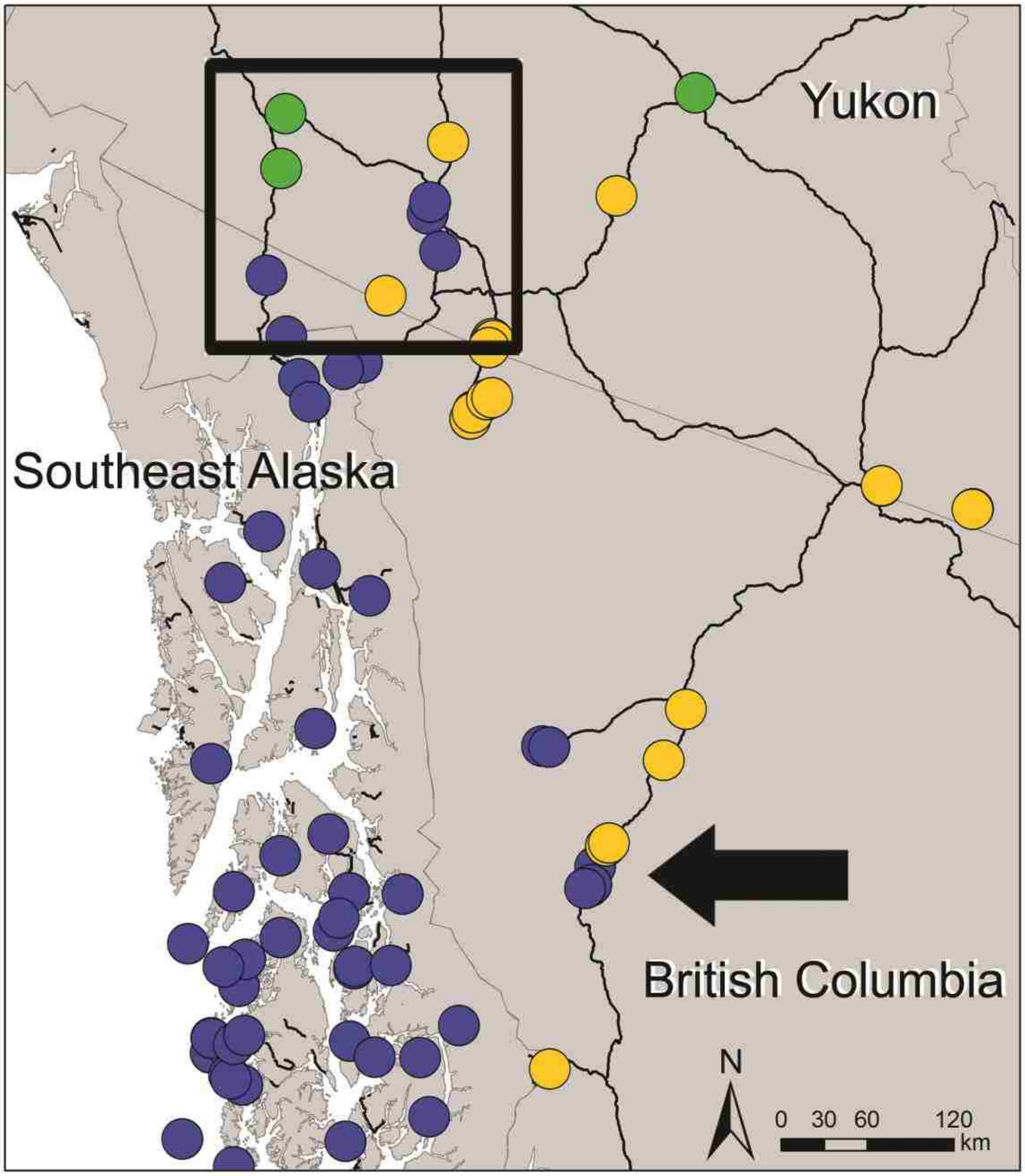

Table 1. Specimens examined. Museum number acronyms are MSB= Museum of Southwestern Biology, UAM=University of Alaska Museum of the North, Fairbanks, HG= Gwaii Haanas National Park Reserve and Haida Heritage Site, and UWBM=University of Washington Burke Museum. GenBank numbers correspond to cyt *b*, and each allele for FGB, IRBP and Zp3, respectively, –= not applicable. GenBank in bold were previously obtained from other studies. Asterisk = additional *P. keeni* used for BAYESASS analyses. Location abbreviations are in parenthesis following locality name.

cyt*b* lineage	Specimen Number	Locality	Latitude	Longitude	GenBank Accession Numbers
Peromyscus sp. nov.					
	MSB144216	Yukon - Central (YTC)	62.39850	-136.55530	KF949162,KF949368/KF949369,KF949702/KF949703,KF950701/KF950702
	MSB144217		63.54310	-137.19480	KF949171,KF949578/KF949579,KF949892/KF949893,KF950909/KF950910
	MSB144263		63.54310	-137.19480	KF949174,KF949580/KF949581,KF949894/KF949895,KF950911/KF950912
	MSB144264		63.54310	-137.19480	KF949175, – / – , – / – , – / –
	MSB144265		63.54310	-137.19480	KF949180, – / – , – / – , – / –
	MSB144270		63.54310	-137.19480	KF949199,KF949582/KF949583,KF949896/KF949897,KF950913/KF950914
	MSB144284		63.54310	-137.19480	KF949163, – / – , – / – , – / –
	MSB144285		64.02590	-138.57890	KF949200, – / – , – / – , – / –
	MSB145250		64.02590	-138.57890	KF949176, – / – , – / – , – / –
	MSB145251		64.02590	-138.57890	KF949207,KF949372/KF949373,KF949706/KF949707,KF950703/KF950704
	MSB145572		63.55510	-137.41230	KF949164,KF949374/KF949375,KF949708/KF949709,KF950705/KF950706
	MSB145618		63.55510	-137.41230	KF949177, – / – , – / – , – / –
	MSB145637		64.04284	-139.41679	KF949178, – / – , – / – , – / –
	MSB145713		63.94020	-138.58258	KF949179, – / – , – / – , – / –
	MSB196683		64.07384	-138.52334	KF949192, – / – , – / – , – / –
	MSB196687		64.07384	-138.52334	KF964333,KF949624/KF949625,KF949940/KF949941, – / –
	MSB196688		63.92972	-138.50384	KF949267,KF949626/KF949627,KF949942/KF949943,KF950945/KF950946
	MSB196689		63.92972	-138.50384	KF949193, – / – , – / – , – / –
	MSB196694		64.05761	-138.94957	KF949194, – / – , – / – , – / –
	MSB231195		61.99575	-132.60938	– ,KF949630/KF949631, – / – ,KF950949/KF950950
	MSB149203	Yukon - South (YTS)	61.99575	-132.60938	KF949181, – / – , – / – , – / –
	MSB149204		61.99575	-132.60938	KF949182,KF949590/KF949591,KF949906/KF949907, – / –
	MSB149205		61.99575	-132.60938	KF949183, – / – , – / – , – / –
	MSB149206		61.99575	-132.60938	KF949165,KF949378/KF949379,KF949712/KF949713,KF950709/KF950657
	MSB149207		61.99575	-132.60938	KF949184,KF949592/KF949593,KF949908/KF949909,KF950920/KF950921
	MSB149208		61.99575	-132.60938	KF949185,KF949594/KF949595,KF949910/KF949911,KF950922/KF950923
	MSB149213		62.11590	-136.14425	KF949186, – / – , – / – , – / –
	MSB149277		62.11590	-136.14425	KF949187,KF949596/KF949597,KF949912/KF949913,KF950924/KF950925
	MSB149278		62.11590	-136.14425	KF949188,KF949598/KF949599,KF949914/KF949915, – / –
	MSB149280		62.11590	-136.14425	KF949189, – / – , – / – , – / –
	MSB149281		60.51450	-137.08170	KF949190, – / – , – / – , – / –
	MSB240539		60.51450	-137.08170	KF949169,KF949406/KF949407,KF949740/KF949741,KF950736/KF950737
	MSB240548		60.51450	-137.08170	KF949195,KF949632/KF949633,KF949946/KF949947,KF950951/KF950952
	MSB240553		60.83833	-137.32917	KF949173,KF949408/KF949409,KF949742/KF949743,KF950738/KF950739
	UAM34604		60.83833	-137.32917	KF949268, – / – ,KF949980/KF949981,KF950985/KF950986
	UAM35344		60.83833	-137.32917	KF949205,KF949668/KF949669,KF949986/KF949987, – / –
	UAM52704		60.83833	-137.32917	KF949206, – / – , – / – , – / –
	UAM52705		58.34307	-134.63975	KF949156,KF949678/KF949679,KF949998/KF949999,KF950995/KF950996

P. keeni			55.71667	-131.85000	
		Alaska			
	UAM20582	Cleveland Peninsula (CP)	55.716667	-131.850000	KF949309, –/–, –/–,KF950770/KF950771
	UAM23771*		55.750405	-132.183333	KF950025, –/–, –/–, –/–
	UAM23773*		55.750405	-132.183333	KF950026, –/–, –/–, –/–
	UAM23774		55.750405	-132.183333	KF949315,KF949468/KF949469,KF949804/KF949805,KF950802/KF950803
	UAM23775*		55.750405	-132.183333	KF950016, –/–, –/–, –/–
	UAM23421	Foggy Bay (FB)	54.983333	-130.960624	KF949263,KF949456/KF949457,KF949790/KF949791,KF950788/KF950789
	UAM23425*		54.983333	-130.960624	KF950008, –/–, –/–, –/–
	UAM30391*		54.983333	-131.000000	KF950131, –/–, –/–, –/–
	UAM42938	Glacier Bay (GB)	58.416667	-135.433333	–,KF949508/KF949509,KF949836/KF949837,KF950840/KF950841
	UAM42939		58.416667	-135.433333	KF949323,KF949510/KF949511,KF949838/KF949839,KF950842/KF950843
	UAM23665*	Haines (HNS)	59.316667	-135.566667	KF950052, –/–, –/–, –/–
	UAM23667*		59.316667	-135.566667	KF950014, –/–, –/–, –/–
	UAM31102		59.574722	-136.156667	KF949159,KF949484/KF949485,KF949818/KF949819,KF950818/KF950819
	UAM31103		59.3661111	-135.799444	KF949319,KF949486/KF949487,KF949820/KF949821,KF950820/KF950821
	UAM31104*		59.3661111	-135.799444	KF950011, –/–, –/–, –/–
	UAM31105*		59.4108333	-136.0025	KF950031, –/–, –/–, –/–
	UAM31106*		59.3661111	-135.799444	KF950032, –/–, –/–, –/–
	UAM31107		59.3661111	-135.799444	KF949320,KF949488/KF949489,KF949822/KF949823,KF950822/KF950823
	UAM48129*		59.261667	-135.559722	KF950012, –/–, –/–, –/–
	UAM50436*		59.5316667	-135.348056	KF950038, –/–, –/–, –/–
	UAM50802		59.531667	-135.348056	KF949288,KF949524/KF949525,KF949848/KF949849,KF950860/KF950861
	UAM52310		59.5316667	-135.348056	KF950039, –/–, –/–, –/–
	UAM52642		59.261667	-135.559722	KF949293,KF949536/KF949537,KF949860/KF949861,KF950872/KF950873
	UAM60272*		59.3661111	-135.799444	KF950040, –/–, –/–, –/–
	UAM76821*		59.5316667	-135.348056	KF950046, –/–, –/–, –/–
	UAM76822*		59.5316667	-135.348056	KF950047, –/–, –/–, –/–
	UAM76823		59.5316667	-135.348056	KF949328,KF949560/KF949561,KF949876/KF949877,KF950891/KF950892
	MSB157000	Juneau (JNO)	58.343070	-134.639750	KF949256,KF949390/KF949391,KF949724/KF949725,KF950719/KF950720
	UAM50751		58.311111	-133.958333	KF949286,KF949520/KF949521,KF949844/KF949845,KF950856/KF950857
	UAM50754*		58.311111	-133.958333	KF950132, –/–, –/–, –/–
	UAM23487*	Misty Fjords (MFD)	56.083333	-131.086460	KF950050, –/–, –/–, –/–
	UAM23490*		56.083333	-131.086460	KF950051, –/–, –/–, –/–
	UAM23491		56.083333	-131.086460	KF949272,KF949460/KF949461,KF949794/KF949795,KF950792/KF950793
	UAM23492		56.083333	-131.086460	KF949273,KF949462/KF949463,KF949796/KF949797,KF950794/KF950795
	UAM20698	Southeast (SEAK)	56.700000	-132.250000	KF949269,KF949444/KF949445,KF949778/KF949779,KF950776/KF950777
	UAM20949		56.700000	-132.250000	KF949270,KF949450/KF949451,KF949784/KF949785,KF950782/KF950783
	UAM50800		59.615833	-135.168333	KF949287,KF949522/KF949523,KF949846/KF949847,KF950858/KF950859
	UAM74125*		57.366667	-133.466667	KF950041, –/–, –/–, –/–
	UAM74128*		57.366667	-133.466667	KF950042, –/–, –/–, –/–

UAM74131*		57.366667	-133.466667	KF950043, –/–, –/–, –/–
	Alaskan islands:			
UAM35318*	Admiralty (ADM)	57.433333	-134.550000	KF950033, –/–, –/–, –/–
UAM44886		57.429444	-133.938889	KF949325, –/–, –/–,KF950848/KF950849
UAM44887*		57.429444	-133.938889	KF950037, –/–, –/–, –/–
UAM44888		57.429444	-133.938889	KF949326,KF949516/KF949517,KF949840/KF949841,KF950850/KF950851
UAM30873*	Baker (BKR)	55.366667	-133.600100	KF950030, –/–, –/–, –/–
UAM30874		55.366667	-133.600100	KF949318,KF949482/KF949483,KF949816/KF949817,KF950816/KF950817
UAM50605		55.366667	-133.600100	–, –/–, –/–,KF950854/KF950855
UAM76353*		55.366667	-133.600100	KF950045, –/–, –/–, –/–
UAM30818	Baranof (BNF)	56.983333	-134.900000	KF949276,KF949478/KF949479,KF949812/KF949813,KF950812/KF950813
UAM30819*		56.983333	-134.900000	KF950029, –/–, –/–, –/–
UAM30820		56.983333	-134.900000	KF949277,KF949480/KF949481,KF949814/KF949815,KF950814/KF950815
UAM30821*		56.983333	-134.900000	KF950056, –/–, –/–, –/–
UAM30822*		56.590278	-134.860278	KF950057, –/–, –/–, –/–
UAM50930	Chichagof (CGF)	58.031339	-135.612055	KF949289,KF949526/KF949527,KF949850/KF949851,KF950862/KF950863
UAM50932*		58.031339	-135.612055	KF950133, –/–, –/–, –/–
UAM50936		58.031339	-135.612055	KF949290,KF949528/KF949529,KF949852/KF949853,KF950864/KF950865
UAM76385*		58.031339	-135.612055	KF950075, –/–, –/–, –/–
MSB198194	Coronation (CRN)	55.920000	-134.319000	KF949306, –/–, –/–,KF950723/KF950724
MSB198221		55.920000	-134.319000	KF949257,KF949396/KF949397,KF949730/KF949731,KF950725/KF950726
UAM42924*		55.883333	-134.233333	KF950066, –/–, –/–, –/–
UAM23730*	Dall (DAL)	54.783333	-132.866667	KF950024, –/–, –/–, –/–
UAM23732		54.783333	-132.866667	KF949314,KF949466/KF949467,KF949802/KF949803,KF950800/KF950801
UAM73711*		55.215556	-133.138056	KF950073, –/–, –/–, –/–
UAM73829*		55.260000	-133.123889	KF950074, –/–, –/–, –/–
UAM73830		55.260000	-133.123889	KF949298,KF949550/KF949551,KF949874/KF949875,KF950887/KF950888
UAM76238*		54.783333	-132.866667	KF950044, –/–, –/–, –/–
UAM20662*	Etolin (ETN)	56.183333	-132.450000	KF950020, –/–, –/–, –/–
UAM20664*		56.183333	-132.450000	KF950021, –/–, –/–, –/–
UAM20665		56.183333	-132.450000	KF949310,KF949442/KF949443, –/–,KF950774/KF950775
UAM34616		56.166667	-132.450000	KF949280,KF949494/KF949495,KF949824/KF949825,KF950826/KF950827
UAM41652*		56.166667	-132.450000	KF950059, –/–, –/–, –/–
UAM42788*	Forrester (FRS)	54.821389	-133.520833	KF950060, –/–, –/–, –/–
UAM42790*		54.821389	-133.520833	KF950061, –/–, –/–, –/–
UAM42792		54.821389	-133.520833	KF949281,KF949500/KF949501,KF949828/KF949829,KF950832/KF950833
UAM42794		54.821389	-133.520833	KF949282,KF949502/KF949503,KF949830/KF949831,KF950834/KF950835
UAM42795*		54.821389	-133.520833	KF950062, –/–, –/–, –/–
UAM70143	Gravina (GRV)	55.178333	-131.805833	KF949294,KF949542/KF949543,KF949866/KF949867,KF950879/KF950880
UAM70144*		55.178333	-131.805833	KF950070, –/–, –/–, –/–
UAM70150*		55.178333	-131.805833	KF950071, –/–, –/–, –/–

UAM70151		55.178333	-131.805833	KF949295,KF949544/KF949545,KF949868/KF949869,KF950881/KF950882
UAM70152*		55.178333	-131.805833	KF950072, – / – , – / – , – / –
UAM23828	Heceta (HEC)	55.803056	-133.591389	KF949274,KF949470/KF949471,KF949806/KF949807,KF950804/KF950805
UAM23829*		55.803056	-133.591389	KF950053, – / – , – / – , – / –
UAM23830*		55.803056	-133.591389	KF950054, – / – , – / – , – / –
UAM23831		55.803056	-133.591389	KF949275,KF949472/KF949473,KF949808/KF949809,KF950806/KF950807
UAM23834*		55.803056	-133.591389	KF950055, – / – , – / – , – / –
UAM49629	Kosciusko (KSC)	55.969167	-133.645833	KF949285,KF949518/KF949519,KF949842/KF949843,KF950852/KF950853
UAM49631*		55.982778	-133.605000	KF950067, – / – , – / – , – / –
UAM70204		55.969167	-133.646944	KF949296,KF949546/KF949547,KF949870/KF949871,KF950883/KF950884
MSB148973*	Kuiu (KUI)	56.631367	-133.737167	KF950017, – / – , – / – , – / –
MSB148974		56.631367	-133.737167	KF949300,KF949376/KF949377,KF949710/KF949711,KF950707/KF950708
UAM43431		56.321389	-134.071667	KF949324,KF949512/KF949513, – / – ,KF950844/KF950845
UAM20945	Kupreanof (KRF)	56.866667	-133.316667	KF949311,KF949446/KF949447,KF949780/KF949781,KF950778/KF950779
UAM20948		56.866667	-133.316667	KF949312,KF949448/KF949449,KF949782/KF949783,KF950780/KF950781
UAM30590*		56.866667	-133.316667	KF950028, – / – , – / – , – / –
UAM42578*	Lulu (LUL)	55.439722	-133.455278	KF950034, – / – , – / – , – / –
UAM42579*		55.439722	-133.455278	KF950035, – / – , – / – , – / –
UAM42580		55.439722	-133.455278	KF949321,KF949496/KF949497,KF949826/KF949827,KF950828/KF950829
UAM42581		55.439722	-133.455278	KF949322,KF949498/KF949499, – / – ,KF950830/KF950831
UAM43024*		55.439722	-133.455278	KF950015, – / – , – / – , – / –
UAM23437*	Mary (MRY)	55.083333	-131.233333	KF950009, – / – , – / – , – / –
UAM23438*		55.083333	-131.233333	KF950010, – / – , – / – , – / –
UAM23104	Mitkof (MIT)	56.583333	-132.833333	KF949265,KF949452/KF949453,KF949786/KF949787,KF950784/KF950785
UAM23106*		56.583333	-132.833333	KF950048, – / – , – / – , – / –
UAM23107*		56.583333	-132.833333	KF950049, – / – , – / – , – / –
UAM23108		56.583333	-132.833333	KF949271,KF949454/KF949455,KF949788/KF949789,KF950786/KF950787
MSB221318	Noyes (NYS)	55.450000	-133.650000	KF949307,KF949400/KF949401, – / – ,KF950729/KF950730
UAM23655		55.451977	-133.659835	KF949313,KF949464/KF949465,KF949798/KF949799,KF950796/KF950797
UAM23656*		55.451977	-133.659835	KF950130, – / – , – / – , – / –
UAM23657*		55.451977	-133.659835	KF950022, – / – , – / – , – / –
UAM23658*		55.451977	-133.659835	KF950023, – / – , – / – , – / –
UAM23717	Prince of Wales (POW)	54.766667	-132.183333	KF949158, – / – ,KF949800/KF949801,KF950798/KF950799
UAM49643*		54.907500	-132.414722	KF950013, – / – , – / – , – / –
UAM74967		56.174444	-133.369167	–,KF949552/KF949553, – / – , – / –
UAM74968		56.174444	-133.369167	KF949299,KF949554/KF949555, – / – , – / –
UAM74969		56.174444	-133.369167	KF949258, – / – , – / – ,KF950889/KF950890
UAM74970		56.174444	-133.369167	KF949329,KF949556/KF949557, – / – , – / –
UAM74972		56.174444	-133.369167	KF949330,KF949558/KF949559, – / – , – / –
UAM23442*	Revillagigedo (REV)	55.502382	-131.028099	KF950129, – / – , – / – , – / –
UAM23443		55.502382	-131.028099	KF949259,KF949458/KF949459,KF949792/KF949793,KF950790/KF950791

UAM23449*		55.502382	-131.028099	KF964334, – / – , – / – , – / –
UAM23956		55.816667	-131.366667	KF949316,KF949474/KF949475, – / – ,KF950808/KF950809
UAM30343*		55.414722	-131.695833	KF950027, – / – , – / – , – / –
MSB221540	San Fernando (SNF)	55.541700	-133.321000	KF949308,KF949402/KF949403,KF949734/KF949735,KF950731/KF950732
UAM42800*		55.467222	-133.389444	KF950063, – / – , – / – , – / –
UAM42801		55.467222	-133.389444	KF949283,KF949504/KF949505,KF949832/KF949833,KF950836/KF950837
UAM42804*		55.467222	-133.389444	KF950064, – / – , – / – , – / –
UAM23992	Suemez (SMZ)	55.283333	-133.307199	KF949317,KF949476/KF949477,KF949810/KF949811,KF950810/KF950811
UAM42831		55.266667	-133.272156	KF949284,KF949506/KF949507,KF949834/KF949835,KF950838/KF950839
UAM42836*		55.266667	-133.272156	KF950065, – / – , – / – , – / –
UAM31725*	Warren (WRN)	55.875000	-133.841667	KF950058, – / – , – / – , – / –
UAM31727		55.875000	-133.841667	KF949278,KF949490/KF949491, – / – , – / –
UAM31729		55.875000	-133.841667	KF949279,KF949492/KF949493, – / – ,KF950824/KF950825
MSB149212*	Wrangell (WRG)	56.474883	-132.375233	KF950018, – / – , – / – , – / –
UAM69665		56.269722	-132.070556	–, – / – , – / – ,KF950877/KF950878
UAM69668*		56.269722	-132.070556	KF950068, – / – , – / – , – / –
UAM69673*		56.269722	-132.070556	KF950069,KF950076/KF950077,KF950078/KF950079, – / –
UAM20619	Zarembo (ZRB)	56.416667	-132.833333	KF949355,KF949440/KF949441,KF949776/KF949777,KF950772/KF950773
UAM20620*		56.416667	-132.833333	KF950019, – / – , – / – , – / –
UAM43440		56.333333	-132.833333	KF949260,KF949514/KF949515, – / – ,KF950846/KF950847
UAM43469*		56.333333	-132.833333	KF950036, – / – , – / – , – / –
	British Columbia			
UAM52511	Central (BCC)	57.135556	-130.286389	KF949291,KF949532/KF949533,KF949856/KF949857,KF950868/KF950869
UAM52512		57.44515	-130.21667	KF949346, – / – , – / – , – / –
UAM52516		57.15512	-130.24492	KF949347,KF949670/KF949671,KF949988/KF949989,KF950989/KF950990
UAM52518		57.135556	-130.286389	KF949292,KF949534/KF949535,KF949858/KF949859,KF950870/KF950871
MSB147174	North (BCN)	57.28230	-130.26880	KF949335,KF949586/KF949587,KF949900/KF949901,KF950915/KF950916
MSB147719		57.155117	-130.244917	KF949160, – / – , – / – , – / –
MSB147720		57.42340	-130.23510	KF949157, – / – ,KF949902/KF949903,KF950917/KF950918
MSB155704		57.16980	-130.23670	KF949336, – / – , – / – , – / –
MSB155836		57.16980	-130.23670	KF949337,KF949602/KF949603,KF949918/KF949919,KF950927/KF950928
MSB155873		59.86972	-136.69028	KF949338, – / – , – / – , – / –
MSB156117		57.86556	-131.28444	KF949339,KF949604/KF949605,KF949920/KF949921,KF950929/KF950930
MSB156119		57.169800	-130.236700	KF949301,KF949382/KF949383,KF949716/KF949717,KF950712/KF950713
UAM50570		57.85472	-131.36944	KF949340, – / – , – / – , – / –
UAM51070		57.865556	-131.284444	KF949327,KF949530/KF949531,KF949854/KF949855,KF950866/KF950867
UAM52661		57.85472	-131.36944	KF949341,KF949672/KF949673,KF949990/KF949991,KF950991/KF950992
UAM52664		57.85472	-131.36944	KF949342,KF949674/KF949675,KF949992/KF949993,KF950993/KF950994
UAM52665		50.05389	-121.70778	KF949343, – / – , – / – , – / –
UAM52666		50.05389	-121.70778	KF949344, – / – , – / – , – / –
UAM52680		57.854722	-131.369444	KF949264,KF949538/KF949539,KF949862/KF949863,KF950874/KF950875

	UWBM75449	South (BCS)	50.053889	-121.707778	KF949333, – / – , – / – , – / –
	UWBM75450		50.053889	-121.707778	KF949334,KF949568/KF949569, – / – ,KF950899/KF950900
	UWBM75463		52.57571	-131.43990	KF949353,KF949686/KF949687, – / – ,KF951003/KF951004
	UWBM75480		52.57571	-131.43990	KF949354,KF949688/KF949689, – / – ,KF951005/KF951006
		British Columbian Islands:			
	HGPeke9701	Hotsprings (HTS)	52.575709	-131.439899	KF949153,KF949362/KF949363,KF949696/KF949697,KF950695/KF950696
	HGPeke9702		52.575709	-131.439899	KF949154, – / – , – / – , – / –
	HGPeke9703		52.575709	-131.439899	KF949155,KF949364/KF949365,KF949698/KF949699,KF950697/KF950698
	HGPeke0306	Ramsay (RMS)	52.569649	-131.398463	KF949302,KF949356/KF949357,KF949690/KF949691,KF950689/KF950690
	HGPeke0307		52.569649	-131.398463	KF949303,KF949358/KF949359,KF949692/KF949693,KF950691/KF950692
	HGPeke0308		52.569649	-131.398463	KF949304,KF949360/KF949361,KF949694/KF949695,KF950693/KF950694
	HGPeke0309		52.569649	-131.398463	KF949305, – / – , – / – , – / –
	UWBM75393	Vancouver (VCR)	50.516667	-127.150000	KF949332,KF949566/KF949567,KF949882/KF949883,KF950897/KF950898
	MSB61426	Washington (WA)	60.63306	-135.16639	**DQ385716**,KF949644/KF949645,KF949958/KF949959,KF950961/KF950962
	UWBM74030		60.63306	-135.16639	– ,KF949684/KF949685,KF950006/KF950007,KF951001/KF951002
	UWBM74932		48.027189	-123.588333	KF949331,KF949564/KF949565,KF949880/KF949881,KF950895/KF950896
	UWBM74954		60.70722	-135.19917	KF949352, – / – , – / – , – / –
	UAM71580	Yukon - South (YTS)	60.44722	-134.83472	KF949348, – / – ,KF950000/KF950001,KF950997/KF950998
	UAM71581		24.45000	-111.83333	KF949349,KF949680/KF949681,KF950002/KF950003,KF950999/KF951000
	UAM71620		60.707222	-135.199167	KF949297,KF949548/KF949549,KF949872/KF949873,KF950885/KF950886
	UAM71622		24.45000	-111.83333	KF949350,KF949682/KF949683,KF950004/KF950005, – / –
	UAM71660		24.45000	-111.83333	KF949351, – / – , – / – , – / –
P. maniculatus - East					
a	CMNH109419	Michigan (MI)	39.75280	-79.08111	**DQ385825**, – / – , – / – , – / –
	CMNH109438	Minnesota (MN)	48.65810	-65.75280	**DQ385737**, – / – , – / – , – / –
	MSB53341	Ontario (ON)	38.56667	-78.36667	**DQ385770**,KF949412/KF949413,KF949746/KF949747,KF950744/KF950745
	MSB71957	Tennessee (TN)	27.97148	-107.60006	**DQ385817**,KF949420/KF949421,KF949754/KF949755,KF950750/KF950751
	MSB71965		19.10167	-99.76750	**DQ385818**,KF949648/KF949649, – / – ,KF950676/KF950964
b	CMNH109330	Maine (ME)	42.15784	-78.71503	**DQ385754**, – / – , – / – , – / –
	MSB229789	New York (NY)	35.61110	-83.42500	– , – / – ,KF949736/KF949737,KF950661/KF950733
	OSM350		35.61110	-83.42500	**DQ385743**, – / – , – / – , – / –
	CMNH109276	Pennsylvania (PA)	38.57667	-78.37500	**DQ385762**, – / – , – / – , – / –
	CMNH109316	Quebec (QC)	38.55000	-78.39667	**DQ385749**, – / – , – / – , – / –
	MSB229872	Vermont (VT)	31.52833	-108.87291	– ,KF949404/KF949405,KF949738/KF949739,KF950734/KF950735
	MSB74926	Virginia (VA)	31.94113	-108.91372	**DQ385759**,KF949426/KF949427,KF949760/KF949761,KF950756/KF950757
	MSB74932		51.02791	-115.03420	**DQ385760**,KF949652/KF949653,KF949966/KF949967,KF950971/KF950972
	MSB74936		51.02791	-115.03420	**DQ385761**,KF949654/KF949655,KF949968/KF949969,KF950973/KF950974
c	OSM430	Labrador (NL)	44.84010	-72.52510	**DQ385731**, – / – , – / – , – / –
	MSB55764	Manitoba (MB)	51.00283	-95.35612	**DQ385723**,KF949414/KF949415,KF949748/KF949749,KF950746/KF950747
	MSB55767		44.80078	-77.67195	**DQ385725**,KF949638/KF949639,KF949952/KF949953,KF950955/KF950956

P. maniculatus - South					
	MSB58334	Chihuahua (CHH)	34.97474	-109.79479	**DQ385717**, – / – , – / – , – / –
	MSB213741	Mexico (MX)	56.03181	-129.93136	– ,KF949628/KF949629,KF949944/KF949945,KF950947/KF950948
	MSB46243	New Mexico (NM)	57.44515	-130.21667	**DQ385718**,KF949634/KF949635,KF949948/KF949949,KF950953/KF950673
	MSB51133		57.42340	-130.23510	**DQ385720**,KF949636/KF949637,KF949950/KF949951,KF950674/KF950954
P. maniculatus - Southwest					
	MSB58325	Baja California (BACA)	34.73966	-120.53967	**DQ385707**,KF949418/KF949419,KF949752/KF949753,KF950683/KF950684
	MSB58326		34.73966	-120.53967	**DQ385709**, – / – , – / – , – / –
	MSB58328		34.73966	-120.53967	**DQ385706**, – / – , – / – , – / –
	MSB58330		34.73966	-120.53967	**DQ385708**,KF949642/KF949643,KF949956/KF949957,KF950685/KF950686
	MSB87462	California (CA)	39.42240	-118.70533	**DQ385710**, – / – , – / – , – / –
	MSB87484		44.88311	-68.67194	**DQ385711**, – / – , – / – , – / –
	MSB87485		54.68750	-101.65278	**DQ385712**, – / – , – / – , – / –
	MSB87486		54.64167	-101.63333	**DQ385713**,KF949434/KF949435,KF949768/KF949769,KF950662/KF950663
	MSB87492		45.86860	-84.72780	**DQ385714**, – / – , – / – ,KF950979/KF950980
	MSB74965	Nevada (NV)	47.05630	-93.91724	**DQ385715**,KF949656/KF949657,KF949970/KF949971, – / –
P. maniculatus - West					
	MSB156150	Alberta (AB)	58.03956	-129.95033	KF949201, – / – , – / – , – / –
	MSB156182		58.03956	-129.95033	KF949166,KF949384/KF949385,KF949718/KF949719,KF950658/KF950714
	MSB156183		58.03956	-129.95033	KF949202, – / – , – / – , – / –
	MSB122918	Arizona (AZ)	58.38253	-129.91877	KF949161,KF949366/KF949367,KF949700/KF949701,KF950699/KF950700
		British Columbia			
	MSB158235	Central (BCC)	59.56000	-133.66694	KF949236,KF949392/KF949393,KF949726/KF949727,KF950721/KF950722
	MSB147166	North (BCN)	59.56000	-133.66694	KF949252, – / – , – / – , – / –
	MSB155835		59.56000	-133.66694	KF949240,KF949600/KF949601,KF949916/KF949917,KF950668/KF950926
	MSB155850		59.60000	-133.66667	KF949241, – / – , – / – , – / –
	MSB158026		59.56000	-133.66694	KF949218, – / – , – / – , – / –
	MSB158027		59.56000	-133.66694	KF949219,KF949606/KF949607,KF949922/KF949923,KF950669/KF950670
	MSB158207		59.56000	-133.66694	KF949220, – / – , – / – , – / –
	MSB199034		59.56000	-133.66694	KF949248,KF949398/KF949399,KF949732/KF949733,KF950727/KF950728
	UAM35335		59.56000	-133.66694	KF949250,KF949666/KF949667,KF949982/KF949983,KF950677/KF950678
	UAM35336		59.71139	-133.56722	KF949251, – / – , – / – , – / –
	UAM35337		59.61306	-133.66722	KF949266, – / – ,KF949984/KF949985,KF950987/KF950988
	UAM35341		59.61306	-133.66778	KF949209, – / – , – / – , – / –
	UAM52689		59.73417	-133.51889	KF949208, – / – ,KF949994/KF949995,KF950679/KF950680
	UAM52690		59.71139	-133.56722	KF949214, – / – , – / – , – / –
	UAM52691		49.20203	-117.89709	KF949215, – / – , – / – , – / –
	UAM52692		49.20203	-117.89709	KF949216, – / – , – / – , – / –
	UAM52693		49.20203	-117.89709	KF949217, – / – , – / – , – / –
	UAM52696		49.20203	-117.89709	KF949210, – / – , – / – , – / –
	UAM52699		49.30000	-115.13040	KF949211,KF949676/KF949677,KF949996/KF949997,KF950681/KF950682

UAM52700		49.30000	-115.13040	KF949212, – / – , – / – , – / –
UAM52701		49.30000	-115.13040	KF949247,KF949540/KF949541,KF949864/KF949865,KF950664/KF950876
UAM52967		41.00403	-124.09161	KF949213, – / – , – / – , – / –
MSB156364	South (BCS)	40.66667	-104.36667	KF949203, – / – , – / – , – / –
MSB156365		40.66667	-104.36667	KF949204, – / – , – / – , – / –
MSB156370		43.40750	-112.80444	KF949167,KF949386/KF949387,KF949720/KF949721,KF950715/KF950716
MSB156589		43.37610	-116.45900	KF949168,KF949388/KF949389,KF949722/KF949723,KF950717/KF950718
MSB56704		43.37610	-116.45900	KF949196, – / – ,KF949954/KF949955,KF950957/KF950958
MSB56705		43.37610	-116.45900	KF949197, – / – , – / – , – / –
MSB56706		43.37610	-116.45900	KF949198,KF949640/KF949641, – / – ,KF950959/KF950960
MSB43630	California (CA)	41.60060	-93.60890	**DQ385703**,KF949410/KF949411,KF949744/KF949745,KF950742/KF950743
MSB74667	Colorado (CO)	38.18430	-99.21550	**DQ385692**,KF949424/KF949425,KF949758/KF949759,KF950754/KF950755
MSB74669		38.18430	-99.21550	**DQ385693**, – / – , – / – , – / –
MSB151511	Idaho (ID)	45.55410	-111.03960	KF949172,KF949380/KF949381,KF949714/KF949715,KF950710/KF950711
MSB74885		39.41658	-118.70098	**DQ385672**, – / – , – / – , – / –
MSB74886		33.99139	-107.15000	**DQ385673**,KF949650/KF949651,KF949964/KF949965,KF950969/KF950970
MSB74894		35.05609	-106.24260	**DQ385674**, – / – , – / – , – / –
MSB74897		32.82235	-106.09322	**DQ385675**, – / – , – / – , – / –
MSB56717	Montana (MT)	60.01000	-111.54000	**DQ385678**,KF949416/KF949417,KF949750/KF949751,KF950748/KF950749
MSB74970	Nevada (NV)	44.39630	-120.42480	**DQ385681**,KF949428/KF949429,KF949762/KF949763,KF950758/KF950759
MSB69326	New Mexico (NM)	40.45556	-112.01139	**DQ385646**,KF949646/KF949647,KF949960/KF949961,KF950675/KF950963
MSB77901		47.22306	-120.99320	**DQ385653**,KF949430/KF949431,KF949764/KF949765,KF950760/KF950761
MSB89198		47.17058	-121.75531	**DQ385661**,KF949436/KF949437,KF949770/KF949771,KF950764/KF950765
MSB89387		48.20000	-121.91670	**DQ385652**,KF949660/KF949661,KF949974/KF949975,KF950981/KF950982
MSB90205		47.71914	-122.71854	**DQ385667**,KF949662/KF949663,KF949976/KF949977,KF950687/KF950688
MSB90219		47.09010	-122.60390	**DQ385670**,KF949664/KF949665,KF949978/KF949979,KF950983/KF950984
UAM77795	Northwest Territories (NWT)	60.13580	-124.05700	KF949170,KF949562/KF949563,KF949878/KF949879,KF950893/KF950894
MSB155558	Oregon (OR)	60.13580	-124.05700	KF949191, – / – , – / – , – / –
MSB72070	Utah (UT)	60.13580	-124.05700	**DQ385685**, – / – ,KF949962/KF949963,KF950965/KF950966
MSB43433	Washington (WA)	60.13580	-124.05700	**DQ385689**, – / – , – / – , – / –
MSB55699		61.10000	-135.29340	**DQ385696**, – / – , – / – , – / –
MSB83456		61.10000	-135.29340	**DQ385695**, – / – , – / – , – / –
MSB83495		61.10000	-135.29340	**DQ385694**,KF949658/KF949659,KF949972/KF949973,KF950975/KF950976
MSB86381		61.10000	-135.29340	**DQ385697**,KF949432/KF949433,KF949766/KF949767,KF950762/KF950763
MSB144139	Yukon - South (YTS)	60.10000	-128.60200	KF949237,KF949570/KF949571,KF949884/KF949885,KF950901/KF950902
MSB144142		60.09700	-128.60300	KF949238,KF949572/KF949573,KF949886/KF949887,KF950903/KF950904
MSB144150		60.09700	-128.60300	KF949253,KF949574/KF949575,KF949888/KF949889,KF950905/KF950906
MSB144151		60.05880	-135.23250	KF949245,KF949576/KF949577,KF949890/KF949891,KF950907/KF950908
MSB144237		61.20045	-133.04693	KF949235,KF949370/KF949371,KF949704/KF949705,KF950655/KF950656
MSB144238		60.06668	-133.78280	KF949242, – / – , – / – , – / –
MSB144239		60.01410	-133.79548	KF949243, – / – , – / – , – / –

	MSB144240		60.05573	-133.80761	KF949244, – / – , – / – , – / –
	MSB144364		60.06656	-133.77998	KF949254, – / – , – / – , – / –
	MSB144366		60.06656	-133.77998	KF949262, – / – , – / – , – / –
	MSB144387		60.07343	-133.80309	KF949255, – / – , – / – , – / –
	MSB144409		60.07343	-133.80309	KF949249,KF949584/KF949585,KF949898/KF949899,KF950665/KF950666
	MSB149188		60.07343	-133.80309	KF949239,KF949588/KF949589,KF949904/KF949905,KF950667/KF950919
	MSB194065		60.01410	-133.79548	KF949221,KF949608/KF949609,KF949924/KF949925,KF950931/KF950932
	MSB194080		60.01410	-133.79548	KF949246,KF949394/KF949395,KF949728/KF949729,KF950659/KF950660
	MSB194085		60.05573	-133.80761	KF949222,KF949610/KF949611,KF949926/KF949927,KF950933/KF950934
	MSB194097		60.15271	-127.43541	KF949223, – / – , – / – , – / –
	MSB194099		60.14992	-127.43530	KF949224,KF949612/KF949613,KF949928/KF949929,KF950935/KF950936
	MSB194102		60.15271	-127.43541	KF949225,KF949614/KF949615,KF949930/KF949931,KF950937/KF950938
	MSB194103		60.06668	-133.78280	KF949226, – / – , – / – , – / –
	MSB194104		60.07343	-133.80309	KF949227,KF949616/KF949617,KF949932/KF949933,KF950939/KF950940
	MSB194105		60.01410	-133.79548	KF949228,KF949618/KF949619,KF949934/KF949935,KF950941/KF950942
	MSB194113		60.01410	-133.79548	KF949229, – / – , – / – , – / –
	MSB194114		60.05573	-133.80761	KF949230,KF949620/KF949621,KF949936/KF949937,KF950671/KF950943
	MSB194127		60.15271	-127.43541	KF949231, – / – , – / – , – / –
	MSB194129		60.14992	-127.43530	KF949232, – / – , – / – , – / –
	MSB194130		60.15271	-127.43541	KF949233, – / – , – / – , – / –
	MSB194166		60.06668	-133.78280	KF949234,KF949622/KF949623,KF949938/KF949939,KF950672/KF950944
	MSB84837	Iowa (IA)	33.50722	-108.54945	**DQ385633**, – / – , – / – ,KF950977/KF950978
	MSB73954	Kansas (KS)	36.75750	-108.18153	**DQ385639**, – / – , – / – ,KF950967/KF950968
	MSB73966		36.19751	-108.31174	**DQ385642**,KF949422/KF949423,KF949756/KF949757,KF950752/KF950753
P. leucopus					
	MSB92216				– ,KF949438/KF949439,KF949772/KF949773,KF950766/KF950767
	MSB92383				– , – / – ,KF949774/KF949775,KF950768/KF950769
					DQ973104, – / – , – / – , – / –
P. melanotis					
	MSB40124				KF949261, – / – , – / – ,KF950740/KF950741
					– ,**FJ214711**/ – , – / – , – / –
					– , – / – ,**EF989891**/ – , – / –

Table 2. Primer list and PCR annealing temperatures. Primers used for amplification and sequencing mtDNA Cytochrome B (cyt *b*), and nuclear loci β-fibrinogen (FGB), interphotoreceptor retinoid-binding protein (IRBP) and zona pellucida 3 (ZP3) in *Peromyscus*, with ^{o}C annealing temperatures indicated in parentheses.

Primer	Sequence (5'-3')	Reference
cyt*b* (50)		
L14734		(Ohdachi et al. 2001)
CytBRev		(Anderson and Yates 2000)
FGB (63)		
MSB_PFGBF	GCCGTTTGGATTGGCTGC	This study, modified from Matocq *et al*. (2007)
MSB_PFGBR	CGACAGGGACAATGATGGC	This study, modified from Matocq *et al*. (2007)
IRBP (60)		
MSB_PIRBPF	CCAGGAGGTACTGAGTGAGC	This study, modified from Stanhope *et al.* (1992)
MSB_PIRBPR	GCTGAGTAGTCCATGCTAGC	This study, modified from Stanhope *et al.* (1992)
Zp3 (56)		
Z36FA		(Turner and Hoekstra 2006)
Z37RA		(Turner and Hoekstra 2006)

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Table 3. Diversity indices, expansion statistics and models of evolution. n=haploid sample size; L=length of sequence; S=variable sites; Eta=#mutations; h=#haplotypes; *Hd*=haplotype diversity; *π*=nucleotide diversity; *D*=Tajima's *D*; *FS*=Fu's *FS*; *R2*=Ramos-Osnin's *R2*; Model=model of evolution as selected by MODELTEST. Bold values are significant at p<0.05 (p<0.02 for *FS*).

Group	Gene	n	L	S	*h*	*Hd*	*π*	*D*	*FS* (p<.02)	*R2*	Model of Evolution
All Samples	Cytb	260	1143	235	155	0.982	0.01861	**-0.10023**	**-0.82321**	**0.07836**	TrN+I+G
	FGB	168	479	23	22	0.309	0.00130	**-0.03746**	**-0.37821**	**0.07790**	HKY
	IRBP	160	421	7	7	0.080	0.00025	**-0.11871**	-0.96319	**0.07576**	HKY+G
	Zp3	176	314	6	8	0.067	0.00029	**-0.08499**	**-0.54854**	**0.07454**	GTR+I+G
NoOG	Cytb	258	1143	191	161	0.984	0.01722	**-0.09987**	**-0.86939**	**0.07861**	
	FGB	166	479	18	21	0.302	0.00117	**-0.02523**	**-0.34750**	**0.07931**	
	IRBP	157	421	7	7	0.081	0.00025	**-0.08041**	-0.61592	**0.07596**	
	Zp3	173	314	5	6	0.057	0.00022	**-0.07028**	-0.43458	**0.07501**	
Peromyscus sp. nov.	Cytb	37	1143	42	22	0.946	0.00487	**-0.08122**	**-0.19581**	**0.11288**	HKY+I
	FGB	20	479	4	3	0.542	0.00312	-0.05602	-0.00642	**0.11819**	HKY
	IRBP	20	421	4	4	0.191	0.00070	**-0.02155**	**0.10754**	**0.13954**	HKY
	Zp3	17	314	10	8	0.574	0.00698	-0.07684	0.01352	**0.12065**	HKY+I
P. keeni	Cytb	103	1143	91	70	0.989	0.00529	**-0.07929**	**-0.33249**	**0.09185**	TrN+I+G
	FGB	86	479	2	3	0.057	0.00013	-0.08379	-0.47951	**0.08348**	HKY+I
	IRBP	74	421	3	4	0.243	0.00064	-0.00699	-0.11345	**0.09694**	HKY+I
	Zp3	89	314	10	12	0.222	0.00100	**-0.02895**	**-0.13447**	**0.09382**	HKY+I
P. maniculatus											
West	Cytb	90	1143	113	61	0.940	0.00860	**-0.09925**	-0.37647	**0.09386**	TrN+I+G
	FGB	44	479	23	21	0.753	0.00381	**-0.05620**	**-0.13547**	**0.09654**	HKY+I
	IRBP	47	421	8	9	0.343	0.00092	**-0.01808**	**-0.05135**	**0.10585**	HKY+I
	Zp3	50	314	4	5	0.153	0.00059	**-0.00082**	**-0.04361**	**0.10990**	HKY+I
East - a	Cytb	5	1143	16	5	1.000	0.00630	-0.05086	0.67799	**0.23149**	
	FGB	3	479	1	2	0.533	0.00111	-0.00688	0.33515	**0.29448**	
	IRBP	2	421	2	3	0.833	0.00238	-0.15870	0.39502	**0.34858**	
	Zp3	3	314	3	3	0.600	0.00391	-0.00619	0.33953	**0.26832**	
East - b	Cytb	7	1143	27	7	1.000	0.00700	**-0.06215**	0.47123	**0.19090**	
	FGB	4	479	1	2	0.250	0.00053	-0.01644	0.31732	**0.26876**	
	IRBP	5	421	2	3	0.511	0.00133	-0.01632	0.26473	**0.22699**	
	Zp3	5	314	6	5	0.867	0.00724	-0.04670	0.20722	**0.18491**	
East - c	Cytb	3	1143	9	3	1.000	0.00525	n/a	1.10130	**0.33813**	
	FGB	2	479	2	3	0.833	0.00209	-0.00377	0.36963	**0.34989**	
	IRBP	2	421	2	3	0.833	0.00317	-0.01828	0.39935	**0.33733**	
	Zp3	2	314	2	3	0.833	0.00319	-0.02415	0.37187	**0.34924**	
South	Cytb	3	1143	10	3	1.000	0.00583	n/a	1.13534	**0.33308**	
	FGB	3	479	2	3	0.600	0.00139	-0.00335	0.32780	**0.28936**	
	IRBP	3	421	7	5	0.933	0.00652	-0.03930	0.41737	**0.23530**	
	Zp3	3	314	8	5	0.933	0.01278	-0.04149	0.41630	**0.22276**	
Southwest	Cytb	10	1143	41	9	0.978	0.01091	-0.86630	0.35640	**0.16183**	
	FGB	4	479	0	1	0.000	0.00000	n/a	n/a	n/a	
	IRBP	4	421	1	2	0.536	0.00129	-0.02545	0.32683	**0.25466**	
	Zp3	4	314	2	2	0.536	0.00361	-0.04456	0.28652	**0.23280**	

Table 4. Cyt *b* and multilocus divergence date estimates for *Peromyscus*.

	cyt*b*			**multilocus**		
Lineage	**95% HPD lower**	**mean**	**95% HPD upper**	**95% HPD lower**	**mean**	**95% HPD upper**
Peromyscus sp. nov./*P. keeni*	299,400	443,000	607,800	136,200	178,600	216,800
Peromyscus sp. nov.	179,878	288,800	403,800	68,400	107,600	149,200
P. keeni	194,472	280,600	378,600	101,800	127,600	153,000
P. maniculatus - West	225,200	323,600	443,600	-	-	-
BC/YT	98,800	149,400	204,600	40,200	68,000	109,600
P. maniculatus - East	171,102	269,800	404,000	-	-	-
P. maniculatus - East - a	59,200	123,000	214,600	-	-	-
P. maniculatus - East - b	66,600	127,200	206,600	-	-	-
P. maniculatus - East - c	33,400	92,600	175,800	-	-	-
P. maniculatus - South	23,684	100,892	199,392	-	-	-
P. maniculatus - Southwest	131,170	257,800	399,800	-	-	-

Table 5. Cyt *b* between group net genetic divergences in *Peromyscus*. The number of base differences per site from estimation of net average between groups of sequences is shown. Standard error estimate(s) are shown above the diagonal. All ambiguous positions were removed for each sequence pair.

	Peromyscus sp. nov.	*P. keeni*	*P. maniculatus* - West	*P. maniculatus* - East - a	*P. maniculatus* - East - b	*P. maniculatus* - East - c	*P. maniculatus* - South	*P. maniculatus* - Southwest	*P. leucopus*	*P. melanotis*
Peromyscus sp. nov.		0.50%	0.50%	0.50%	0.60%	0.60%	0.50%	0.50%	0.90%	1.00%
P. keeni	3.60%		0.50%	0.60%	0.60%	0.60%	3.60%	0.40%	0.90%	1.00%
P. maniculatus - West	3.60%	3.90%		3.60%	4.30%	4.00%	3.30%	0.50%	9.90%	13.40%
P. maniculatus - East - a	4.20%	4.40%	0.50%		0.40%	0.40%	3.10%	0.50%	10.10%	1.00%
P. maniculatus - East - b	4.60%	4.40%	0.50%	1.70%		1.50%	3.20%	0.50%	9.60%	13.70%
P. maniculatus - East - c	4.80%	4.50%	0.50%	2.00%	0.30%		3.60%	0.50%	9.70%	13.60%
P. maniculatus - South	3.60%	0.50%	0.50%	0.50%	0.50%	0.50%		0.40%	0.90%	1.00%
P. maniculatus - Southwest	3.70%	2.40%	3.30%	3.90%	4.10%	4.00%	2.50%		9.50%	12.90%
P. leucopus	10.80%	10.00%	0.90%	0.90%	0.90%	0.90%	9.60%	0.90%		1.00%
P. melanotis	13.40%	13.30%	1.00%	13.30%	1.00%	1.00%	13.40%	1.00%	14.00%	

Table 6. Yukon populations of *Peromyscus* sp. nov., *P. keeni* and *P. maniculatus* West cyt*b* lineage populations. Bayesian migration estimates determined in BAYESASS. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows).

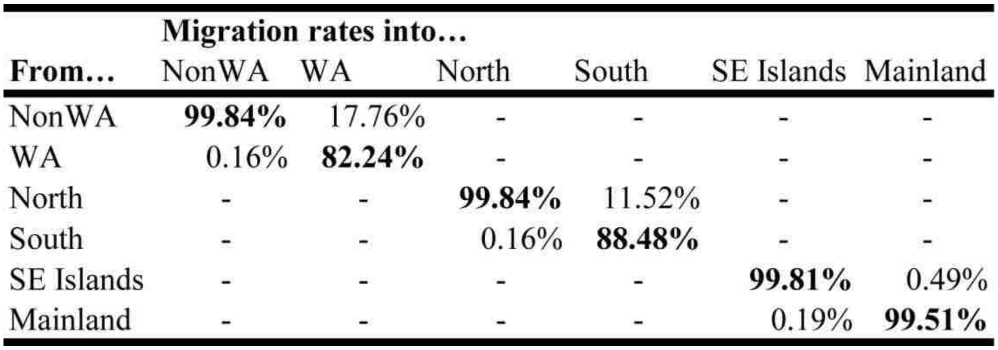
	Migration rates into…		
From…	***Peromyscus* sp. nov.**	***P. keeni***	***P. maniculatus* - West**
***Peromyscus* sp. nov.**	**0.868**	0.011	0.013
P. keeni	0.096	**0.686**	0.024
***P. maniculatus* - West**	0.010	0.008	**0.901**

Table 7. Southeast Alaskan population Bayesian migration estimates determined in BAYESASS for *P. keeni* and nearby *Peromyscus*. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows). Location abbreviations are in Table 1 and preceding notations are: Y=*Peromyscus* sp. nov., K=*P. keeni* and MW=*P. maniculatus* West.

	Migration rates into…																							
From…	**Y_YTS**	**K_ADM**	**K_BCC**	**K_BCN**	**K_BCS**	**K_BKR**	**K_BNF**	**K_CGF**	**K_CRN**	**K_DAL**	**K_ETN**	**K_FST**	**K_GRV**	**K_HEC**	**K_HTS**	**K_KRF**	**K_KSC**	**K_KUI**	**K_LUL**	**K_MIT**	**K_MLCP**	**K_MLFB**	**K_MLGB**	**K_MLHNS**
Y_YTS	**0.6734**	0.0066	0.0066	0.0066	0.0066	0.0068	0.0066	0.0066	0.0066	0.0068	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0110	0.0066	0.0069	0.0066	0.0066	0.0066
K_ADM	0.0065	**0.6733**	0.0064	0.0064	0.0066	0.0073	0.0065	0.0064	0.0064	0.0072	0.0064	0.0064	0.0065	0.0064	0.0064	0.0064	0.0064	0.0064	0.0108	0.0065	0.0070	0.0064	0.0065	0.0065
K_BCC	0.0067	0.0067	**0.6734**	0.0066	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0066	0.0067	0.0067	0.0067	0.0067	0.0066	0.0067	0.0109	0.0067	0.0067	0.0066	0.0067	0.0067
K_BCN	0.0064	0.0064	0.0064	**0.6732**	0.0065	0.0066	0.0065	0.0064	0.0064	0.0066	0.0064	0.0064	0.0065	0.0064	0.0064	0.0064	0.0064	0.0065	0.0140	0.0064	0.0065	0.0064	0.0064	0.0064
K_BCS	0.0067	0.0067	0.0067	0.0066	**0.6736**	0.0069	0.0067	0.0067	0.0067	0.0069	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0098	0.0067	0.0068	0.0067	0.0067	0.0067
K_BKR	0.0065	0.0065	0.0065	0.0065	0.0066	**0.6739**	0.0064	0.0064	0.0064	0.0070	0.0065	0.0065	0.0065	0.0065	0.0065	0.0065	0.0065	0.0065	0.0118	0.0065	0.0068	0.0064	0.0065	0.0065
K_BNF	0.0063	0.0063	0.0063	0.0063	0.0064	0.0067	**0.6731**	0.0063	0.0063	0.0067	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0064	0.0063	0.0143	0.0063	0.0066	0.0063	0.0063	0.0063
K_CGF	0.0065	0.0064	0.0064	0.0065	0.0065	0.0067	0.0064	**0.6732**	0.0064	0.0067	0.0064	0.0065	0.0065	0.0064	0.0064	0.0064	0.0065	0.0065	0.0132	0.0065	0.0066	0.0065	0.0065	0.0064
K_CRN	0.0066	0.0066	0.0066	0.0066	0.0068	0.0071	0.0066	0.0066	**0.6733**	0.0071	0.0066	0.0066	0.0065	0.0066	0.0066	0.0066	0.0066	0.0066	0.0102	0.0066	0.0069	0.0066	0.0065	0.0066
K_DAL	0.0062	0.0062	0.0062	0.0062	0.0063	0.0065	0.0062	0.0062	0.0062	**0.6739**	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0158	0.0062	0.0065	0.0062	0.0062	0.0062
K_ETN	0.0063	0.0063	0.0063	0.0063	0.0065	0.0067	0.0063	0.0063	0.0063	0.0068	**0.6731**	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0142	0.0063	0.0067	0.0063	0.0063	0.0063
K_FST	0.0063	0.0064	0.0064	0.0063	0.0065	0.0067	0.0063	0.0063	0.0063	0.0066	0.0063	**0.6731**	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0148	0.0064	0.0065	0.0063	0.0063	0.0063
K_GRV	0.0063	0.0064	0.0063	0.0063	0.0064	0.0066	0.0063	0.0063	0.0063	0.0067	0.0063	0.0063	**0.6731**	0.0063	0.0063	0.0063	0.0063	0.0063	0.0150	0.0063	0.0065	0.0063	0.0063	0.0063
K_HEC	0.0063	0.0064	0.0063	0.0063	0.0064	0.0068	0.0063	0.0063	0.0063	0.0066	0.0063	0.0063	0.0063	**0.6731**	0.0063	0.0063	0.0063	0.0063	0.0144	0.0064	0.0066	0.0064	0.0063	0.0063
K_HTS	0.0065	0.0065	0.0065	0.0065	0.0066	0.0067	0.0066	0.0066	0.0066	0.0066	0.0065	0.0065	0.0065	0.0065	**0.6733**	0.0065	0.0066	0.0066	0.0126	0.0066	0.0066	0.0065	0.0066	0.0066
K_KRF	0.0066	0.0066	0.0066	0.0065	0.0066	0.0068	0.0066	0.0066	0.0065	0.0067	0.0066	0.0065	0.0066	0.0066	0.0066	**0.6733**	0.0066	0.0065	0.0116	0.0066	0.0067	0.0066	0.0065	0.0066
K_KSC	0.0066	0.0066	0.0066	0.0066	0.0066	0.0068	0.0066	0.0066	0.0066	0.0068	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	**0.6733**	0.0066	0.0116	0.0066	0.0067	0.0066	0.0066	0.0066
K_KUI	0.0066	0.0066	0.0066	0.0065	0.0066	0.0067	0.0065	0.0066	0.0065	0.0067	0.0066	0.0066	0.0065	0.0066	0.0066	0.0066	0.0066	**0.6733**	0.0121	0.0066	0.0066	0.0066	0.0065	0.0066
K_LUL	0.0063	0.0063	0.0063	0.0063	0.0064	0.0066	0.0063	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0064	0.0063	**0.6829**	0.0063	0.0064	0.0063	0.0063	0.0062
K_MIT	0.0064	0.0065	0.0064	0.0064	0.0066	0.0069	0.0065	0.0064	0.0064	0.0068	0.0064	0.0065	0.0064	0.0064	0.0064	0.0064	0.0065	0.0065	0.0125	**0.6733**	0.0067	0.0065	0.0065	0.0064
K_MLCP	0.0063	0.0063	0.0063	0.0063	0.0064	0.0065	0.0063	0.0063	0.0063	0.0065	0.0064	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0152	0.0063	**0.6736**	0.0063	0.0063	0.0063
K_MLFB	0.0066	0.0066	0.0065	0.0065	0.0067	0.0069	0.0066	0.0066	0.0065	0.0069	0.0066	0.0066	0.0065	0.0066	0.0066	0.0066	0.0066	0.0066	0.0110	0.0066	0.0068	**0.6733**	0.0066	0.0066
K_MLGB	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0066	0.0066	0.0067	0.0110	0.0067	0.0067	0.0067	**0.6734**	0.0067
K_MLHNS	0.0063	0.0064	0.0063	0.0063	0.0065	0.0067	0.0063	0.0063	0.0063	0.0069	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0064	0.0138	0.0063	0.0067	0.0063	0.0063	**0.6731**
K_MLJNO	0.0066	0.0065	0.0065	0.0065	0.0066	0.0067	0.0066	0.0065	0.0066	0.0067	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0065	0.0066	0.0121	0.0066	0.0066	0.0066	0.0066	0.0065
K_MLKLU	0.0062	0.0062	0.0062	0.0062	0.0063	0.0066	0.0062	0.0062	0.0062	0.0073	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0120	0.0062	0.0071	0.0062	0.0062	0.0062
K_MLMFD	0.0065	0.0064	0.0065	0.0064	0.0065	0.0067	0.0064	0.0065	0.0064	0.0067	0.0064	0.0064	0.0064	0.0064	0.0065	0.0064	0.0065	0.0064	0.0132	0.0064	0.0066	0.0064	0.0064	0.0065
K_MLSEC	0.0063	0.0063	0.0063	0.0063	0.0064	0.0067	0.0063	0.0063	0.0063	0.0067	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0063	0.0063	0.0144	0.0063	0.0066	0.0063	0.0063	0.0063
K_MLSKW	0.0062	0.0062	0.0062	0.0062	0.0063	0.0064	0.0062	0.0062	0.0062	0.0064	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0062	0.0172	0.0062	0.0064	0.0062	0.0062	0.0062
K_MLWP	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0090	0.0068	0.0068	0.0068	0.0068	0.0068
K_MRY	0.0067	0.0067	0.0067	0.0067	0.0069	0.0072	0.0067	0.0067	0.0067	0.0072	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0083	0.0067	0.0071	0.0067	0.0067	0.0067
K_NYS	0.0063	0.0063	0.0063	0.0063	0.0064	0.0068	0.0063	0.0064	0.0063	0.0069	0.0063	0.0064	0.0064	0.0063	0.0063	0.0063	0.0063	0.0063	0.0143	0.0063	0.0066	0.0063	0.0063	0.0063
K_POW	0.0061	0.0061	0.0061	0.0060	0.0062	0.0064	0.0061	0.0061	0.0061	0.0064	0.0061	0.0061	0.0061	0.0061	0.0061	0.0061	0.0061	0.0061	0.0185	0.0061	0.0063	0.0061	0.0061	0.0061
K_REV	0.0064	0.0064	0.0063	0.0063	0.0066	0.0072	0.0063	0.0063	0.0064	0.0072	0.0063	0.0064	0.0063	0.0064	0.0063	0.0063	0.0064	0.0063	0.0122	0.0064	0.0068	0.0063	0.0063	0.0064
K_RMS	0.0064	0.0064	0.0064	0.0064	0.0065	0.0066	0.0065	0.0064	0.0064	0.0066	0.0064	0.0064	0.0064	0.0064	0.0064	0.0065	0.0065	0.0064	0.0138	0.0064	0.0067	0.0064	0.0064	0.0064
K_SMZ	0.0066	0.0066	0.0066	0.0066	0.0066	0.0067	0.0065	0.0066	0.0066	0.0067	0.0066	0.0066	0.0066	0.0065	0.0065	0.0066	0.0065	0.0066	0.0117	0.0066	0.0067	0.0065	0.0066	0.0066
K_SNF	0.0064	0.0065	0.0064	0.0064	0.0065	0.0068	0.0064	0.0065	0.0064	0.0067	0.0065	0.0065	0.0065	0.0064	0.0064	0.0064	0.0065	0.0064	0.0131	0.0065	0.0067	0.0064	0.0064	0.0065
K_VCR	0.0068	0.0068	0.0068	0.0069	0.0068	0.0069	0.0068	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0085	0.0068	0.0069	0.0068	0.0068	0.0068
K_WA	0.0068	0.0068	0.0069	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0085	0.0068	0.0069	0.0068	0.0068	0.0068
K_WRG	0.0065	0.0064	0.0065	0.0065	0.0066	0.0070	0.0065	0.0065	0.0065	0.0071	0.0065	0.0065	0.0064	0.0065	0.0065	0.0065	0.0065	0.0065	0.0109	0.0065	0.0069	0.0065	0.0065	0.0064
K_WRN	0.0066	0.0066	0.0066	0.0066	0.0067	0.0069	0.0066	0.0065	0.0066	0.0068	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0066	0.0112	0.0066	0.0068	0.0067	0.0066	0.0066
K_YTS	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0089	0.0068	0.0068	0.0068	0.0068	0.0068
K_ZRB	0.0064	0.0064	0.0064	0.0064	0.0065	0.0067	0.0064	0.0064	0.0064	0.0067	0.0065	0.0065	0.0064	0.0064	0.0064	0.0065	0.0065	0.0064	0.0133	0.0064	0.0066	0.0065	0.0064	0.0064
MW_BCC	0.0068	0.0069	0.0068	0.0068	0.0070	0.0073	0.0069	0.0068	0.0069	0.0073	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0069	0.0069	0.0071	0.0068	0.0068	0.0068
MW_BCN	0.0067	0.0068	0.0067	0.0067	0.0070	0.0078	0.0067	0.0068	0.0067	0.0075	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0068	0.0067	0.0068	0.0067	0.0072	0.0067	0.0067	0.0067
MW_BCS	0.0067	0.0068	0.0067	0.0067	0.0069	0.0074	0.0067	0.0067	0.0068	0.0073	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0078	0.0067	0.0071	0.0067	0.0067	0.0067
MW_WA	0.0069	0.0068	0.0068	0.0068	0.0070	0.0072	0.0068	0.0069	0.0068	0.0072	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0071	0.0069	0.0070	0.0068	0.0068	0.0068
MW_YTS	0.0067	0.0068	0.0067	0.0067	0.0070	0.0076	0.0067	0.0067	0.0068	0.0075	0.0067	0.0067	0.0068	0.0067	0.0067	0.0067	0.0067	0.0067	0.0068	0.0068	0.0072	0.0067	0.0067	0.0067

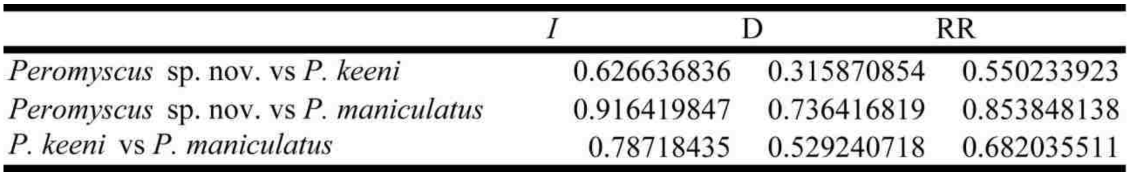
K_MLJNO	K_MLKLU	K_MLMFD	K_MLSEC	K_MLSKW	K_MLWP	K_MRY	K_NYS	K_POW	K_REV	K_RMS	K_SMZ	K_SNF	K_VCR	K_WA	K_WRG	K_WRN	K_YTS	K_ZRB	MW_BCC	MW_BCS	MW_WA	MW_YTS	From…
0.0066	0.0114	0.0066	0.0067	0.0066	0.0066	0.0066	0.0068	0.0069	0.0066	0.0066	0.0067	0.0066	0.0066	0.0066	0.0082	0.0066	0.0065	0.0107	0.0066	0.0066	0.0067	0.0066	**Y_YTS**
0.0065	0.0110	0.0064	0.0070	0.0065	0.0065	0.0065	0.0071	0.0079	0.0065	0.0064	0.0067	0.0064	0.0064	0.0065	0.0120	0.0064	0.0064	0.0107	0.0065	0.0064	0.0065	0.0064	**K_ADM**
0.0067	0.0108	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0069	0.0067	0.0067	0.0066	0.0067	0.0067	0.0067	0.0069	0.0067	0.0067	0.0109	0.0067	0.0067	0.0067	0.0067	**K_BCC**
0.0064	0.0140	0.0064	0.0065	0.0065	0.0065	0.0064	0.0065	0.0067	0.0064	0.0065	0.0064	0.0064	0.0065	0.0064	0.0074	0.0065	0.0064	0.0140	0.0064	0.0064	0.0064	0.0064	**K_BCN**
0.0067	0.0100	0.0066	0.0068	0.0067	0.0067	0.0067	0.0068	0.0071	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0082	0.0067	0.0067	0.0097	0.0067	0.0067	0.0067	0.0067	**K_BCS**
0.0064	0.0114	0.0065	0.0068	0.0065	0.0065	0.0065	0.0069	0.0077	0.0065	0.0065	0.0066	0.0064	0.0065	0.0065	0.0106	0.0064	0.0065	0.0112	0.0064	0.0065	0.0064	0.0064	**K_BKR**
0.0063	0.0145	0.0063	0.0066	0.0063	0.0063	0.0063	0.0066	0.0070	0.0063	0.0063	0.0065	0.0063	0.0063	0.0063	0.0093	0.0064	0.0064	0.0140	0.0063	0.0064	0.0064	0.0063	**K_BNF**
0.0064	0.0135	0.0064	0.0066	0.0064	0.0065	0.0064	0.0068	0.0069	0.0065	0.0064	0.0065	0.0064	0.0065	0.0064	0.0085	0.0065	0.0064	0.0129	0.0065	0.0064	0.0064	0.0064	**K_CGF**
0.0066	0.0104	0.0066	0.0068	0.0066	0.0066	0.0066	0.0069	0.0075	0.0066	0.0066	0.0067	0.0066	0.0066	0.0066	0.0099	0.0065	0.0066	0.0102	0.0065	0.0066	0.0066	0.0066	**K_CRN**
0.0062	0.0166	0.0062	0.0064	0.0062	0.0062	0.0062	0.0065	0.0070	0.0063	0.0062	0.0063	0.0062	0.0062	0.0062	0.0091	0.0062	0.0062	0.0159	0.0062	0.0062	0.0062	0.0062	**K_DAL**
0.0063	0.0144	0.0063	0.0065	0.0063	0.0063	0.0063	0.0067	0.0072	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0095	0.0063	0.0063	0.0140	0.0063	0.0063	0.0063	0.0063	**K_ETN**
0.0063	0.0146	0.0063	0.0066	0.0063	0.0063	0.0063	0.0066	0.0071	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0090	0.0063	0.0063	0.0142	0.0063	0.0064	0.0063	0.0063	**K_FST**
0.0063	0.0152	0.0063	0.0064	0.0063	0.0063	0.0063	0.0066	0.0069	0.0064	0.0063	0.0064	0.0063	0.0063	0.0063	0.0085	0.0063	0.0063	0.0148	0.0063	0.0064	0.0063	0.0063	**K_GRV**
0.0063	0.0147	0.0063	0.0064	0.0063	0.0063	0.0063	0.0065	0.0071	0.0063	0.0063	0.0064	0.0063	0.0063	0.0063	0.0091	0.0063	0.0063	0.0144	0.0063	0.0063	0.0063	0.0063	**K_HEC**
0.0065	0.0124	0.0066	0.0066	0.0065	0.0065	0.0065	0.0066	0.0067	0.0065	0.0065	0.0066	0.0066	0.0066	0.0065	0.0072	0.0066	0.0065	0.0123	0.0065	0.0066	0.0066	0.0066	**K_HTS**
0.0066	0.0117	0.0066	0.0067	0.0066	0.0065	0.0066	0.0068	0.0069	0.0066	0.0065	0.0067	0.0066	0.0066	0.0066	0.0081	0.0066	0.0066	0.0115	0.0066	0.0066	0.0066	0.0065	**K_KRF**
0.0066	0.0117	0.0066	0.0067	0.0066	0.0065	0.0066	0.0067	0.0070	0.0066	0.0065	0.0066	0.0066	0.0066	0.0065	0.0080	0.0066	0.0066	0.0114	0.0066	0.0066	0.0066	0.0066	**K_KSC**
0.0065	0.0121	0.0065	0.0067	0.0066	0.0065	0.0066	0.0067	0.0068	0.0065	0.0066	0.0066	0.0066	0.0066	0.0065	0.0077	0.0065	0.0065	0.0119	0.0065	0.0065	0.0066	0.0065	**K_KUI**
0.0063	0.0151	0.0063	0.0065	0.0063	0.0063	0.0063	0.0066	0.0071	0.0064	0.0063	0.0063	0.0063	0.0063	0.0063	0.0077	0.0063	0.0063	0.0150	0.0063	0.0063	0.0063	0.0063	**K_LUL**
0.0065	0.0122	0.0065	0.0068	0.0064	0.0064	0.0065	0.0068	0.0077	0.0065	0.0065	0.0065	0.0064	0.0064	0.0064	0.0095	0.0064	0.0064	0.0121	0.0064	0.0064	0.0064	0.0064	**K_MIT**
0.0063	0.0156	0.0063	0.0064	0.0063	0.0063	0.0063	0.0064	0.0067	0.0063	0.0064	0.0063	0.0063	0.0063	0.0063	0.0078	0.0063	0.0063	0.0153	0.0063	0.0063	0.0064	0.0063	**K_MLCP**
0.0066	0.0111	0.0066	0.0068	0.0065	0.0066	0.0066	0.0068	0.0073	0.0066	0.0066	0.0067	0.0065	0.0066	0.0065	0.0089	0.0066	0.0066	0.0109	0.0066	0.0066	0.0066	0.0066	**K_MLFB**
0.0066	0.0109	0.0066	0.0067	0.0067	0.0067	0.0067	0.0067	0.0067	0.0066	0.0067	0.0066	0.0067	0.0067	0.0067	0.0068	0.0067	0.0067	0.0108	0.0066	0.0067	0.0066	0.0066	**K_MLGB**
0.0064	0.0140	0.0063	0.0066	0.0063	0.0064	0.0063	0.0067	0.0073	0.0063	0.0063	0.0065	0.0063	0.0063	0.0064	0.0103	0.0063	0.0063	0.0131	0.0064	0.0063	0.0063	0.0064	**K_MLHNS**
0.6733	0.0121	0.0065	0.0067	0.0065	0.0066	0.0065	0.0067	0.0069	0.0065	0.0065	0.0066	0.0066	0.0066	0.0066	0.0077	0.0066	0.0066	0.0119	0.0066	0.0066	0.0066	0.0065	**K_MLJNO**
0.0062	**0.6830**	0.0062	0.0063	0.0062	0.0062	0.0062	0.0072	0.0069	0.0063	0.0062	0.0063	0.0062	0.0062	0.0062	0.0157	0.0062	0.0062	0.0111	0.0062	0.0062	0.0062	0.0062	**K_MLKLU**
0.0065	0.0133	**0.6732**	0.0066	0.0065	0.0065	0.0065	0.0066	0.0070	0.0064	0.0064	0.0065	0.0065	0.0064	0.0064	0.0086	0.0064	0.0065	0.0130	0.0064	0.0064	0.0065	0.0064	**K_MLMFD**
0.0063	0.0145	0.0064	**0.6735**	0.0063	0.0063	0.0063	0.0066	0.0071	0.0063	0.0063	0.0065	0.0063	0.0063	0.0063	0.0092	0.0063	0.0063	0.0141	0.0064	0.0063	0.0064	0.0063	**K_MLSEC**
0.0062	0.0173	0.0062	0.0063	**0.6730**	0.0062	0.0062	0.0064	0.0066	0.0062	0.0062	0.0062	0.0062	0.0063	0.0062	0.0079	0.0062	0.0062	0.0167	0.0062	0.0062	0.0062	0.0062	**K_MLSKW**
0.0068	0.0090	0.0068	0.0068	0.0068	**0.6736**	0.0068	0.0068	0.0068	0.0068	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0090	0.0068	0.0068	0.0068	0.0068	**K_MLWP**
0.0067	0.0084	0.0067	0.0069	0.0067	0.0067	**0.6735**	0.0071	0.0077	0.0067	0.0067	0.0069	0.0067	0.0067	0.0067	0.0103	0.0067	0.0067	0.0081	0.0067	0.0067	0.0067	0.0067	**K_MRY**
0.0063	0.0144	0.0063	0.0066	0.0063	0.0063	0.0063	**0.6737**	0.0072	0.0064	0.0063	0.0065	0.0064	0.0063	0.0063	0.0090	0.0063	0.0063	0.0139	0.0063	0.0063	0.0064	0.0063	**K_NYS**
0.0061	0.0170	0.0061	0.0063	0.0061	0.0061	0.0061	0.0064	**0.6749**	0.0061	0.0061	0.0061	0.0061	0.0061	0.0061	0.0084	0.0061	0.0061	0.0178	0.0061	0.0061	0.0061	0.0061	**K_POW**
0.0064	0.0117	0.0064	0.0068	0.0064	0.0063	0.0063	0.0071	0.0087	**0.6733**	0.0063	0.0065	0.0063	0.0063	0.0064	0.0128	0.0063	0.0063	0.0110	0.0064	0.0063	0.0064	0.0063	**K_REV**
0.0064	0.0140	0.0064	0.0065	0.0064	0.0064	0.0064	0.0066	0.0067	0.0064	**0.6732**	0.0065	0.0064	0.0064	0.0064	0.0075	0.0065	0.0065	0.0138	0.0064	0.0064	0.0064	0.0064	**K_RMS**
0.0066	0.0118	0.0066	0.0066	0.0066	0.0066	0.0066	0.0067	0.0069	0.0066	0.0066	**0.6734**	0.0066	0.0066	0.0065	0.0078	0.0066	0.0066	0.0117	0.0066	0.0065	0.0066	0.0066	**K_SMZ**
0.0064	0.0133	0.0064	0.0066	0.0065	0.0064	0.0065	0.0067	0.0069	0.0065	0.0064	0.0066	**0.6732**	0.0064	0.0064	0.0084	0.0064	0.0064	0.0129	0.0065	0.0065	0.0064	0.0065	**K_SNF**
0.0068	0.0083	0.0068	0.0069	0.0068	0.0068	0.0068	0.0069	0.0071	0.0068	0.0068	0.0068	0.0068	**0.6736**	0.0068	0.0075	0.0068	0.0068	0.0085	0.0068	0.0068	0.0068	0.0068	**K_VCR**
0.0068	0.0084	0.0068	0.0068	0.0068	0.0067	0.0069	0.0069	0.0071	0.0068	0.0068	0.0068	0.0068	0.0068	**0.6736**	0.0075	0.0068	0.0068	0.0084	0.0068	0.0068	0.0068	0.0068	**K_WA**
0.0064	0.0122	0.0065	0.0067	0.0065	0.0064	0.0065	0.0068	0.0075	0.0065	0.0065	0.0066	0.0065	0.0065	0.0064	**0.6788**	0.0064	0.0065	0.0101	0.0064	0.0065	0.0065	0.0065	**K_WRG**
0.0066	0.0113	0.0066	0.0067	0.0066	0.0065	0.0066	0.0068	0.0071	0.0066	0.0066	0.0067	0.0066	0.0066	0.0066	0.0084	**0.6734**	0.0066	0.0109	0.0066	0.0066	0.0066	0.0066	**K_WRN**
0.0068	0.0090	0.0068	0.0068	0.0068	0.0069	0.0069	0.0068	0.0069	0.0068	0.0068	0.0068	0.0068	0.0068	0.0068	0.0070	0.0068	**0.6736**	0.0089	0.0068	0.0068	0.0068	0.0068	**K_YTS**
0.0064	0.0133	0.0064	0.0066	0.0064	0.0064	0.0064	0.0066	0.0070	0.0065	0.0064	0.0065	0.0065	0.0065	0.0064	0.0080	0.0064	0.0065	**0.6804**	0.0064	0.0065	0.0064	0.0064	**K_ZRB**
0.0068	0.0069	0.0068	0.0070	0.0068	0.0069	0.0068	0.0071	0.0076	0.0068	0.0068	0.0069	0.0068	0.0069	0.0068	0.0095	0.0068	0.0068	0.0069	**0.6736**	0.0068	0.0068	0.0068	**MW_BCC**
0.0067	0.0068	0.0067	0.0071	0.0067	0.0067	0.0067	0.0072	0.0080	0.0068	0.0067	0.0070	0.0067	0.0067	0.0067	0.0121	0.0067	0.0067	0.0068	0.0067	0.0067	0.0068	0.0067	**MW_BCN**
0.0067	0.0077	0.0067	0.0071	0.0067	0.0067	0.0067	0.0071	0.0078	0.0067	0.0068	0.0068	0.0067	0.0067	0.0067	0.0105	0.0068	0.0067	0.0077	0.0067	**0.6735**	0.0068	0.0068	**MW_BCS**
0.0068	0.0072	0.0068	0.0071	0.0069	0.0068	0.0068	0.0071	0.0075	0.0069	0.0068	0.0069	0.0068	0.0068	0.0068	0.0094	0.0068	0.0068	0.0070	0.0068	0.0068	**0.6736**	0.0068	**MW_WA**
0.0067	0.0068	0.0067	0.0072	0.0068	0.0068	0.0067	0.0071	0.0079	0.0067	0.0067	0.0070	0.0067	0.0068	0.0067	0.0115	0.0067	0.0068	0.0068	0.0067	0.0067	0.0068	**0.6735**	**MW_YTS**

Table 8. Recent historical migration rates under three models of hypothesized migration based on potential refugial locations for *P. keeni*. 1) Southern coastal refugium: Washington versus the remaining range, 2) either Southern or Northern coastal island refugium: Southern (southern British Columbia, Vancouver Island and Washington) versus Northern (northern British Columbia, Yukon and Alaska), and 3) Southeast Alaska coastal refugium: Southeast Alaskan islands versus all mainland populations. Non-migrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows).



	Migration rates into…					
From…	NonWA	WA	North	South	SE Islands	Mainland
NonWA	**99.84%**	17.76%	-	-	-	-
WA	0.16%	**82.24%**	-	-	-	-
North	-	-	**99.84%**	11.52%	-	-
South	-	-	0.16%	**88.48%**	-	-
SE Islands	-	-	-	-	**99.81%**	0.49%
Mainland	-	-	-	-	0.19%	**99.51%**

Table 9. Measures of niche overlap (ecological exchangeability) for *Peromyscus* sp. nov., *P. keeni* and *P. maniculatus* - West . Schoener's *D*, Warren's *I* and Relative Ranks (RR) between lineages. Values near 1.0 reflect highly exchangeable niches 263 whereas near 0.0 are considered in-exchangeable.



	I	D	RR
Peromyscus sp. nov. vs *P. keeni*	0.626636836	0.315870854	0.550233923
Peromyscus sp. nov. vs *P. maniculatus*	0.916419847	0.736416819	0.853848138
P. keeni vs *P. maniculatus*	0.78718435	0.529240718	0.682035511

CHAPTER 4

Living on the edge: exploring the role of coastal refugia and island biology in the Alexander Archipelago of Alaska

Abstract

Although islands are of long-standing interest to biologists, only a handful of studies have investigated the roles of island area, isolation, and climatic history in shaping evolutionary diversification in high latitude archipelagos. In this study of the Alexander Archipelago (AA) of Southeast Alaska, we address the degree of insularity and the impact of historical climate variability on geographic structure using multiple loci for three co-distributed mammals throughout the AA and adjacent mainland. We examined mitochondrial and nuclear loci for long-tailed voles (*Microtus longicaudus*), northwestern deer mice (*Peromyscus keeni*), and dusky shrews (*Sorex monticolus*), and integrated Species Distribution Models, reconstructions of paleo-shorelines, and island area and isolation. Changes in sea level and glacial cover resulted in genetic signatures of coastal refugia, with varying influence of island isolation and area on genetic diversity. All three species were determined to have paleoendemic clades that originated from multiple coastal refugia within the AA during the Late Pleistocene. This approach can be extended to other island systems or fragmented habitats to help identify and conserve regionally distinct biota and ecosystems.

Introduction

The varied features of island biomes such as isolation, area, topography, and biogeographic history, make them of long-standing interest to studies in evolution, ecology and conservation biology (Berry 1986; Fattorini 2009). Limited connectivity can lower genetic exchange between islands, leading to divergent populations and potentially higher endemism (Dobzhansky 1963; Adler 1992; Whittaker 1998). However, because many insular biomes remain understudied diversity is poorly documented and islands may account for a greater proportion of biodiversity than currently appreciated (Bickford et al. 2007).

Genetic diversity is often influenced by both physical geographic features and historical climate. Tropical oceanic islands have provided key insights into our understanding of diversity, especially in relation to how island area and isolation may shape species richness, community assembly, or diversification (e.g., Hamilton 1963; Gifford and Larson 2008; Gillespie et al. 2008). Additionally, in high latitudes, Quaternary (2.6 Ma – present) climate change impacted species' distributions and altered genetic variation and associated demographic signatures (Eddingsaas et al. 2004; Lomolino et al. 2006; Hope et al. 2010). However, few studies have investigated the role of island area, isolation, and climatic history in evolutionary diversification in high latitude archipelagos (e.g., Sota and Nagata 2008; Pedreschi et al. 2014).

During the Last Glacial Maximum (LGM; between 26.5 kya and 19 kya) ice covered most of North America (Dyke and Prest 1987; Mandryk et al. 2001), restricting distributions to ice-free regions in the north (Beringia), south, or along the coasts (Marr et al. 2008). As the glaciers receded, periglacial populations re-colonized previously glaciated regions, greatly influencing the genetic composition of these newly formed communities (Eddingsaas et al. 2004). Due to eustatic and isostatic fluxes at the LGM, the Alexander Archipelago (AA) of Alaska and Haida Gwaii of British Columbia experienced sea levels up to 165 meters lower (Mobley 1988; Hetherington et al. 2003; Baichtal et al. 2008). Although many of the islands were buried under 1000 m of ice, potential refugia existed along the western edge where continental shelf was exposed (Carrara et al. 2007; Baichtal and Carlson 2010).

Colonization and extinction dynamics of the land bridge islands of the AA more closely resemble those of oceanic islands (Conroy et al. 1999; Whittaker and Fernández-Palacios 2007) in that glacial cover effectively created a clean slate, with multiple ice-free regions (Beringian, southern continental) proposed as potential sources for colonization in the Holocene. Recolonization from these regions partially shaped the contemporary genetic structure of coastal biota. More controversial is the contribution of coastal refugia as a source for recolonization of deglaciated areas in Northwestern North America (Byun et al. 1997; Byun et al. 1999; Demboski et al. 1999).

In addition to recolonization dynamics, as glaciers receded and sea levels rose during the late Pleistocene-early Holocene (14 kya to 10 kya), the connectivity across the islands of the AA became highly fragmented (Carrara et al. 2007). Subsequent *in situ* diversification may have produced endemic populations on islands across the AA for either long-term occupants of the region (paleoendemic) or recent colonizers from outside the region (neoendemic) (Cook et al. 2006; MacDonald and Cook 2007; Cook and MacDonald 2013).

The AA is one of the planet's most extensive archipelagos with >1,100 named islands including 7 of the 15 largest United States islands. Most of this archipelago is within the Tongass National Forest (6.9 million ha; United States Geological Survey 2010). Together with Haida Gwaii to the south, these archipelagos support part of the largest remaining coastal temperate rainforest worldwide (Ecostrust and Conservation International 1992; DellaSala et al. 2011). Many of these islands have been highly modified by industrial timber harvesting and associated road building over the past 60 years (List 2000; Schoen and Dovichin, eds. 2007; Albert and Schoen 2013). The rugged and ice-laden Coastal and Wrangell-St. Elias mountain ranges border the adjacent mainland, which acted as barriers to dispersal and effectively filtered the species that colonized the islands from the continent (Cook and MacDonald 2013).

Previous regional studies identified divergent, endemic populations of various taxa including, but not limited to, vascular and non-vascular plants (Soltis et al. 1997; Brodo and Sloan 2004; Hannon et al. 2010), terrestrial invertebrates (Clarke et al. 2001), several fish (O'Reilly et al. 1993; Kondzela et al. 1994; Smith et al. 2001), birds (Barry and Tallmon 2010; Bull et al. 2010; de Volo et al. 2013), and an array of terrestrial mammals, including northern flying squirrels (*Glaucomys sabrinus*) (Bidlack and Cook 2002), red-backed voles (genus *Myodes*) (Runck et al. 2009), ermine (*Mustela erminea*) (Fleming and Cook 2002; Dawson et al. 2014), black bear (*Ursus americanus*) (Peacock et al. 2007), and mountain goats (*Oreamnos americanus*) (Shafer et al. 2011).

In this study, we use multiple DNA loci to explore the interplay of insularity and historical climate variability on contemporary genetic structure of three mammals that are widely co-distributed throughout the AA and adjacent mainland. *Microtus longicaudus*, *Peromyscus keeni*, and *Sorex monticolus* were chosen because they are widespread and preliminary analyses identified inter-population variation across the mainland and Alexander Archipelago (Conroy and Cook 2000; Demboski and Cook 2001; Lucid and Cook 2004). These species are sympatric, but *Microtus longicaudus* prefers open herbaceous habitats, *P. keeni* prefers a variety of forest and scrub habitats, and *S. monticolus* prefers forested and non-forested habitats with dense ground cover (Smolen and Keller 1987; Smith and Belk 1996; Zheng et al. 2003). Comparative study of multiple species allows us to explore the combination of climatic variability and individual niches (abiotic requirements) to genetic structure across this fragmented landscape. If all three species expanded from shared refugia, genetic signatures should track the common influence of climatic events, regardless of individual niche requirements.

We also evaluate how genetic structure is partitioned in these species across the islands of Southeast Alaska to determine the role of island size and isolation. The theory of island biogeography (MacArthur and Wilson 1967; Brown 1971) has been expanded to reflect expectations for the distribution of genetic diversity (Kimura and Weiss 1964; Johnson et al. 2000). We focus on how island area and isolation, in combination with the potential role of coastal refugia as historical sources for colonization, shaped diversity across the archipelago.

More specifically, we ask: are the genetic signatures of *M. longicaudus*, *P. keeni*, and *S. monticolus* a result of shared historical climatic and geologic events? Based on species distribution models (SDMs; Figure 1) and historical bathymetric reconstructions (Figure 2; see Methods and Results) we identify potential refugia in the AA during the

LGM for each species. We hypothesize all three species have similar phylogenetic topologies and similar signatures of demographic and spatial expansion. We explore the possibility of coastal refugia west of the ice in the AA and predict deeper genetic divergence in the populations in refugial regions proposed by the coastal refugia hypothesis (CRH; Fladmark 1979). Additionally, gene trees may reflect changes in island connectivity due to lowered sea-levels during glacial periods. Signatures of expansion should be observed in hypothesized non-refugial island populations as a result of post-glacial colonization.

Lastly, we assess genetic divergence among insular populations of each species to determine whether island remoteness and area conform to models of island biogeography. Genetic signals should be driven by island colonization (as expected for oceanic islands) and we expect a nested pattern, such that intra-island genetic diversity will decrease with increasing geographic distance from the mainland source population (Kimura and Weiss 1964). If genetic signals are influenced by extinction (as expected for land-bridge islands), we expect a non-nested pattern and decrease in genetic diversity with decrease in island area (Dawson and Hamner 2005; Zhang et al. 2012).

Phylogeographic studies help us understanding how climate has influenced the genetic structure of insular communities and provide the historical context necessary to investigate endemism and island biology (Grant and Grant 2003). Environmental changes, such as habitat conversion or those predicted under climate-warming scenarios elevate the extinction risk for small insular populations due to their limited mobility and modest ranges (Olson 1989; Fahrig 2003; Christensen et al. 2007). The genetic footprints of *M. longicaudus*, *P. keeni*, and *S. monticolus* aid the assessment of the paleoecology of past refugial locations that harbored endemic lineages and geographic barriers that structured populations. In addition to investigating historical climatic and island effects on a high latitude archipelago, we also utilize SDMs to identify regions of conservation priority under future climate change scenarios.

Materials and Methods

Sample collection and sequencing

Specimens were collected between 1991 and 2012 and archived at the Museum of Southwestern Biology (MSB), University of New Mexico and the University of Alaska Museum of the North (n= 137 *M. longicaudus*, 146 *P. keeni*, and 149 *S. monticolus*; Table 1). Tissues were also loaned from the University of Washington Burke Museum and Gwaii Haanas National Park Reserve and Haida Heritage Site (13 *P. keeni*, and 3 *S. monticolus*). Sampling covered 44 localities across Southeast Alaska and Haida Gwaii. All recognized subspecies (Hall 1981) found in or near Southeast Alaska for each study species were represented. Outgroup taxa (n= 3 *Microtus*, 40 *Peromyscus*, and 9 *Sorex*) were also included. Additionally, we used GenBank sequences representing 41 *M. longicaudus*, and 18 outgroup *P. maniculatus* (Table 1).

We extracted total genomic DNA to a final concentration of 50ng µl^{-1} using either Omega Bio-Tek (Norcross, GA) E.Z.N.A. or standard salt extraction (Fleming and Cook 2002). Polymerase chain reactions (PCR) amplified mitochondrial (mtDNA) cytochrome *b* (cyt *b*) and three nuclear loci per genus (*Microtus*: Protein C-est-2 (ETS2), β-fibrinogen (FGB), and Recombination Activating Protein 1 (Rag1); *Peromyscus*: β-fibrinogen (FGB), interphotoreceptor retinoid-binding protein (IRBP) and zona pellucida 3 (ZP3);

Sorex: Alcohol Dehydrogenase 2 (ADH2), Apolipoprotein B (ApoB) and β-fibrinogen (FGB); Table 2) with reaction mixtures of 1µl DNA extract, 1 µl of primer each (2mM), 1.5 µl PCR buffer (10x), 1.5 µl $MgCl_2$ (25mM), 1.25 µl of dNTP's (10mM), 1.25 µl of Bovine Serum Albumen (BSA, 1.5mM), and 0.08 µl of Ampli*Taq* DNA polymerase (Applied Biosystems, Foster City, CA, USA) and were adjusted to a final volume of 15 µl with ddH_2O. After cleaning PCR products with ExoSap-IT (Affymetrix, Santa Clara, CA), automated sequencing was conducted at either the High Throughput Genomic Center (Seattle, WA, USA) or using an Applied Biosystems 3110 DNA sequencer (Molecular Biology Facility, UNM) using original PCR primers and BigDye v3.1 (Applied Biosystems) terminator reaction chemistry.

Nuclear heterozygotes were inferred with PHASE v2.1 (Stephens et al. 2001; Stephens and Scheet 2005) using five runs with 1000 iterations (different seeds) and a burn-in of 1000. Iterations with the best goodness-of-fit were chosen. Posterior probabilities for nucleotides ≥0.85 were chosen; otherwise ambiguous sites were coded as N. All analysis used phased sequence data. Sequences were edited in SEQUENCHER v4.2 (GeneCodes Corporation), aligned in MEGA v5.2 (Tamura et al. 2011) using the MUSCLE algorithm and confirmed by eye.

Phylogenetic and demographic analyses

To explore the phylogenetic relationship within each species, we performed Maximum Likelihood (ML) and Bayesian phylogenetic reconstructions for cyt *b* for each species. We used MODELTEST (Posada and Crandall 1998; Posada and Buckley 2004) to determine genetic models of evolution for each locus (Table 3). ML estimations were performed in MEGA with 1000 bootstrap replicates. Using BEAST v1.7.5 (Drummond et al. 2012), we generated Bayesian phylogenies and divergence dates estimates with input files prepared in BEAUTI v1.7.5., part of the BEAST software package. A mutation rate of 4% Myr^{-1} was assigned to *M. longicaudus* and *P. keeni* (Conroy and Cook 1999; Brunhoff et al. 2003) and a rate of 5.5% Myr^{-1} for *S. monticolus* (Hope et al. 2013). We applied a coalescent constant size tree prior with a random start tree, using an uncorrelated lognormal relaxed clock because relationships with non-insular populations are deeper in time, for 60 million generations, sampled every 2000. Time to Most Recent Common Ancestor (TMRCA) was determined with a 95% posterior probability distribution in TRACER v1.5 (Rambaut and Drummond 2007). For each tree, convergence statistics were assessed with both a minimum effective sample size (ESS) value of 200 and trace graphs in TRACER. Three independent runs were combined using LOGCOMBINER v1.7.5, with a 10% burin-in and tree files were annotated in TREEANNOTATOR v1.7.5 (part of BEAST software package). Tree topology was visualized in FIGTREE v1.4.0 (Rambaut 2009).

Species history, rather than individual gene accounts, can be obtained even for recently diverged taxa through the use of a multilocus coalescent approach (Maddison 1997; Carstens and Knowles 2007; Edwards et al. 2007) such as *BEAST (Heled and Drummond 2010) which co-estimates species trees and gene trees using a Bayesian Markov chain Monte Carlo (MCMC) algorithm implemented in BEAST. Phased loci were assigned as independent and unlinked and set with substitution models calculated in MODELTEST (Table 3). *A priori* groupings were designated based on cyt *b* Bayesian supported lineages (≥0.95 posterior probability). Cyt *b* was designated a lognormal relaxed clock with the same rates as the BEAST analysis, while all rates for phased nuclear loci were estimated and assigned strict clocks . Each run consisted of random start trees with a Species Tree: Yule process prior and piecewise linear and constant root population size model with MCMC chain lengths of 2 billion iterations, sampling every 2 million. TRACER, LOGCOMBINER and TREEANNOTATOR were used as above. PHYLOGEOVIZ (Tsai 2011) was used to visualize phased nuclear haplotype frequencies across the landscape.

Net genetic distances among major clades of cyt *b* were calculated in MEGA. To test for recent demographic change, we computed standard summary statistics (segregating sites (*S*), number of haplotypes (*h*), haplotype diversity (*Hd*), and nucleotide diversity (π)), and selection and expansion statistics Tajima's (1989) *D*, Fu's (1997) F*s*, and R_2 (Ramos-Onsins and Rozas 2002) with 10 thousand coalescent simulations for each phased locus in DNASP 5.10.1 (Librado and Rozas 2009). Selection potential was also assessed through an HKA Test (Hudson et al. 1987). Additionally, we computed pairwise mismatch distributions for cyt *b* data.

To identify signals of population fluctuation, we estimated historical demography for the Island clades with both a multilocus Extended Bayesian Skyline Plots (EBSP, Heled and Drummond 2008) implemented in BEAST. Three runs per analysis used a MCMC chain of 2 billion steps, sampled every 2 million, with strict molecular clocks and models of evolution (Table 3) calculated via MODELTEST. As above, TRACER was used to assess convergence. For EBSPs, we determined that significant population size change occurred if zero was excluded from the 95% confidence interval (CI) of the estimate of the number of size-change steps (Lim and Sheldon 2011).

If *M. longicaudus*, *P. keeni* and *S. monticolus* experienced shared effects of climatic change and glacial cover, we would expect the phylogenetic topologies to be similar. To test for congruence in Island clades across the three species, we performed three Shimodaira-Hasegawa tests (1999) using each respective species as the constrained tree, implemented in PAUP*. Compared to the phylogenetic trees produced above, *a priori* ML and Bayesian trees were generated using two individuals per island, limited to islands with at least two of the three species (Table 4). These trees included four Northern clade and three Southern clade representatives, with sequences comprised of ambiguous bases used as place holders when island representatives were not available (e.g., *S. monticolus* for Chichagof). Trees were constructed in MEGA (ML) with 1000 replicates and BEAST (Bayesian) as above.

Testing phylogenetic models under the coastal refugia hypothesis

If species persisted in refugia, genetic relationships between refugial island populations will be similar to those found on land-bridge systems (Cardillo et al. 2008) with measures of divergence larger than the divergence between non-refugial island populations. As above, cyt *b* net genetic divergences between hypothesized refugial and non-refugial island populations were calculated in MEGA and standard demographic statistics and mismatch distributions (cyt *b* only) were calculated in DNASP for all phased loci to test for varying histories between potentially refugial and non-refugial insular populations. Populations were designated as refugial or non-refugial based on paleo-shoreline reconstructions (see below).

To determine if climatic conditions in the AA were within each species' threshold, we generated SDMs for each species under current, mid-Holocene (~6ka), LGM (~21 kya) (http://pmip2.lsce.ipsl.fr/; Braconnot et al. 2007), last inter-glacial (LIG; ~120 – 140 kya), and future conditions (twice the current levels of CO2, ~2080, Christensen et al. 2007). Bioclimatic variables were obtained from WORLDCLIM (www.worldclim.org, Hijmans et al. 2005) at a resolution of 2.5 arc-minutes and clipped to incorporate only Southeast Alaska and the surrounding mainland. ENMTOOLS (Warren et al. 2008; Warren et al. 2010) was used to determine highly correlated variables (Pearson correlation coefficient ≥0.75), which we then selected based on those most biologically relevant, which may over-parameterize models. We obtained species localities from natural history collection databases (e.g., ARCTOS http://arctos.data-base.uaf.edu and MaNIS http://manisnet.org/, Stein and Wieczorek 2004) in October 2013 and removed those <12 km distant by removing intervening samples (Hope et al. 2011) to reduce potential spatial autocorrelation from sampling bias, leading to over-fitting of the model (Reddy and Davalos 2003). This resulted in 127 *M. longicaudus*, 150 *P. keeni*, and 145 *S. monticolus* sample localities. SDMs for each species were constructed at each time period using MAXENT v3.3.3k (Elith et al. 2006; Phillips et al. 2006; Phillips and Dudik 2008). Final runs were performed using cross-validation across 10 replicates, with a regularization parameter of 5 (Hope et al. 2011; Warren and Seifert 2011) and 1000 iterations. All other values were set as default. Models of LGM were averaged for final results using raster calculator in ARCGIS 10.1 (ESRI, Redlands, CA, USA). Climate suitability was limited by the low median threshold values over all replicates (Pearson et al. 2007).

We estimated potential island refugia, connectivity, and potential colonization pathways at different points since the LGM. To do so, we used ARCGIS 10.1 to change Southeast Alaska sea levels to levels suggested by estimates of historic sea levels and current bathymetry information (Baichtal and Carlson 2010; Baichtal pers. com.) to re-create paleo-shorelines at 20 kya which included LGM glacial cover, 14 kya and 10 kya (Ehlers and Gibbard 2004; Carrara et al. 2007).

Testing models under the equilibrium and non-equilibrium island biogeography

To test for influences of island area and isolation on genetic diversity within islands, we performed regression analyses with MICROSOFT EXCEL (2010). Values for island area and isolation were obtained either from literature (Conroy et al. 1999; Lucid and Cook 2004; Cook and MacDonald 2013) or island isolation was calculated by hand using GOOGLE EARTH (Google Inc. 2013) as the shortest over-water distance between each island and from the mainland (Conroy et al. 1999), which assumes the mainland as the location of source populations (Table 4). Because of the low variability in the nuclear loci, cyt *b* genetic diversity measures (*S, h, Hd* and *π* obtained above) were used to test for associations with log area and log distance to mainland for Island clades of both continental (mainland Southeast Alaska, central British Columbia through southern Yukon and south-central Alaska) and insular populations of *M. longicaudus, P. keeni*, and *S. monticolus*. We performed Holm-Bonferroni sequential corrections for multiple comparisons (Holm 1979) on resulting p-values to determine if isolation and area significantly affected genetic variation.

Results

Sampling and phylogenetic and demographic analyses

All loci across all species had varying levels of polymorphism and genetic diversity (Table 3), with the mtDNA cyt *b* the most variable locus. Among Island clades of all three species, *M. longicaudus* had the highest mtDNA haplotype diversity (98.4%), followed by *P. keeni* (97.8%), and *S. monticolus* (76.4%). Nuclear haplotype diversity for *M. longicaudus* ranged from 12.4 – 18.2%, for *P. keeni* 6.5 – 39.1%, and for *S. monticolus* 4.1 – 33.8%. Selection was not detected through the HKA tests.

Cyt *b* phylogenetic reconstructions supported an Island clade within both *M. longicaudus* and *S. monticolus*, while *P. keeni* represents the Island clade in the peromyscine phylogeny (Figure 3). Populations of the *M. longicaudus* Island clade are restricted to Southeast Alaska, southern Yukon, and south-central Alaska (Figure 4). This species is notably absent from Baranof Island as well as Haida Gwaii and Vancouver Island to the south. The *M. longicaudus* Island clade contains 16 lineages and is restricted to mainland Southeast Alaska, adjacent British Columbia and south-central Alaska (Figure 4). Representatives of the Island and Northern clades make contact in the vicinities of Haines and Juneau and are in close geographic proximity along the central and southern mainland coast.

Peromyscus keeni ranges from southern Yukon through Southeast Alaska and coastal British Columbia to Washington's Olympic Peninsula (Figure 4) and contains substantial structure (25 lineages). There is contact with *P. maniculatus* in British Columbia along the east side of the Coast Mountains and in northern Washington, and close geographic proximity to *P. maniculatus* and *Peromyscus* sp. nov. (Sawyer et al. *submitted*) in southern Yukon.

The *S. monticolus* Island clade is highly structured (10 lineages), ranging from Southeast Alaska (but not Chichagof, Baranof or other outer northern islands) and eastern British Columbia southward into Washington, with possible contact with the Northern clade near Haines and Juneau, Alaska and Washington (Figure 4).

Within *M. longicaudus*, the Island clade is sister to the North Pacific Coast (NPC) and Northern clades at 1.2 ± 0.3% net genetic distance, and highly diverged from the Southern clade (3.7 ± 0.5%; Table 5). For *P. keeni*, the coastal group of *P. maniculatus* (2.3 ± 0.4%) is closest, followed by the Yukon *Peromyscus* sp. (3.6 ± 0.5%), and the rest of *P. maniculatus* (3.8 ± 0.5%). The Island clade of *S. monticolus* is least diverged from the Northern clade (4.8 ± 0.5%), and most diverged from the Southern clade (5.4 ± 0.6%).

The multilocus species trees (Figure 5) for *M. longicaudus* reveals a single supported clade which contains the Island and Northern cyt *b* clades. The species tree for *Peromyscus* supports the Island clade (*P. keeni*) and the *Peromyscus* sp. nov. clade. Species tree for *S. monticolus* supports the Island clade and the Southern clade, and indicates that *S. monticolus* is monophyletic.

Nuclear haplotypes within the AA are broadly distributed across the archipelago and exhibit little geographic structure for all loci and all species, with the exception of ETS2. *Microtus longicaudus* populations on Forrester and Chichagof Island each have unique haplotypes for this locus (Figures 6 and 7). Multilocus divergence dates (Table 6) for the Island-Northern clade of *M. longicaudus* are post-LGM, although cyt *b* TMRCA for the Island clade is well before the LIG. *Peromyscus keeni* multilocus TMRCA places divergence around the LIG, with cyt *b* TMRCA well before this. The Island clade for *S. monticolus* diverged between the LGM and LIG, with cyt *b* estimates around the LIG.

Overall, measures of genetic diversity for the Island clades were low for all three species (Table 3), indicative of population demographic expansion or selection. Although significant expansion statistics can indicate selection, negative HKA tests suggest significantly negative *D* and *FS* for all cyt *b*, a result of recently expanded populations. Cyt *b* mismatch distributions for all species are unimodal with a multimodal tail for *M. longicaudus* suggesting reduced ancestral populations (Figure 8).

Shared geologic histories should result in congruent phylogenetic topologies. The Shimodaira Hasegawa test (Table 7) when performed on the ML trees alone, identified the *P. keeni* topology ($p<0.01$) as optimal for all three species. However, when performed on only the Bayesian trees or in combination with ML trees, each test selected their respective tree as the best ($p<0.01$) with the exception of *P. keeni,* which indicated both *P. keeni* trees as equally likely ($p=0.52$ ML versus Bayesian, $p<0.01$ for all other tree comparisons). Topologies are similar in that populations of each species represent an Island clade restricted to high-latitude coastal and island regions, a Northern clade that occupies high latitudes and southern continental clades. The calculation of nodal support in ML analysis compared to Bayesian methods (Douady et al. 2003) can result in less structured ML topology.

Testing phylogenetic models under the coastal refugia hypothesis

Mean net genetic divergence was greatest between non-refugial populations of *M. longicaudus* and *P. keeni* and least divergent for *S. monticolus* (Table 9). Contrary to expectations, refugial to non-refugial divergence was not statistically different than refugial to refugial or non-refugial to non-refugial populations. Fu's *FS* and Tajima's *D* and diversity indices (Table 3) varied in significance and (Figure 8) for all non-refugial and refugial populations not noticeably different from each. The mismatch distributions (Figure 8) for all non-refugial locations, and *M. longicaudus* refugial populations, were unimodal, with a bimodal topology for refugial populations of *P. keeni* and *S. monticolus*.

Predictive performance for SDMs had mean AUC values of 0.801 ± 0.067 for *M. longicaudus*, 0.777 ± 0.080 for *P. keeni*, and 0.754 ± 0.082 for *S. monticolus* across replicate runs. No model clamping was detected. Suitable climate conditions for all three species in Southeast Alaska were present across all four time periods (Figure 1), including in areas west of the glacial ice during the LGM. Greatest suitability was for *P. keeni* for all historic periods. Future distributions suggest a decrease in habitat suitability for the outer southern islands and increased suitability for mainland regions for all three species (Figure 9). Paleo-shoreline reconstructions (Figure 2) suggest a northern coastal refugium and a southern coastal refugium at the LGM, four major island groupings (outer northern, inner northern, inner southern, and outer southern and middle islands) at 10 kya, and by 8 kya contemporary island topography was present. Post-glacial interisland colonization pathways from refugial locations were inferred from island connectivity (Figure 10).

Testing genetic models under the theory of island biogeography

The relationship of genetic diversity and island area and isolation (Figure 11 and Table 8), detected significant (Holm-Bonferroni corrected p-value ≤ 0.05) effects of island area on *M. longicaudus S*, *h*, *Hd*, and π, and *P. keeni S*. Island isolation significantly affected *M. longicaudus* π, and *P. keeni S* and *h*. All other relationships among genetic diversity indices and island area and isolation were non-significant. Although eight significant relationships were detected, adjusted R^2 values were no greater than 0.515.

Discussion

Few studies have explored the effects of both contemporary insularity and historical climate dynamics on genetic structure of the biota of high latitude island systems. We found that northern island inhabitants maintain signals of colonization history, thus providing the ability to study how historical climate has structured populations. In the case of the AA, terrestrial mammalian genetic diversity was primarily influenced by glacial cover and lower sea levels that resulted in endemic glacial relics acting as source populations that had persisted in coastal refugia to the west of this archipelago. In contrast, in the case of *M. longicaudus*, and possibly *S. monticolus*, the adjoining mainland to the east was primarily recolonized by populations that crossed the Coastal Range. However, island area and distance to mainland have influenced some of the genetic structure.

Shared geologic and climatic history

SDMs indicate that suitable environmental conditions existed in Southeast Alaska for *M. longicaudus*, *P. keeni* and *S. monticolus* during both the LIG and LGM (Figure 1). Suitability is consistent with signals of long-term persistence for the insular populations found in each of these species. Multilocus estimates of divergence for *M. longicaudus*, *P. keeni* and *S. monticolus* suggest pre-LGM initiation of regional divergence (Table 6). Other signals (i.e., EBSP, diversity indices) within *M. longicaudus* suggest a deeper history in Southeast Alaska, including persistence and divergence in coastal refugia. Recent divergence of *M. longicaudus* could also reflect geographic proximity and admixture between contemporary populations representing the Island and Northern cyt b clades, rather than post-glacial expansion into the AA. The Island clade of *S. monticolus* is highly differentiated from other conspecific clades, more so even than between the two peromyscine species, *P. keeni* and *P. maniculatus*. Within each Island clade, *P. keeni* has the most intralineage structure which is consistent with longer term persistence in the region, while the Island clade of *S. monticolus* had the least variability and relatively shallow intraclade relationship (Figures 3 and 5).

EBSPs and expansion statistics indicate demographic expansion in Island clades of all three species, which is consistent with deglaciation of these areas (Figure 8; Table 3). Consistent with recent expansion, all three Island clades have lower estimates of mitochondrial and nuclear diversity compared to their continental counterparts. However, if populations are in Hardy-Weinberg equilibrium, but have a fragmented structure like those of islands, heterozygosity may appear artificially low (Wahlund 1928). Higher heterozygosity and more interisland differentiation are in accordance with continued habitation in the region for much of the late Pleistocene for all three species.

Tree topologies across the three species are generally similar, with identifiable southern continental clades, Northern clade populations that occupy high latitudes, and Island clade populations restricted to coastal and high-latitude island regions. Also, some island-specific lineages are consistently recorded among the three species for Forrester, Noyes and Revillagigedo islands. There are distinct island-specific lineages for Coronation, Dall, Kuiu, Lulu, Prince of Wales, and Zarembo between *M. longicaudus* and *P. keeni*, and San Fernando between *P. keeni* and *S. monticolus* (Figure 3; Table 4). Supported island lineages for Kupreanof, Suemez and Wrangell were unique to *M. longicaudus*; Admiralty, Baranof, Chichagof, Gravina, Heceta, and Warren were unique to *P. keeni;* and Etolin was unique to *S. monticolus*. Within *P. keeni*, the presence of a lineage representing the northern islands of Admiralty, Baranof and Chichagof islands is consistent with proposed biogeographic subregions (Swarth 1936; but see MacDonald and Cook 1996). Relatively high numbers of endemic lineages within each species may be due to extended persistence in the region, differential selective pressures on distinct islands, and genetic drift that is accentuated by the fragmented nature of the islands.

Lack of multilocus geographic structure across the region for all three species (Figures 5 -7), coupled with their limited migration among islands (Sawyer and Cook, submitted; Sawyer et al., submitted) is most likely due to incomplete lineage sorting rather than contemporary gene flow. We hypothesize that repeated genetic exchange during periods of lowered sea levels throughout the late-Pleistocene and early Holocene was followed by segregation. This hypothesis is contrary to our original predictions that

P. keeni would have relatively high levels of gene flow across the region because it is the most widely distributed mammalian species in the AA. Overall, there are signals of shared history across *M. longicaudus*, *P. keeni* and *S. monticolus,* but individualistic responses to historical climate, timing of isolation in the AA, and colonization pathways are potentially recorded in the incongruent phylogeographic patterns and levels of variation.

Coastal refugia hypothesis

Although much remains unknown, a growing number of studies have suggested the importance of northern coastal refugial isolation on contemporary genetic structure (e.g., Hannon et al. 2010; Shafer et al. 2011; de Volo et al. 2013), including that of humans and their colonization of the Americas (e.g., Fladmark 1979; Baichtal and Carlson 2010). Reconstruction of paleo-shorelines, historical island connectivity, and potential colonization pathways suggests multiple regions of LGM glacial refugia within the region of Southeast Alaska (Figures 2 and 10): 1) mainland near Glacier Bay, 2) outer Baranof and Chichagof islands, 3) Forrester refugial complex, which would result post-glacial colonization through Prince of Wales, Zarembo and Mitkof, 4) Coronation refugial complex, colonization through Kuiu and Kupreanof, or 5) Annette-Duke refugium, south of Gravina. Re-colonization of Admiralty, as well as Wrangell and Etolin would necessarily be from the mainland originating from one of the refugial regions.

Each species' SDM (Figure 1) suggest suitable climate offshore on the exposed shelf and select western islands (Table 4) since at least the LIG. Given the climate suitability, level of genetic differentiation, and timing of divergence within *M.*

longicaudus and *S. monticolus*, these species most likely persisted in at least two southern AA refugia throughout the glacial-interglacial cycles, not just that of the LGM. *Peromyscus keeni* however, likely persisted in a combination of northern and southern refugia in the AA, as suggested by the distinct cyt *b* lineage for the northern islands and differentiation across the southern islands. The unique haplotypes for *P. keeni* individuals from the islands of Haida Gwaii present the option of coastal refugia within Haida Gwaii.

Cowan (1935) suggested both *P. keeni* and *S. monticolus* survived the Wisconsinan glaciation in coastal refugia in the AA. Although Heaton and Grady (2007) conclude all small mammals failed to survive the LGM (Heaton et al. 2003; Heaton and Grady 2007), there are pre-LGM, as well as some undated, fossil evidence from Prince of Wales Island suggests the possibility that all three species occupied the region prior the LGM, but. The lack of fossils on Prince of Wales immediately surrounding the LGM does not eliminate the possibility, however, that these species persisted further west in coastal refugia, rather than on Prince of Wales Island, throughout Pleistocene glacial cycles, including the LGM.

The Island clade of *M. longicaudus* is limited to the AA and nearby mainland, a geographic range consistent with paleoendemism in the region (Figure 4). Although there are wider distributions in both *P. keeni* and the Island clade of *S. monticolus* (south to Washington), divergence dates, net genetic distance, genetic diversity, and expansion statistics, as well as opposing models of refugial migration for *P. keeni* (Sawyer et al. submitted) suggest paleoendemism. The cyt *b* phylogenies indicate most, but not all, refugial areas supported lineages for all three species. Furthermore, there is genetic evidence of coastal refugia followed by rapid expansion; however, both the mtDNA and multilocus relationships suggest a deeper than LGM influence for all three species. The repeated connectivity and fragmentation of the AA has undoubtedly contributed to the loss of clear specific refugial island signatures. That is, higher gene flow during periods of low sea level would eliminate island-specific genetic signatures.

The Alexander Archipelago and island biogeography

The effects of island area and isolation on the genetic diversity of *M. longicaudus*, *P. keeni* and *S. monticolus* are mixed. Given the number of supported lineages without predictable geographic distribution in the cyt *b* phylogenies (Figure 3), the distribution of genetic variation would suggest vicariance played a large role in shaping the observed patterns (Whittaker 1998).

There is an increase in genetic diversity with increased island area and proximity to the mainland, as expected, but most of the relationships are not statistically significant (Figure 11, Table 8). Although the regression analysis detected significant effects of island area on all diversity indices for *M. longicaudus,* isolation on π for *M. longicaudus*, and S and h for *P. keeni*, a maximum of only 50% of the variation observed is explained by either island area or isolation.

The isolation measurement assumes the source population is from the mainland. If source populations were actually from coastal refugia, this changes the expected distribution of variation. However, we cannot simply invert the distance measurements because of the possibility of multiple refugial locations and post-colonization pathways (Figure 10). For example, the distance of Admiralty populations would traditionally be measured from the mainland, but if the source population was from Chichagof refugia, or perhaps Forrester or Coronation complexes, the determination of distance to source populations is much less certain and more complex. Overall, isolation and area appear to be factors influencing some of the observed genetic variation, but it is clear these attributes are not the only variables at play in the AA.

Conclusion

Historical climate (coastal refugia) and island topography (area and isolation) contribute to the genetic diversity of the high-latitude islands of the Alexander Archipelago. Multiple lines of evidence suggest all three species in this study are paleoendemic to the region with earliest habitation by *P. keeni*, followed by *M. longicaudus*, and finally *S. monticolus*. Failure to detect clear genetic signatures of specific island refugia within the coastal region or relationships with island area and isolation is most likely the result of repeated connectivity and fragmentation across the AA, plus non-equilibrium populations and recent diversification as indicated by incomplete lineage sorting.

A closer analysis of genetic structure within an array of species between islands can help provide a framework for scientifically defensible management decisions (Gutrich et al. 2005; Pritchard et al. 2007), especially in the context of historical divergence patterns and predicted climate change. For example, the outer islands of the AA not only house a disproportionate number of endemic lineages, mammalian and otherwise, but future SDMs predicted that these three species on these islands will be seriously impacted by future climate change (Figure 9). Additionally, regional endemics

(Cook and MacDonald 2001; Sikes and Stockbridge 2013) face challenges posed by anthropogenic activities that are facilitating habitat conversion.

More generally, similarities across species are more readily identifiable through the use of multiple analyses (i.e., phylogenetic reconstructions, EBSP, SDMs) rather than assumptions or decisions based on any single characteristic (i.e., life history characteristics) or result (i.e., relationship with island area and isolation). Ultimately, this comparative and integrative multi-locus approach can be extended to various taxa in other high-latitude island systems or fragmented habitats, like those of the Haida Gwaii (Reimchen and Byun 2006), the Japanese Archipelago (Millien-Parra and Jaeger 1999), and British Isles (Vincent 1990) to help identify and conserve species, ecosystems, and regionally distinct biota experiencing dynamic environmental change (Avise 2008; Hendry et al. 2010).

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Figures and Tables

Figure 1. . SDM for *M. longicaudus*, *P. keeni* and *S. monticolus* from the LIG to Current. Solid blue covering at the LGM is glacial ice cover. SDM's climate suitability at each time period.

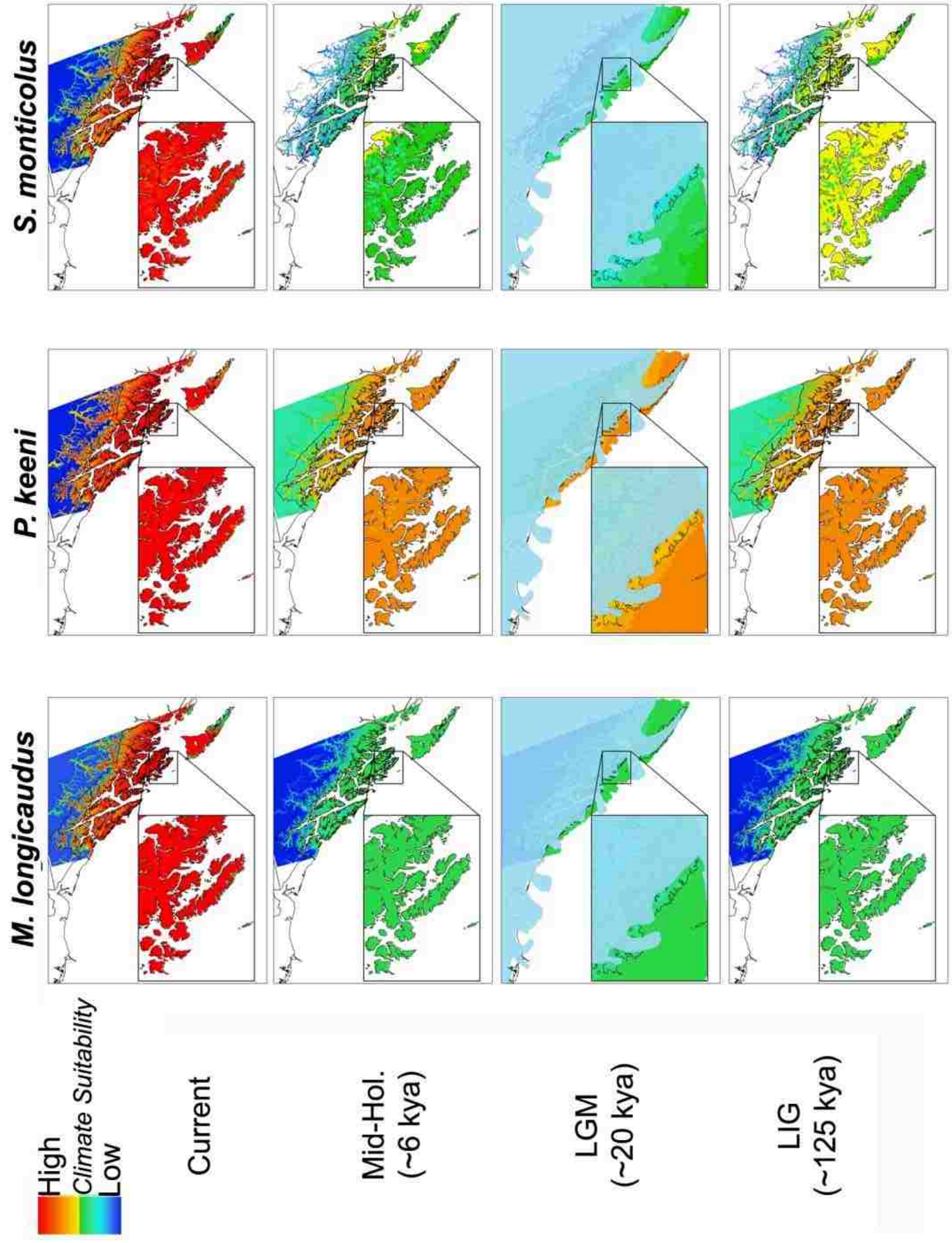

Figure 2. Islands and surrounding mainland Alaska locations, paleo-shorelines, and hypothesized island groups (also see Table 4).

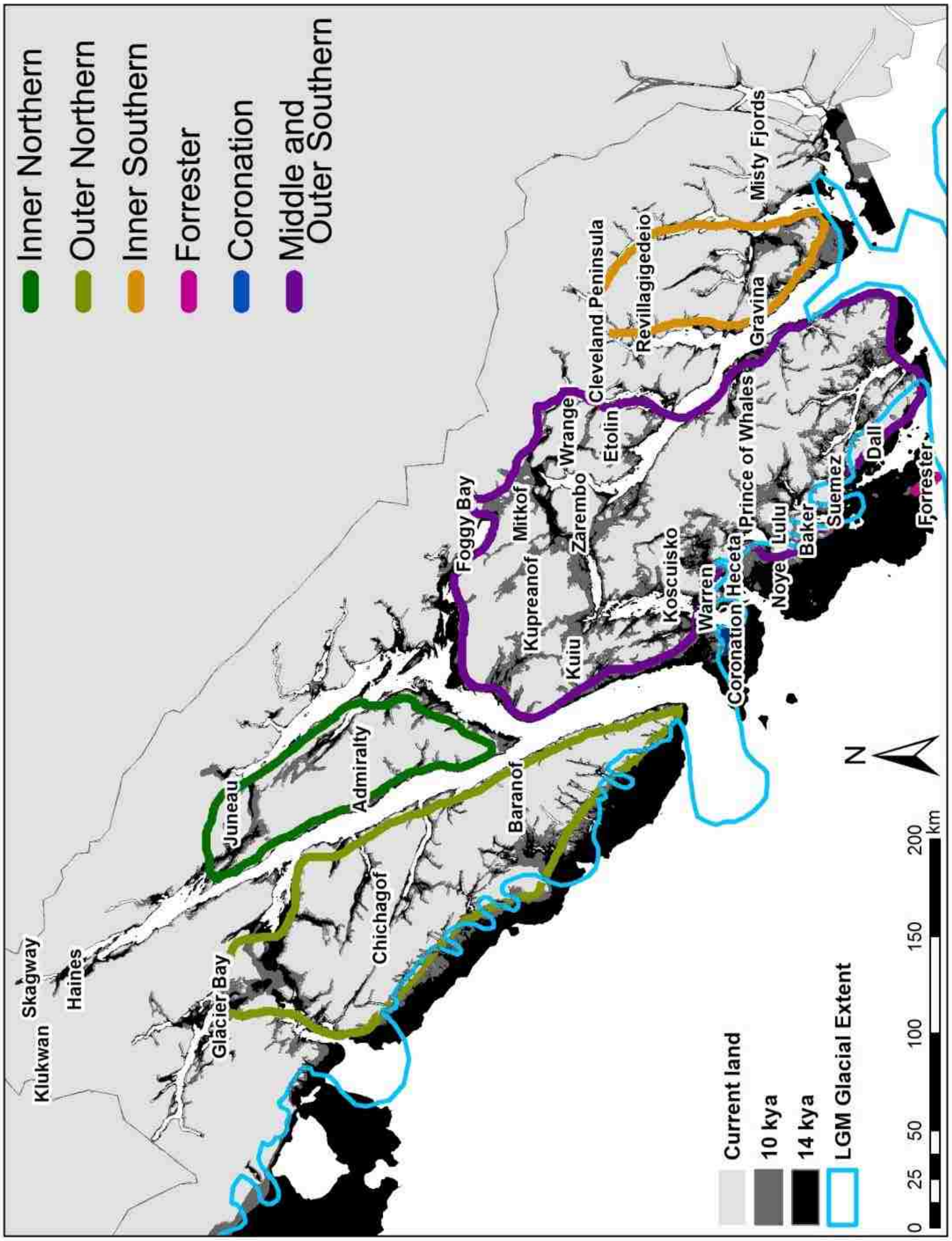

Figure 3. . Dated Bayesian cyt*b* trees for *M. longicaudus*, *P. keeni* and *S. monticolus*. Posterior probability ≥0.95 represented with open circles and Maximum Likelihood bootstraps of ≥0.7 with asterisks are shown on branches. Vertical light gray bars represent the LIG (left) and LGM (right). Dark gray horizontal bars = 95% CI for TMRCA for the Island clade for each species. Geographic location (Table 4) for supported intralineage clades are immediately right taxon tips. Major lineage abbreviations are: COP=Colorado Plateau; NPC=North Pacific Coast, PeMa=*P. maniculatus*, E (East), W (West) and SW (Southwest); S=South.

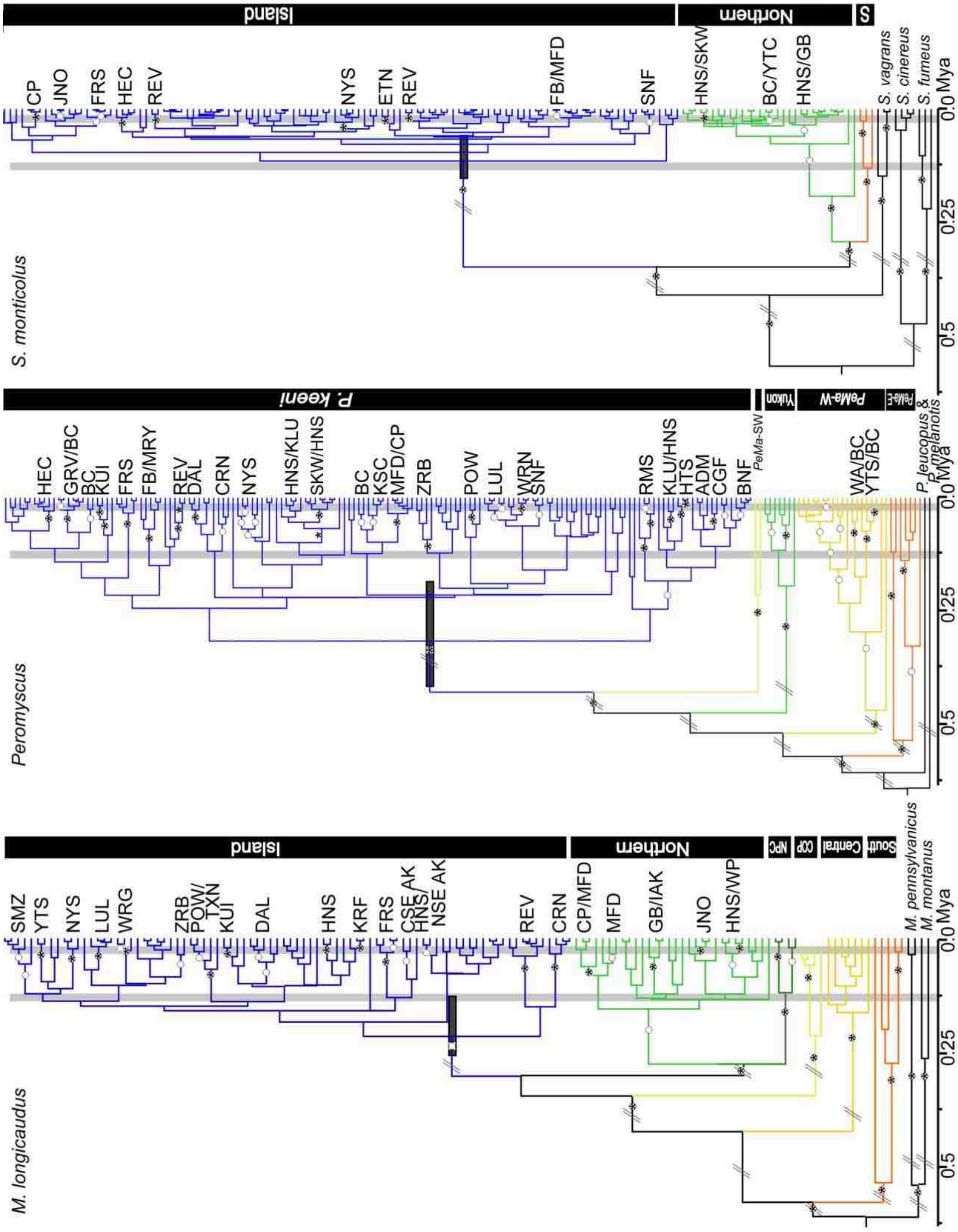
S. monticolus
CP
JNO
FRS
HEC
REV
NYS
ETN
REV
FB/MFD
SNF
HNS/SKW
BC/YTC
HNS/GB
Island
Northern
S
S. vagrans
S. cinereus
S. fumeus
0.0
0.25
0.5
Mya
Peromyscus
HEC
GRV/BC
BC
KUI
FRS
FB/MRY
REV
DAL
CRN
NYS
HNS/KLU
SKW/HNS
BC
KSC
MFD/CP
ZRB
POW
LUL
WRN
SNF
RMS
KLU/HNS
HTS
ADM
CGF
BNF
PeMa-SW
WA/BC
YTS/BC
P. keeni
Yukon
PeMa-W
PeMa-E
P. leucopus &
P. melanotis
0.0
0.25
0.5
Mya
M. longicaudus
SMZ
YTS
NYS
LUL
WRG
ZRB
POW/
TXN
KUI
DAL
HNS
KRF
FRS
CSE AK
HNS/
NSE AK
REV
CRN
CP/MFD
MFD
GB/IAK
JNO
HNS/WP
Island
Northern
NPC
COP
Central
South
M. pennsylvanicus
M. montanus
0.0
0.25
0.5
Mya

Figure 4. Sampling scheme, range maps and North American LGM glacial cover. Sampling localities are shown by major cyt*b* lineage. The thick black lines are the current range for each species, with the addition of *P. maniculatus* (white line) on the *Peromyscus* map. The light blue in the bottom right image is LGM glacial ice cover. NPC=North Pacific Coast; COP=Colorado Plateau.

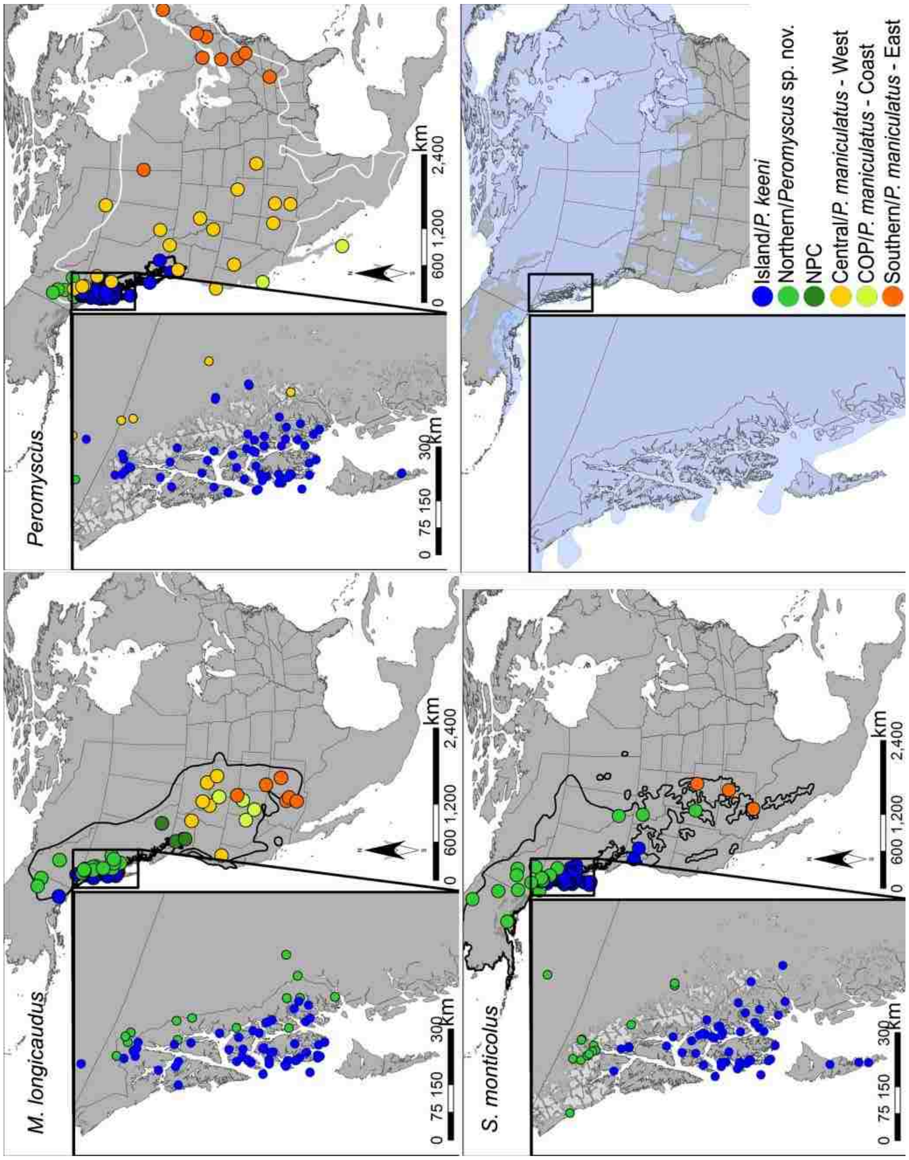

Figure 5. Multilocus Bayesian Species Tree. Posterior probabilities of ≥0.95 are represented with open circles on branches of the consensus tree. *A priori* groupings were designated based on cyt *b* Bayesian supported (≥0.95 posterior probability) clades. Blue = Island/*P. keeni*, bright green = Northern/*Peromyscus* sp. nov. (Yukon), dark green = North Pacific Coast, light yellow-green = Colorado Plateau/ *P. maniculatus* Southwest, golden = Central/*P. maniculatus* West, orange = Southern/*P. maniculatus* East, black = outgroups. Horizontal gray bars represent divergence date estimates and vertical bars indicate approximate time for the LIG and LGM.

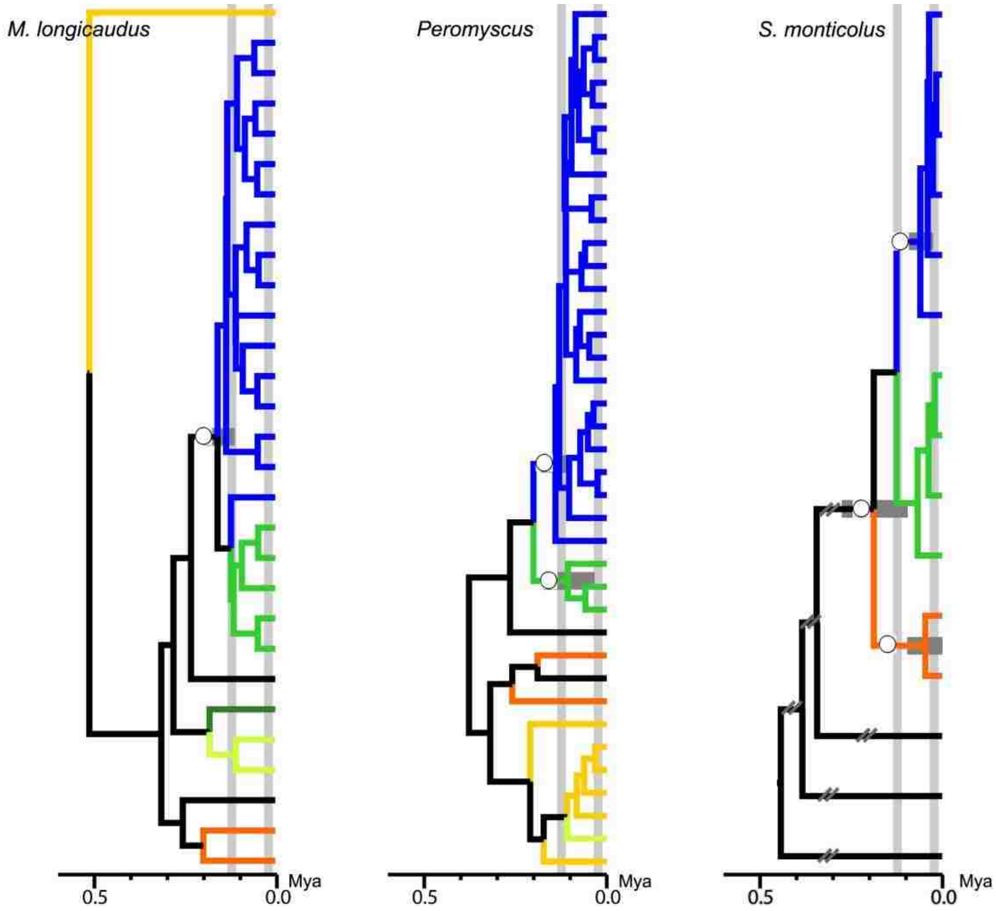

Figure 6. Island phased nuclear haplotype distribution for *M. longicaudus*, *P. keeni* and *S. monticolus* as prepared by PHYLOGEOVIZ.

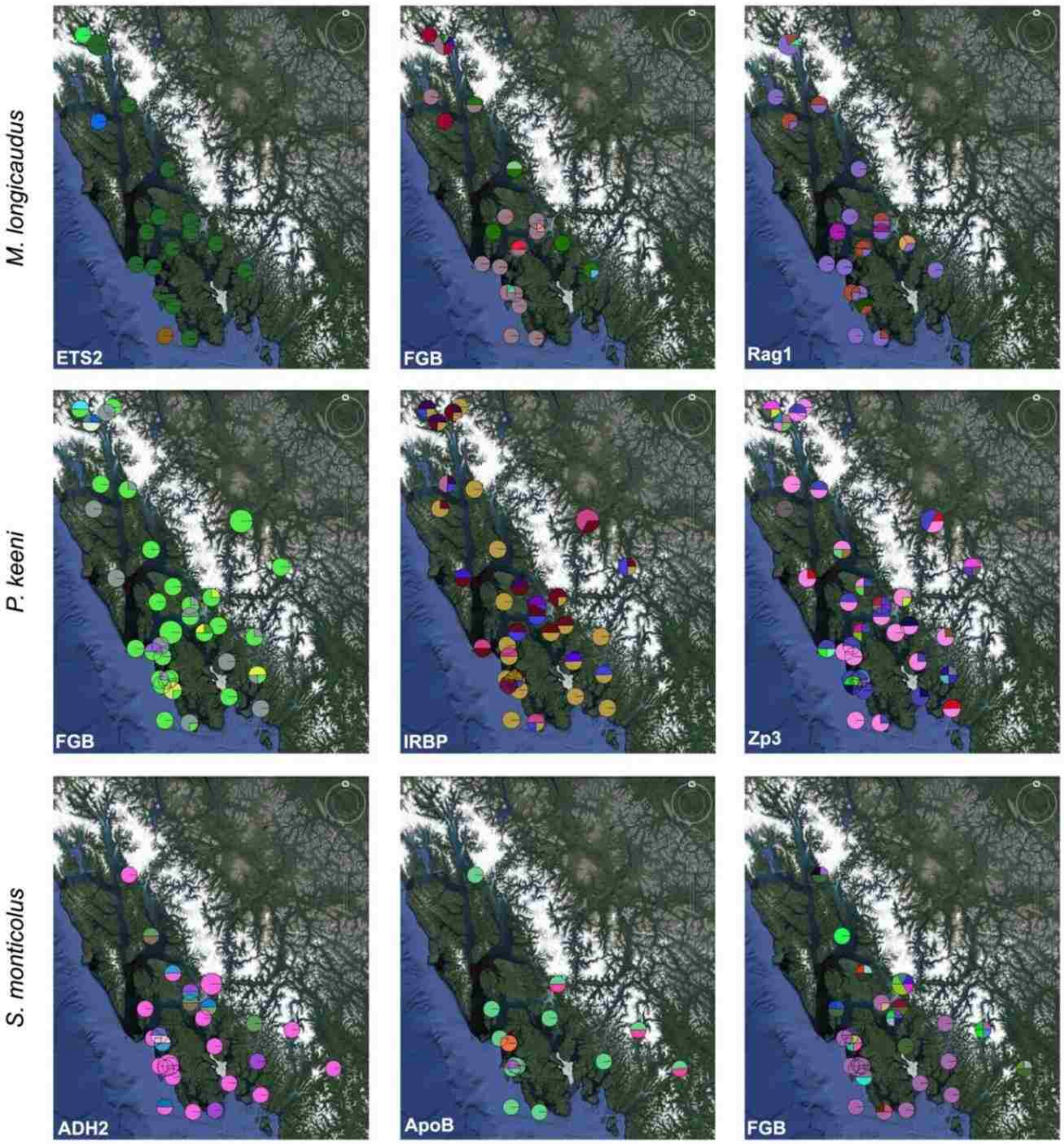

Figure 7. Bayesian gene trees for phased nuclear loci for *M. longicaudus* (a. ETS2, b. FGB, and c. Rag1), *Peromyscus* (d. FGB, e. IRBP, and f. Zp3) and *S. monticolus* (g. ADH2, h. ApoB, and i. FGB) with posterior probabilities of ≥0.95 represented with open circles on branches. Geographic locations for supported intralineage clades are provided. Blue = Island/*P. keeni*, bright green = Northern/*Peromyscus* sp. (Yukon), dark green = North Pacific Coast, light yellow-green = Colorado Plateau/ *P. maniculatus* Southwest, golden = Central/*P. maniculatus* West, orange = Southern/*P. maniculatus* East, black = outgroups.

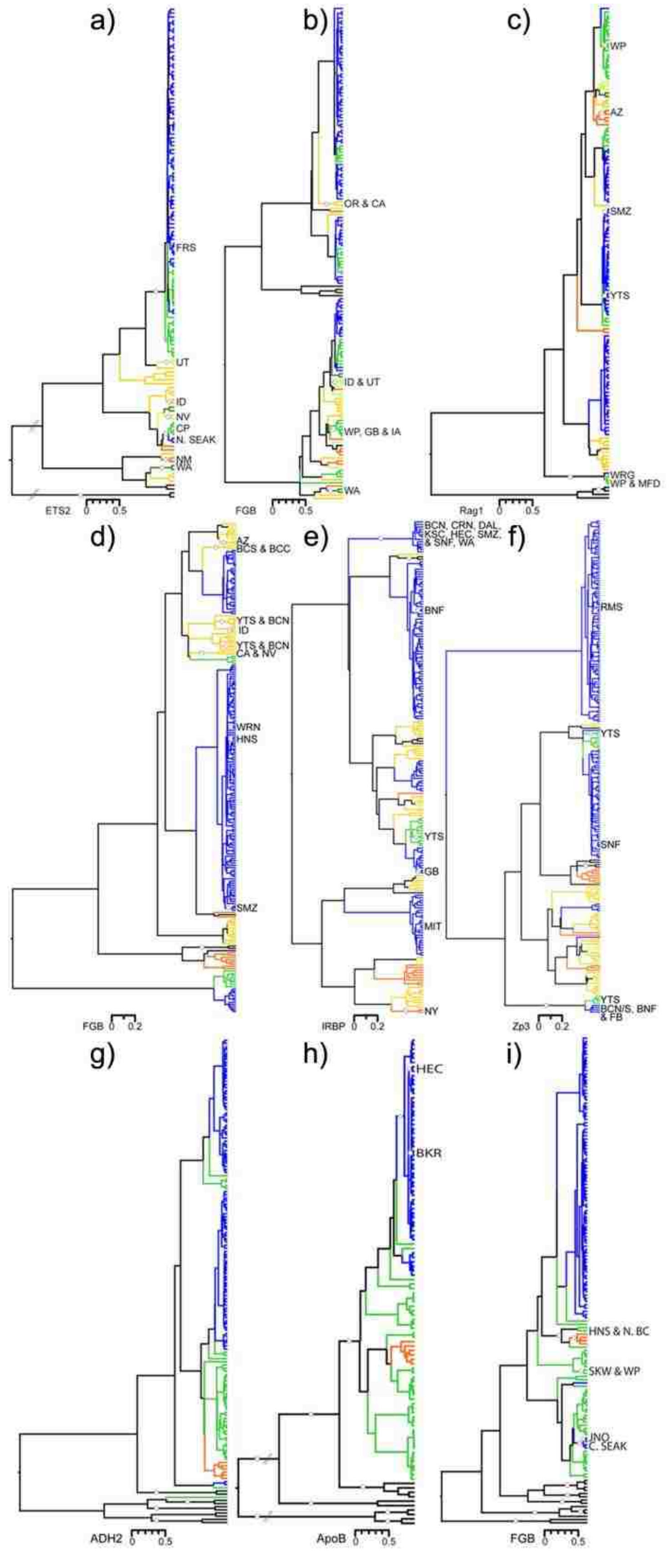
a)
FRS
UT
ID
NV
CP
N. SEAK
NM
WA
ETS2 0 0.5
b)
OR & CA
ID & UT
WP, GB & IA
WA
FGB 0 0.5
c)
WP
AZ
SMZ
YTS
WRG
WP & MFD
Rag1 0 0.5
d)
AZ
BCS & BCC
YTS & BCN
ID
YTS & BCN
CA & NV
WRN
HNS
SMZ
FGB 0 0.2
e)
BCN, CRN, DAL,
KSC, HEC, SMZ,
& SNF, WA
BNF
YTS
GB
MIT
NY
IRBP 0 0.2
f)
RMS
YTS
SNF
YTS
BCN/S, BNF
& FB
Zp3 0 0.2
g)
ADH2 0 0.5
h)
HEC
BKR
ApoB 0 0.5
i)
HNS & N. BC
SKW & WP
JNO
C. SEAK
FGB 0 0.5

Figure 8. Cyt *b* mismatch distributions and EBSPs for *P. keeni* and Island lineages of *M. longicaudus*, *S. monticolus*, as well as Refugial islands and non-refugial islands (see Table 4). Observed curves (dotted line) and expected curves (solid line) are the number of pairwise differences under rapid population growth. EBSP (Island/*P. keeni* insets) central line indicates mean change in effective population size through time, with upper and lower lines sowing the 95% posterior density. The x-axis (right-to-left) extends from past (TMRCA) to present and is scaled in millions of years and the y-axis is the effective population size scaled by generation time. Vertical gray bars indicate the LIG (when applicable, right) and LGM (left) for reference.

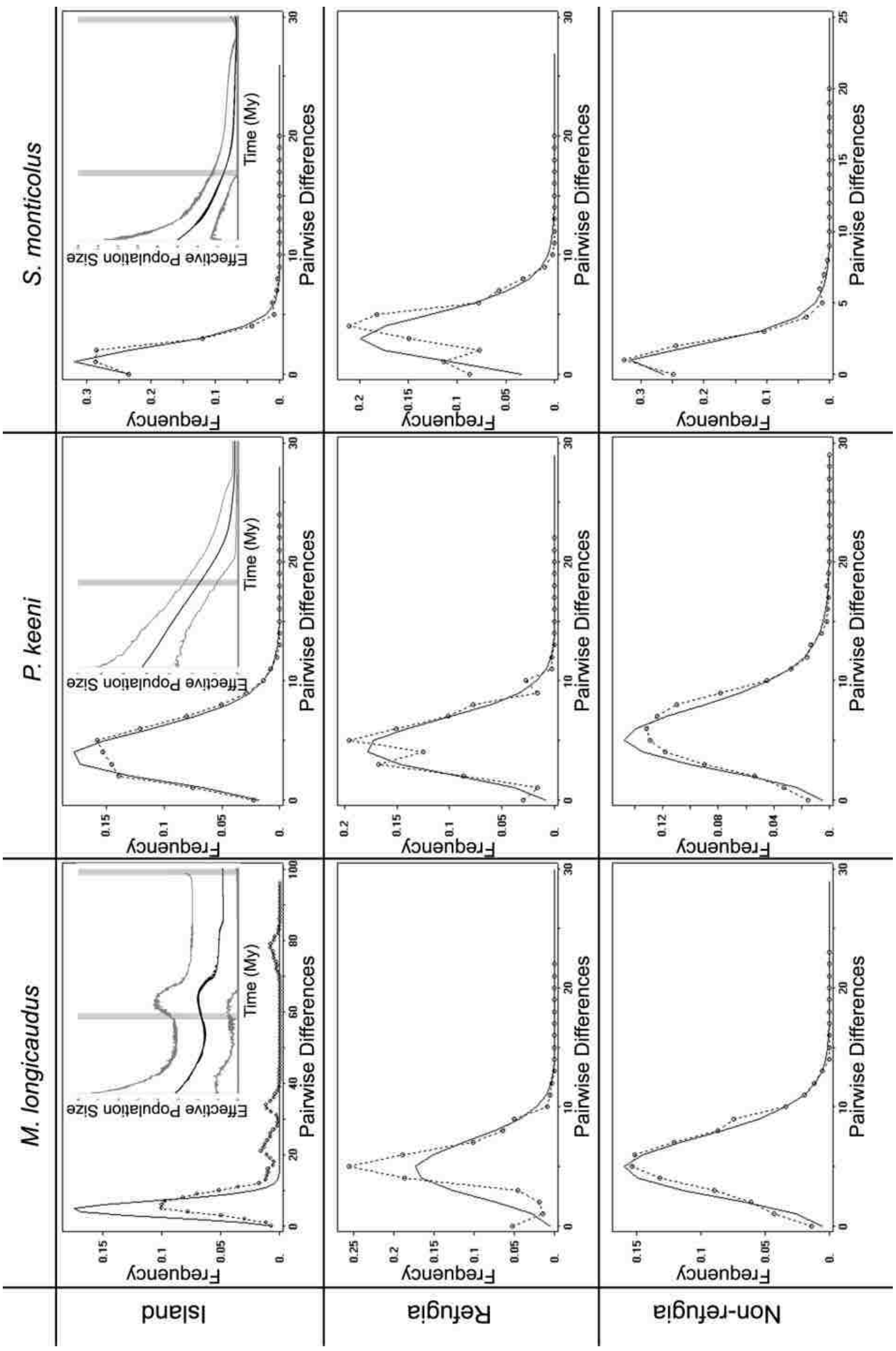
M. longicaudus
P. keeni
S. monticolus
Island
Refugia
Non-refugia
Frequency
Pairwise Differences
Effective Population Size
Time (My)

Figure 9. SDM for *M. longicaudus*, *P. keeni* and *S. monticolus* for Current and Future, as well as the change in climate suitability between the two time periods.

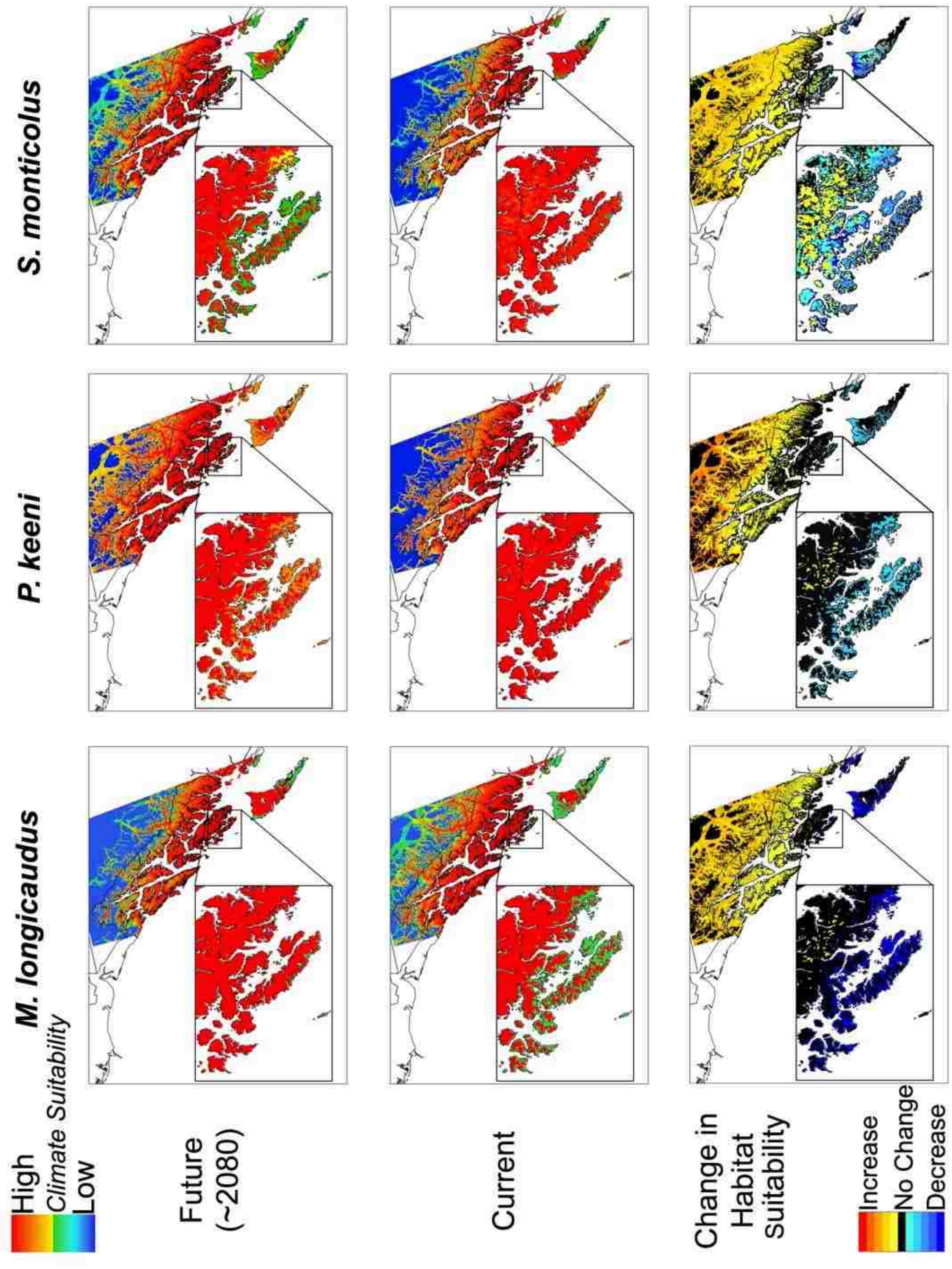

Figure 10. Historical island connectivity and potential colonization across the Alexander Archipelago as a result of change in sea level and glacial cover.

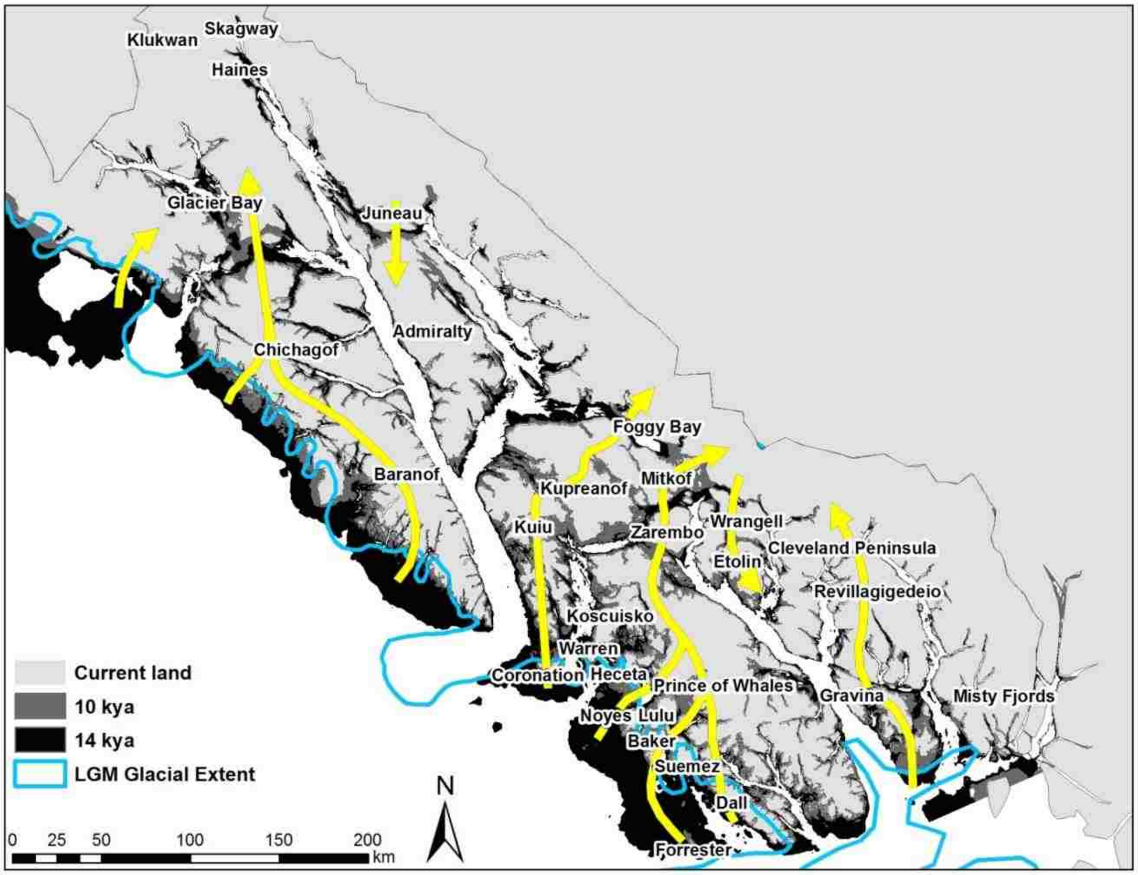

Figure 11. Cyt *b* genetic diversity (S, *h*, *Hd* and π) by log island area and isolation for *M. longicaudus* (red), *P. keeni* (blue) and *S. monticolus* (green) with regression lines. See Table 8 for regression results.

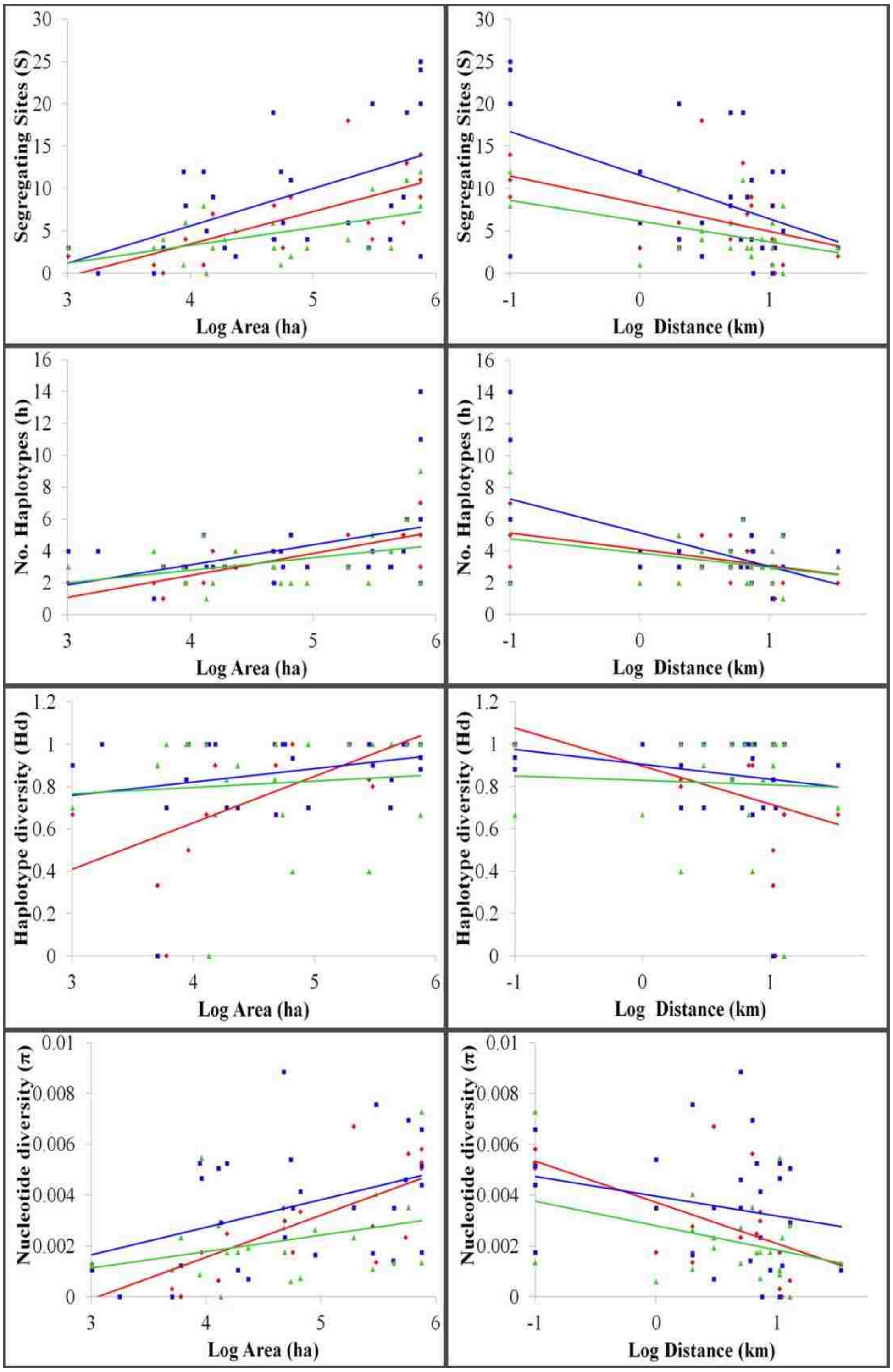

Table 1. Specimens examined. Museum number acronyms are MSB= Museum of Southwestern Biology, UAM=University of Alaska Museum of the North, Fairbanks, HG= Gwaii Haanas National Park Reserve and Haida Heritage Site, and UWBM=University of Washington Burke Museum. GenBank numbers correspond to cyt *b*, and each phased allele for *M. longicaudus* (ETS2, FGB and Rag1), *Peromyscus* (FGB, IRBP and Zp3) and *S. monticolus* (ADH2, ApoB and FGB) respectively, –= not applicable. GenBank in bold were previously obtained from other studies.

Species	*cytb* lineage	Locality	Specimen Number	Latitude	Longitude	GenBank Accession Numbers
Microtus longicaudus						
	Central	California	UAM77991	41.409444	-122.193889	**AF187176**, – / – , – / – , – / –
			UAM77992	41.409444	-122.193889	**AF187174**, – / – , – / – , – / –
		Idaho	MSB227995	44.658860	-113.215840	KF948609,KF948677/KF948678,KF948845/KF948846,KF949027/KF949028
			UAM77997	46.732387	-117.000165	**AF187173**, – / – , – / – , – / –
		Montana	UAM34299	45.520000	-108.820000	**AF187172**, – / – , – / – , – / –
			MSB156351	45.731000	-112.676000	KF948534, – / – , – / – , – / –
		Wyoming	MSB225915	44.226300	-107.234700	KF948607,KF948673/KF948674,KF948841/KF948842,KF949023/KF949024
	Colorado Plateau	Idaho	MSB143745	43.553000	-111.243000	KF948533, – / – ,KF948785/KF948786, – / –
		Nevada	MSB227146	39.237500	-114.689200	KF948608,KF948675/KF948676,KF948843/KF948844,KF949025/KF949026
		Utah	MSB76827	38.344170	-112.491110	KF948610, – / – ,KF948859/KF948860, – / –
			MSB77127	40.186140	-111.139530	KF948611,KF948683/KF948684,KF948861/KF948862,KF949035/KF949036
	Island	Alaska - Chichagof Island	UAM32929	57.816667	-136.150000	**AF187205**, – / – , – / – , – / –
			UAM32932	57.816667	-136.150000	KF964338, – / – , – / – , – / –
			UAM51686	57.957500	-134.307222	KF964342, – / – , – / – , – / –
			UAM20507	58.066667	-135.233333	**AF187211**, – / – ,KF948867/KF948868,KF949041/KF949042
			UAM36269	58.079167	-135.477778	**AF187219**,KF948729/KF948730,KF948921/KF948922,KF949093/KF949094
		Alaska - Coronation Island	UAM22920	55.917778	-134.320833	KF964335, – / – , – / – , – / –
			UAM22921	55.917778	-134.320833	**AF187223**, – / – , – / – , – / –
			UAM23410	55.917778	-134.320833	**AF187222**, – / – , – / – , – / –
			UAM23606	55.917778	-134.320833	**AF187213**,KF948697/KF948698,KF948883/KF948884,KF949057/KF949058
		Alaska - Dall Island	UAM42372	54.744167	-132.771111	KF948622, – / – , – / – , – / –
			UAM23728	54.783333	-132.866667	**AF187206**,KF948699/KF948700,KF948887/KF948888,KF949061/KF949062
			UAM49658	54.806944	-132.769167	KF948579,KF948747/KF948748,KF948945/KF948946,KF949117/KF949118
			UAM49660	54.806944	-132.769167	KF948627, – / – , – / – , – / –
			UAM42429	55.215556	-133.138056	KF948569, – / – , – / – , – / –
		Alaska - Forrester Island	UAM42727	54.821389	-133.520833	KF948624, – / – , – / – , – / –
			UAM42380	54.821389	-133.520833	KF948566,KF948737/KF948738,KF948929/KF948930,KF949101/KF949102
			UAM42381	54.821389	-133.520833	**AF187221**,KF948739/KF948740, – / – ,KF949103/KF949104
			UAM42728	54.821389	-133.520833	KF948581, – / – ,KF948931/KF948932, – / –
		Alaska - Kosciusko Island	UAM42385	55.918889	-133.685000	KF948567, – / – , – / – , – / –
			UAM30506	56.150000	-133.350000	KF948559, – / – , – / – , – / –
			UAM30507	56.150000	-133.350000	KF948560,KF948709/KF948710,KF948899/KF948900,KF949073/KF949074
			UAM30508	56.150000	-133.350000	KF948561,KF948711/KF948712,KF948901/KF948902,KF949075/KF949076
			UAM30721	56.150000	-133.350000	KF948619, – / – , – / – , – / –
		Alaska - Kuiu Island	UAM42376	56.321389	-134.071667	KF948565, – / – , – / – , – / –
			UAM22912	56.410354	-134.033333	**AF187224**,KF948691/KF948692, – / – , – / –
			UAM22913	56.410354	-134.033333	KF948555, – / – ,KF948875/KF948876,KF949049/KF949050
			UAM42377	56.583333	-134.000000	KF948640, – / – , – / – , – / –
			MSB149385	56.667600	-134.265500	KF948547, – / – , – / – , – / –
		Alaska - Kupreanof Island	MSB148983	56.642000	-133.700700	KF948546,KF948647/KF948648,KF948793/KF948794,KF948991/KF948992
			UAM20918	56.866667	-133.316667	**AF187208**, – / – , – / – , – / –
			UAM20919	56.866667	-133.316667	KF948554, – / – , – / – , – / –
			UAM23871	56.974830	-133.941160	**AF187227**, – / – , – / – , – / –
		Alaska - Lulu Island	MSB221446	55.468500	-133.425800	KF948553,KF948671/KF948672,KF948837/KF948838,KF949021/KF949022
			MSB221498	55.468500	-133.425800	KF948604, – / – , – / – , – / –
			MSB221521	55.468500	-133.425800	KF948605, – / – , – / – , – / –
			MSB221545	55.468500	-133.425800	KF948606, – / – ,KF948839/KF948840, – / –
		Alaska - Mitkof Island	UAM22918	56.583333	-132.833333	KF948556,KF948693/KF948694,KF948877/KF948878,KF949051/KF949052

Alaska - Noyes Island	UAM23659	55.451977	-133.659835	KF948615, – / – ,KF948885/KF948886,KF949059/KF949060
	MSB221332	55.488000	-133.631200	KF948602, – / – , – / – , – / –
	MSB221340	55.488000	-133.631200	KF948603,KF948669/KF948670,KF948835/KF948836,KF949019/KF949020
Alaska - Orr Island	UAM52256	55.950000	-133.383333	**AF187209**, – / – , – / – , – / –
Alaska - Prince of Wales Island	UAM23726	54.766667	-132.183333	KF948616, – / – , – / – , – / –
	UAM23727	54.766667	-132.183333	KF948557, – / – , – / – , – / –
	UAM70243	54.888333	-132.366111	KF948572,KF948775/KF948776,KF948977/KF948978,KF949143/KF949144
	UAM41767	55.461111	-132.691667	**AF187207**, – / – , – / – , – / –
	UAM36579	56.166667	-133.316667	**AF187215**,KF948731/KF948732,KF948923/KF948924,KF949095/KF949096
	UAM34288	56.174444	-133.369167	KF948621, – / – , – / – , – / –
Alaska - Revillagigedo Island	UAM97289	55.343889	-131.498333	KF948575, – / – , – / – , – / –
	UAM30504	55.414722	-131.695833	KF948618, – / – , – / – , – / –
	UAM23455	55.502382	-131.028099	KF964344, – / – , – / – , – / –
	UAM23804	55.766667	-131.016667	**AF187212**, – / – , – / – , – / –
	UAM23943	55.816667	-131.366667	KF964336,KF948703/KF948704,KF948891/KF948892,KF949065/KF949066
	UAM23944	55.816667	-131.366667	KF948617,KF948705/KF948706,KF948893/KF948894,KF949067/KF949068
Alaska - Suemez Island	UAM42392	55.266667	-133.272156	KF948623, – / – , – / – , – / –
	UAM42393	55.266667	-133.272156	KF948568, – / – , – / – , – / –
	UAM43227	55.266667	-133.272156	KF948582, – / – , – / – , – / –
	UAM41768	55.283333	-133.307199	**AF187226**,KF948733/KF948734,KF948925/KF948926,KF949097/KF949098
	UAM49638	55.283333	-133.307199	KF948578,KF948745/KF948746,KF948943/KF948944,KF949115/KF949116
Alaska - Sukkwan Island	UAM31826	55.100000	-132.833333	**AF187230**, – / – , – / – , – / –
Alaska - Tuxekan Island	UAM52262	55.900000	-133.333333	**AF187220**, – / – , – / – , – / –
Alaska - Warren Island	UAM31755	55.874782	-133.841667	KF948542,KF948713/KF948714,KF948903/KF948904,KF949077/KF949078
	UAM31784	55.874782	-133.841667	**AF187218**, – / – , – / – , – / –
	UAM31785	55.874782	-133.841667	KF948537, – / – , – / – , – / –
	UAM31787	55.874782	-133.841667	KF948543, – / – , – / – , – / –
	UAM31788	55.874782	-133.841667	KF948538,KF948715/KF948716,KF948905/KF948906,KF949079/KF949080
	UAM31786	55.875000	-133.841667	**AF187214**, – / – , – / – , – / –
Alaska - Wrangell Island	UAM62899	56.233333	-132.133333	KF948540,KF948755/KF948756,KF948953/KF948954,KF949125/KF949126
	UAM72153	56.318333	-132.286111	KF948541, – / – , – / – , – / –
	UAM23063	56.350000	-132.333333	KF948536,KF948695/KF948696,KF948879/KF948880,KF949053/KF949054
Alaska - Zarembo Island	UAM20611	56.416667	-132.833333	KF948544, – / – ,KF948873/KF948874,KF949047/KF949048
	UAM42375	56.416667	-132.833333	KF948539,KF948735/KF948736,KF948927/KF948928,KF949099/KF949100
Alaska - Glacier Bay	UAM30499	58.450000	-135.916667	**AF187225**, – / – ,KF948897/KF948898,KF949071/KF949072
Alaska - Haines	UAM68284	59.162500	-135.777778	KF948636,KF948773/KF948774,KF948975/KF948976,KF949141/KF949142
	MSB193312	59.217640	-135.448180	KF948589, – / – ,KF948807/KF948808, – / –
	MSB195212	59.245900	-135.175300	KF948600, – / – ,KF948831/KF948832,KF949015/KF949016
	UAM52711	59.261667	-135.559722	KF964341,KF948749/KF948750,KF948947/KF948948,KF949119/KF949120
	MSB193328	59.266710	-135.603360	KF948591,KF948655/KF948656,KF948811/KF948812,KF948999/KF949000
	MSB193439	59.266710	-135.603360	KF948594,KF948661/KF948662,KF948817/KF948818,KF949005/KF949006
	UAM64609	59.414722	-136.061944	KF948632,KF948763/KF948764,KF948965/KF948966, – / –
Alaska - interior	UAM57777	61.317933	-144.235317	KF948628,KF948751/KF948752,KF948949/KF948950,KF949121/KF949122
Alaska - Juneau	MSB156999	58.343070	-134.639750	KF948550,KF948653/KF948654,KF948803/KF948804,KF948995/KF948996
Alaska - Southeast	UAM74134	57.366667	-133.466667	KF948573,KF948779/KF948780,KF948981/KF948982,KF949147/KF949148
	UAM74413	57.366667	-133.466667	KF948639,KF948781/KF948782,KF948983/KF948984,KF949149/KF949150
	UAM74283	57.366667	-133.466667	KF948638, – / – , – / – , – / –
Yukon - south	UAM34297	60.400000	-137.050000	**AF187228**,KF948725/KF948726,KF948915/KF948916,KF949089/KF949090
	UAM34298	60.400000	-137.050000	**AF187229**,KF948727/KF948728,KF948917/KF948918,KF949091/KF949092

	Northern	Alaska - Cleveland Peninsula	UAM23751	55.750405	-132.183333	**AF187198**, – / – , – / – , – / –
			UAM23752	55.750405	-132.183333	KF964343,KF948701/KF948702,KF948889/KF948890,KF949063/KF949064
			UAM30495	55.750405	-132.183330	KF948558,KF948707/KF948708,KF948895/KF948896,KF949069/KF949070
		Alaska - Glacier Bay	UAM34593	65.227500	-144.500278	**AF187190**, – / – , – / – , – / –
			UAM34594	65.227500	-144.500278	**AF187189**, – / – ,KF948919/KF948920, – / –
		Alaska - Haines	UAM48471	59.500278	-135.354167	KF964340,KF948743/KF948744,KF948939/KF948940,KF949111/KF949112
			UAM64427	59.623222	-136.089333	KF948630,KF948757/KF948758,KF948955/KF948956,KF949127/KF949128
		Alaska - interior	UAM60319	65.302722	-142.037306	KF948629,KF948753/KF948754,KF948951/KF948952,KF949123/KF949124
		Alaska - Juneau	UAM32822	58.183333	-133.316667	**AF187203**, – / – , – / – , – / –
			UAM75497	58.306881	-134.416667	KF948574,KF948783/KF948784,KF948985/KF948986,KF949151/KF949152
			UAM34292	58.533333	-133.683333	KF948563,KF948719/KF948720,KF948909/KF948910,KF949083/KF949084
			UAM34293	58.533333	-133.683333	KF948564,KF948721/KF948722,KF948911/KF948912,KF949085/KF949086
			UAM34294	58.533333	-133.683333	KF964337,KF948723/KF948724,KF948913/KF948914,KF949087/KF949088
		Alaska - Misty Fjords	UAM34284	54.943611	-130.333611	KF948562,KF948717/KF948718,KF948907/KF948908,KF949081/KF949082
			UAM34285	54.943611	-130.333611	KF948620, – / – , – / – , – / –
			UAM34286	54.943611	-130.333611	**AF187194**, – / – , – / – , – / –
			UAM23883	55.766667	-130.883333	**AF187199**, – / – , – / – , – / –
			UAM76246	55.766667	-130.883333	**AF187197**, – / – , – / – , – / –
			UAM23496	56.083333	-131.086460	**AF187191**, – / – ,KF948881/KF948882,KF949055/KF949056
			UAM23552	56.083333	-131.086460	KF964339, – / – , – / – , – / –
		Alaska - Southeast	UAM48474	56.026944	-130.070556	**AF187200**, – / – , – / – , – / –
			UAM30496	57.008333	-132.983333	**AF187193**, – / – , – / – , – / –
			UAM30497	57.008333	-132.983333	**AF187201**, – / – , – / – , – / –
			UAM48463	59.614167	-135.166944	**AF187192**, – / – , – / – , – / –
			UAM48465	59.614167	-135.166944	KF948625,KF948741/KF948742,KF948933/KF948934,KF949105/KF949106
			UAM48466	59.614167	-135.166944	KF948580, – / – ,KF948935/KF948936,KF949107/KF949108
			UAM48467	59.614167	-135.166944	KF948626, – / – ,KF948937/KF948938,KF949109/KF949110
		British Columbia - central	MSB158239	56.496278	-129.425333	KF948535, – / – , – / – , – / –
		British Columbia - north	UAM68182	59.529167	-134.907778	KF948635,KF948771/KF948772,KF948973/KF948974,KF949139/KF949140
		Yukon - central	MSB144481	63.841300	-135.461400	KF948585,KF948645/KF948646,KF948791/KF948792,KF948989/KF948990
	North Pacific Coast	British Columbia - south	UAM69492	50.816667	-118.966667	**AF187188**, – / – , – / – , – / –
		Washington	UAM41789	47.000000	-120.950000	**AF187181**, – / – , – / – , – / –
			MSB43445	47.22306	-120.9932	**AF187180**,KF948679/KF948680,KF948847/KF948848, – / –
			MSB80232	48.200000	-121.916700	KF948612,KF948685/KF948686,KF948863/KF948864,KF949037/KF949038
	Southern	New Mexico	MSB50701	35.2667993	-106.1994019	**AF187163**,KF948681/KF948682,KF948851/KF948852,KF949031/KF949032
		Arizona	MSB88783	32.668700	-109.881200	–, – / – ,KF948865/KF948866,KF949039/KF949040
			MSB53559	33.7954	-109.4188	**AF187165**, – / – , – / – , – / –
			MSB50495	34.125300	-110.0431	**AF187164**, – / – ,KF948849/KF948850,KF949029/KF949030
		Colorado	MSB155126	37.238800	-107.758600	KF948548, – / – ,KF948801/KF948802, – / –
		Wyoming	MSB155085	41.036500	-110.404400	KF948588,KF948651/KF948652,KF948799/KF948800,KF948993/KF948994
Microtus montanus			MSB121523			KF948532, – / – , – / – , – / –
Microtus pennsylvanicus						
			MSB110998			KF948531, – / – , – / – , – / –
			MSB149290			–,KF948649/KF948650, – / – , – / –
Peromyscus sp. nov.						
		Yukon - central	MSB144216	62.398500	-136.555300	KF949162,KF949368/KF949369,KF949702/KF949703,KF950701/KF950702
			MSB144284	63.543100	-137.194800	KF949163, – / – , – / – , – / –
			MSB145251	64.025900	-138.578900	KF949207,KF949372/KF949373,KF949706/KF949707,KF950703/KF950704
			MSB145572	64.025900	-138.578900	KF949164,KF949374/KF949375,KF949708/KF949709,KF950705/KF950706

	Yukon - south	MSB240539	60.514500	-137.081700	KF949169,KF949406/KF949407,KF949740/KF949741,KF950736/KF950737
		MSB240553	60.514500	-137.081700	KF949173,KF949408/KF949409,KF949742/KF949743,KF950738/KF950739
		MSB149206	61.995750	-132.609383	KF949165,KF949378/KF949379,KF949712/KF949713,KF950709/KF950657
Peromyscus keeni					
	Alaska - Admiralty Island	UAM44886	57.429444	-133.938889	KF949325, – / – , – / – ,KF950848/KF950849
		UAM44887	57.429444	-133.938889	KF950037, – / – , – / – , – / –
		UAM44888	57.429444	-133.938889	KF949326,KF949516/KF949517,KF949840/KF949841,KF950850/KF950851
		UAM35318	57.433333	-134.550000	KF950033, – / – , – / – , – / –
	Alaska - Baker Island	UAM30873	55.366667	-133.600100	KF950030, – / – , – / – , – / –
		UAM30874	55.366667	-133.600100	KF949318,KF949482/KF949483,KF949816/KF949817,KF950816/KF950817
		UAM50605	55.366667	-133.600100	–, – / – , – / – ,KF950854/KF950855
		UAM76353	55.366667	-133.600100	KF950045, – / – , – / – , – / –
	Alaska - Baranof Island	UAM30822	56.590278	-134.860278	KF950057, – / – , – / – , – / –
		UAM30818	56.983333	-134.900000	KF949276,KF949478/KF949479,KF949812/KF949813,KF950812/KF950813
		UAM30819	56.983333	-134.900000	KF950029, – / – , – / – , – / –
		UAM30820	56.983333	-134.900000	KF949277,KF949480/KF949481,KF949814/KF949815,KF950814/KF950815
		UAM30821	56.983333	-134.900000	KF950056, – / – , – / – , – / –
	Alaska - Chichagof Island	UAM50930	58.031339	-135.612055	KF949289,KF949526/KF949527,KF949850/KF949851,KF950862/KF950863
		UAM50932	58.031339	-135.612055	KF950133, – / – , – / – , – / –
		UAM50936	58.031339	-135.612055	KF949290,KF949528/KF949529,KF949852/KF949853,KF950864/KF950865
		UAM76385	58.031339	-135.612055	KF950075, – / – , – / – , – / –
	Alaska - Coronation Island	UAM42924	55.883333	-134.233333	KF950066, – / – , – / – , – / –
		MSB198194	55.920000	-134.319000	KF949306, – / – , – / – ,KF950723/KF950724
		MSB198221	55.920000	-134.319000	KF949257,KF949396/KF949397,KF949730/KF949731,KF950725/KF950726
	Alaska - Dall Island	UAM23730	54.783333	-132.866667	KF950024, – / – , – / – , – / –
		UAM23732	54.783333	-132.866667	KF949314,KF949466/KF949467,KF949802/KF949803,KF950800/KF950801
		UAM76238	54.783333	-132.866667	KF950044, – / – , – / – , – / –
		UAM73711	55.215556	-133.138056	KF950073, – / – , – / – , – / –
		UAM73829	55.260000	-133.123889	KF950074, – / – , – / – , – / –
		UAM73830	55.260000	-133.123889	KF949298,KF949550/KF949551,KF949874/KF949875,KF950887/KF950888
	Alaska - Etolin Island	UAM34616	56.166667	-132.450000	KF949280,KF949494/KF949495,KF949824/KF949825,KF950826/KF950827
		UAM41652	56.166667	-132.450000	KF950059, – / – , – / – , – / –
		UAM20662	56.183333	-132.450000	KF950020, – / – , – / – , – / –
		UAM20664	56.183333	-132.450000	KF950021, – / – , – / – , – / –
		UAM20665	56.183333	-132.450000	KF949310,KF949442/KF949443, – / – ,KF950774/KF950775
	Alaska - Forrester Island	UAM42788	54.821389	-133.520833	KF950060, – / – , – / – , – / –
		UAM42790	54.821389	-133.520833	KF950061, – / – , – / – , – / –
		UAM42792	54.821389	-133.520833	KF949281,KF949500/KF949501,KF949828/KF949829,KF950832/KF950833
		UAM42794	54.821389	-133.520833	KF949282,KF949502/KF949503,KF949830/KF949831,KF950834/KF950835
		UAM42795	54.821389	-133.520833	KF950062, – / – , – / – , – / –
	Alaska - Gravina Island	UAM70143	55.178333	-131.805833	KF949294,KF949542/KF949543,KF949866/KF949867,KF950879/KF950880
		UAM70144	55.178333	-131.805833	KF950070, – / – , – / – , – / –
		UAM70150	55.178333	-131.805833	KF950071, – / – , – / – , – / –
		UAM70151	55.178333	-131.805833	KF949295,KF949544/KF949545,KF949868/KF949869,KF950881/KF950882
		UAM70152	55.178333	-131.805833	KF950072, – / – , – / – , – / –
	Alaska - Heceta Island	UAM23828	55.803056	-133.591389	KF949274,KF949470/KF949471,KF949806/KF949807,KF950804/KF950805
		UAM23829	55.803056	-133.591389	KF950053, – / – , – / – , – / –
		UAM23830	55.803056	-133.591389	KF950054, – / – , – / – , – / –
		UAM23831	55.803056	-133.591389	KF949275,KF949472/KF949473,KF949808/KF949809,KF950806/KF950807
		UAM23834	55.803056	-133.591389	KF950055, – / – , – / – , – / –

Alaska - Kosciusko Island	UAM70204	55.969167	-133.646944	KF949296,KF949546/KF949547,KF949870/KF949871,KF950883/KF950884
	UAM49629	55.969167	-133.645833	KF949285,KF949518/KF949519,KF949842/KF949843,KF950852/KF950853
	UAM49631	55.982778	-133.605000	KF950067, – / – , – / – , – / –
Alaska - Kuiu Island	UAM43431	56.321389	-134.071667	KF949324,KF949512/KF949513, – / – ,KF950844/KF950845
	MSB148973	56.631367	-133.737167	KF950017, – / – , – / – , – / –
	MSB148974	56.631367	-133.737167	KF949300,KF949376/KF949377,KF949710/KF949711,KF950707/KF950708
Alaska - Kupreanof Island	UAM20945	56.866667	-133.316667	KF949311,KF949446/KF949447,KF949780/KF949781,KF950778/KF950779
	UAM20948	56.866667	-133.316667	KF949312,KF949448/KF949449,KF949782/KF949783,KF950780/KF950781
	UAM30590	56.866667	-133.316667	KF950028, – / – , – / – , – / –
Alaska - Lulu Island	UAM42578	55.439722	-133.455278	KF950034, – / – , – / – , – / –
	UAM42579	55.439722	-133.455278	KF950035, – / – , – / – , – / –
	UAM42580	55.439722	-133.455278	KF949321,KF949496/KF949497,KF949826/KF949827,KF950828/KF950829
	UAM42581	55.439722	-133.455278	KF949322,KF949498/KF949499, – / – ,KF950830/KF950831
	UAM43024	55.439722	-133.455278	KF950015, – / – , – / – , – / –
Alaska - Mary Island	UAM23437	55.083333	-131.233333	KF950009, – / – , – / – , – / –
	UAM23438	55.083333	-131.233333	KF950010, – / – , – / – , – / –
Alaska - Mitkof Island	UAM23104	56.583333	-132.833333	KF949265,KF949452/KF949453,KF949786/KF949787,KF950784/KF950785
	UAM23106	56.583333	-132.833333	KF950048, – / – , – / – , – / –
	UAM23107	56.583333	-132.833333	KF950049, – / – , – / – , – / –
	UAM23108	56.583333	-132.833333	KF949271,KF949454/KF949455,KF949788/KF949789,KF950786/KF950787
Alaska - Noyes Island	MSB221318	55.450000	-133.650000	KF949307,KF949400/KF949401, – / – ,KF950729/KF950730
	UAM23655	55.451977	-133.659835	KF949313,KF949464/KF949465,KF949798/KF949799,KF950796/KF950797
	UAM23656	55.451977	-133.659835	KF950130, – / – , – / – , – / –
	UAM23657	55.451977	-133.659835	KF950022, – / – , – / – , – / –
	UAM23658	55.451977	-133.659835	KF950023, – / – , – / – , – / –
Alaska - Prince of Wales Island	UAM23717	54.766667	-132.183333	KF949158, – / – ,KF949800/KF949801,KF950798/KF950799
	UAM49643	54.907500	-132.414722	KF950013, – / – , – / – , – / –
	UAM74967	56.174444	-133.369167	–,KF949552/KF949553, – / – , – / –
	UAM74968	56.174444	-133.369167	KF949299,KF949554/KF949555, – / – , – / –
	UAM74969	56.174444	-133.369167	KF949258, – / – , – / – ,KF950889/KF950890
	UAM74970	56.174444	-133.369167	KF949329,KF949556/KF949557, – / – , – / –
	UAM74972	56.174444	-133.369167	KF949330,KF949558/KF949559, – / – , – / –
Alaska - Revillagigedo Island	UAM30343	55.414722	-131.695833	KF950027, – / – , – / – , – / –
	UAM23442	55.502382	-131.028099	KF950129, – / – , – / – , – / –
	UAM23443	55.502382	-131.028099	KF949259,KF949458/KF949459,KF949792/KF949793,KF950790/KF950791
	UAM23449	55.502382	-131.028099	KF964334, – / – , – / – , – / –
	UAM23956	55.816667	-131.366667	KF949316,KF949474/KF949475, – / – ,KF950808/KF950809
Alaska - San Fernando Island	UAM42800	55.467222	-133.389444	KF950063, – / – , – / – , – / –
	UAM42801	55.467222	-133.389444	KF949283,KF949504/KF949505,KF949832/KF949833,KF950836/KF950837
	UAM42804	55.467222	-133.389444	KF950064, – / – , – / – , – / –
	MSB221540	55.541700	-133.321000	KF949308,KF949402/KF949403,KF949734/KF949735,KF950731/KF950732
Alaska - Suemez Island	UAM42831	55.266667	-133.272156	KF949284,KF949506/KF949507,KF949834/KF949835,KF950838/KF950839
	UAM42836	55.266667	-133.272156	KF950065, – / – , – / – , – / –
	UAM23992	55.283333	-133.307199	KF949317,KF949476/KF949477,KF949810/KF949811,KF950810/KF950811
Alaska - Warren Island	UAM31725	55.875000	-133.841667	KF950058, – / – , – / – , – / –
	UAM31727	55.875000	-133.841667	KF949278,KF949490/KF949491, – / – , – / –
	UAM31729	55.875000	-133.841667	KF949279,KF949492/KF949493, – / – ,KF950824/KF950825
Alaska - Wrangell Island	UAM69665	56.269722	-132.070556	–, – / – , – / – ,KF950877/KF950878
	UAM69668	56.269722	-132.070556	KF950068, – / – , – / – , – / –
	UAM69673	56.269722	-132.070556	KF950069,KF950076/KF950077,KF950078/KF950079, – / –
	MSB149212	56.474883	-132.375233	KF950018, – / – , – / – , – / –

Alaska - Zarembo Island	UAM43440	56.333333	-132.833333	KF949260,KF949514/KF949515, – / – ,KF950846/KF950847
	UAM43469	56.333333	-132.833333	KF950036, – / – , – / – , – / –
	UAM20619	56.416667	-132.833333	KF949355,KF949440/KF949441,KF949776/KF949777,KF950772/KF950773
	UAM20620	56.416667	-132.833333	KF950019, – / – , – / – , – / –
British Columbia - Hotsprings Island	HGPeke9701	52.575709	-131.439899	KF949153,KF949362/KF949363,KF949696/KF949697,KF950695/KF950696
	HGPeke9702	52.575709	-131.439899	KF949154, – / – , – / – , – / –
	HGPeke9703	52.575709	-131.439899	KF949155,KF949364/KF949365,KF949698/KF949699,KF950697/KF950698
British Columbia - Ramsay Island	HGPeke0306	52.569649	-131.398463	KF949302,KF949356/KF949357,KF949690/KF949691,KF950689/KF950690
	HGPeke0307	52.569649	-131.398463	KF949303,KF949358/KF949359,KF949692/KF949693,KF950691/KF950692
	HGPeke0308	52.569649	-131.398463	KF949304,KF949360/KF949361,KF949694/KF949695,KF950693/KF950694
	HGPeke0309	52.569649	-131.398463	KF949305, – / – , – / – , – / –
Alaska - Cleveland Peninsula	UAM20582	55.716667	-131.850000	KF949309, – / – , – / – ,KF950770/KF950771
	UAM23771	55.750405	-132.183333	KF950025, – / – , – / – , – / –
	UAM23773	55.750405	-132.183333	KF950026, – / – , – / – , – / –
	UAM23774	55.750405	-132.183333	KF949315,KF949468/KF949469,KF949804/KF949805,KF950802/KF950803
	UAM23775	55.750405	-132.183333	KF950016, – / – , – / – , – / –
Alaska - Foggy Bay	UAM30391	54.983333	-131.000000	KF950131, – / – , – / – , – / –
	UAM23421	54.983333	-130.960624	KF949263,KF949456/KF949457,KF949790/KF949791,KF950788/KF950789
	UAM23425	54.983333	-130.960624	KF950008, – / – , – / – , – / –
Alaska - Glacier Bay	UAM42938	58.416667	-135.433333	–,KF949508/KF949509,KF949836/KF949837,KF950840/KF950841
	UAM42939	58.416667	-135.433333	KF949323,KF949510/KF949511,KF949838/KF949839,KF950842/KF950843
Alaska - Haines	UAM48129	59.261667	-135.559722	KF950012, – / – , – / – , – / –
	UAM52642	59.261667	-135.559722	KF949293,KF949536/KF949537,KF949860/KF949861,KF950872/KF950873
	UAM23665	59.316667	-135.566667	KF950052, – / – , – / – , – / –
	UAM23667	59.316667	-135.566667	KF950014, – / – , – / – , – / –
	UAM31103	59.3661111	-135.799444	KF949319,KF949486/KF949487,KF949820/KF949821,KF950820/KF950821
	UAM31104	59.3661111	-135.799444	KF950011, – / – , – / – , – / –
	UAM31106	59.3661111	-135.799444	KF950032, – / – , – / – , – / –
	UAM31107	59.3661111	-135.799444	KF949320,KF949488/KF949489,KF949822/KF949823,KF950822/KF950823
	UAM60272	59.3661111	-135.799444	KF950040, – / – , – / – , – / –
	UAM31105	59.4108333	-136.0025	KF950031, – / – , – / – , – / –
	UAM50802	59.531667	-135.348056	KF949288,KF949524/KF949525,KF949848/KF949849,KF950860/KF950861
	UAM50436	59.5316667	-135.348056	KF950038, – / – , – / – , – / –
	UAM52310	59.5316667	-135.348056	KF950039, – / – , – / – , – / –
	UAM76821	59.5316667	-135.348056	KF950046, – / – , – / – , – / –
	UAM76822	59.5316667	-135.348056	KF950047, – / – , – / – , – / –
	UAM76823	59.5316667	-135.348056	KF949328,KF949560/KF949561,KF949876/KF949877,KF950891/KF950892
	UAM31102	59.574722	-136.156667	KF949159,KF949484/KF949485,KF949818/KF949819,KF950818/KF950819
Alaska - Juneau	UAM50751	58.311111	-133.958333	KF949286,KF949520/KF949521,KF949844/KF949845,KF950856/KF950857
	UAM50754	58.311111	-133.958333	KF950132, – / – , – / – , – / –
	MSB157000	58.343070	-134.639750	KF949256,KF949390/KF949391,KF949724/KF949725,KF950719/KF950720
Alaska - Misty Fjords	UAM23487	56.083333	-131.086460	KF950050, – / – , – / – , – / –
	UAM23490	56.083333	-131.086460	KF950051, – / – , – / – , – / –
	UAM23491	56.083333	-131.086460	KF949272,KF949460/KF949461,KF949794/KF949795,KF950792/KF950793
	UAM23492	56.083333	-131.086460	KF949273,KF949462/KF949463,KF949796/KF949797,KF950794/KF950795
Alaska - Southeast	UAM20698	56.700000	-132.250000	KF949269,KF949444/KF949445,KF949778/KF949779,KF950776/KF950777
	UAM20949	56.700000	-132.250000	KF949270,KF949450/KF949451,KF949784/KF949785,KF950782/KF950783
	UAM74125	57.366667	-133.466667	KF950041, – / – , – / – , – / –
	UAM74128	57.366667	-133.466667	KF950042, – / – , – / – , – / –
	UAM74131	57.366667	-133.466667	KF950043, – / – , – / – , – / –
	UAM50800	59.615833	-135.168333	KF949287,KF949522/KF949523,KF949846/KF949847,KF950858/KF950859

	Britihs Columbia - Vancouver Island	UWBM75393	50.516667	-127.150000	KF949332,KF949566/KF949567,KF949882/KF949883,KF950897/KF950898
	British Columbia - central	UAM52518	57.135556	-130.286389	KF949292,KF949534/KF949535,KF949858/KF949859,KF950870/KF950871
		UAM52511	57.135556	-130.286389	KF949291,KF949532/KF949533,KF949856/KF949857,KF950868/KF950869
	British Columbia - north	MSB147719	57.155117	-130.244917	KF949160,–/–,–/–,–/–
		MSB156119	57.169800	-130.236700	KF949301,KF949382/KF949383,KF949716/KF949717,KF950712/KF950713
		UAM52680	57.854722	-131.369444	KF949264,KF949538/KF949539,KF949862/KF949863,KF950874/KF950875
		UAM51070	57.865556	-131.284444	KF949327,KF949530/KF949531,KF949854/KF949855,KF950866/KF950867
	British Columbia - south	UWBM75449	50.053889	-121.707778	KF949333,–/–,–/–,–/–
		UWBM75450	50.053889	-121.707778	KF949334,KF949568/KF949569,–/–,KF950899/KF950900
	Washington	UWBM74932	48.027189	-123.588333	KF949331,KF949564/KF949565,KF949880/KF949881,KF950895/KF950896
	Yukon - south	UAM71620	60.707222	-135.199167	KF949297,KF949548/KF949549,KF949872/KF949873,KF950885/KF950886
Peromyscus maniculatus - East					
	Manitoba	MSB55764	54.687500	-101.652780	**DQ385723**,KF949414/KF949415,KF949748/KF949749,KF950746/KF950747
	New York	OSM330	42.157840	-78.715031	**DQ385743**,–/–,–/–,–/–
		MSB229789	43.595000	-75.685000	–,–/–,KF949736/KF949737,KF950661/KF950733
	Ontario	MSB53341	44.800780	-77.671950	**DQ385770**,KF949412/KF949413,KF949746/KF949747,KF950744/KF950745
	Pennsylvania	CMNH109276	39.752800	-79.081110	**DQ385762**,–/–,–/–,–/–
	Quebec	CMNH109316	48.658100	-65.752800	**DQ385749**,–/–,–/–,–/–
	Tennessee	MSB71957	35.611100	-83.425000	**DQ385817**,KF949420/KF949421,KF949754/KF949755,KF950750/KF950751
	Vermont	MSB229872	44.840100	-72.525100	–,KF949404/KF949405,KF949738/KF949739,KF950734/KF950735
	Virginia	MSB74926	38.366670	-78.366670	**DQ385759**,KF949426/KF949427,KF949760/KF949761,KF950756/KF950757
Peromyscus maniculatus - West					
	Alberta	MSB156182	51.027910	-115.034200	KF949166,KF949384/KF949385,KF949718/KF949719,KF950658/KF950714
	Arizona	MSB122918	34.974736	-109.794788	KF949161,KF949366/KF949367,KF949700/KF949701,KF950699/KF950700
	British Columbia - central	MSB158235	56.031806	-129.931360	KF949236,KF949392/KF949393,KF949726/KF949727,KF950721/KF950722
	British Columbia - north	MSB199034	58.382528	-129.918770	KF949248,KF949398/KF949399,KF949732/KF949733,KF950727/KF950728
		UAM52701	59.734167	-133.518889	KF949247,KF949540/KF949541,KF949864/KF949865,KF950664/KF950876
	British Columbia - south	MSB156370	49.202030	-117.897090	KF949167,KF949386/KF949387,KF949720/KF949721,KF950715/KF950716
		MSB156588	49.202030	-117.897090	KF949168,KF949388/KF949389,KF949722/KF949723,KF950717/KF950718
	California	MSB43630	41.004030	-124.091610	**DQ385703**,KF949410/KF949411,KF949744/KF949745,KF950742/KF950743
	Colorado	MSB74667	40.666667	-104.366667	**DQ385692**,KF949424/KF949425,KF949758/KF949759,KF950754/KF950755
	Idaho	MSB151511	43.407500	-112.804440	KF949172,KF949380/KF949381,KF949714/KF949715,KF950710/KF950711
	Kansas	MSB73966	38.184300	-99.215500	**DQ385642**,KF949422/KF949423,KF949756/KF949757,KF950752/KF950753
	Montana	MSB56717	45.554100	-111.039600	**DQ385678**,KF949416/KF949417,KF949750/KF949751,KF950748/KF950749
	Nevada	MSB74970	39.416584	-118.700981	**DQ385681**,KF949428/KF949429,KF949762/KF949763,KF950758/KF950759
	New Mexico	MSB89198	32.822334	-106.093220	**DQ385661**,KF949436/KF949437,KF949770/KF949771,KF950764/KF950765
		MSB77901	35.056091	-106.242682	**DQ385653**,KF949430/KF949431,KF949764/KF949765,KF950760/KF950761
	Northwest Territories	UAM77795	60.010000	-111.540000	KF949170,KF949562/KF949563,KF949878/KF949879,KF950893/KF950894
	Washington	MSB86381	47.090100	-122.603900	**DQ385697**,KF949432/KF949433,KF949766/KF949767,KF950762/KF950763
	Yukon - south	MSB194080	60.014103	-133.795475	KF949246,KF949394/KF949395,KF949728/KF949729,KF950659/KF950660
		MSB144237	61.100000	-135.293400	KF949235,KF949370/KF949371,KF949704/KF949705,KF950655/KF950656
Peromyscus maniculatus - Southwest					
	Baja California	MSB58325	24.450000	-111.833333	**DQ385707**,KF949418/KF949419,KF949752/KF949753,KF950683/KF950684
	California	MSB87486	34.739658	-120.539674	**DQ385713**,KF949434/KF949435,KF949768/KF949769,KF950662/KF950663
Peromyscus leucopus					
		MSB92216			–,KF949438/KF949439,KF949772/KF949773,KF950766/KF950767
		MSB92383			–,–/–,KF949774/KF949775,KF950768/KF950769
Peromyscus melanotis		MSB40124			KF949261,–/–,–/–,KF950740/KF950741

Sorex monticolus						
	Island	Alaska - Admiralty Island	UAM44653	57.429444	-133.938889	KF950196, – / – , – / – , – / –
			UAM44654	57.429444	-133.938889	KF950197,KF950367/KF950368, – / – ,KF950627/KF950628
			UAM44655	57.429444	-133.938889	KF950198, – / – , – / – , – / –
			UAM44656	57.429444	-133.938889	KF950199, – / – , – / – , – / –
		Alaska - Baker Island	MSB221326	55.420000	-133.498000	KF950235,KF950289/KF950290,KF950439/KF950440,KF950547/KF950548
			MSB221335	55.420000	-133.498000	KF950236,KF950291/KF950292,KF950441/KF950442,KF950549/KF950550
		Alaska - Coronation Island	UAM23968	55.917778	-134.320833	KF950106, – / – , – / – , – / –
			UAM24726	55.917778	-134.320833	KF950180, – / – , – / – , – / –
		Alaska - Dall Island	UAM42079	54.744167	-132.771111	KF950188, – / – , – / – , – / –
			UAM42347	54.744167	-132.771111	KF950189,KF950363/KF950364,KF950477/KF950478,KF950621/KF950622
			UAM23750	54.783333	-132.866667	KF950167,KF950335/KF950336,KF950461/KF950462,KF950591/KF950592
			UAM73714	55.215556	-133.138056	KF950101, – / – , – / – , – / –
			UAM42080	55.250497	-133.116667	KF950095, – / – , – / – , – / –
		Alaska - Etolin Island	UAM20639	56.183333	-132.483333	KF950145,KF950313/KF950314, – / – ,KF950569/KF950570
			UAM69891	56.186667	-132.632778	KF950100,KF950387/KF950388,KF950499/KF950500,KF950647/KF950648
		Alaska - Forrester Island	UAM42083	54.821389	-133.520833	KF950080, – / – , – / – , – / –
			UAM42086	54.821389	-133.520833	KF950083,KF950359/KF950360,KF950475/KF950476,KF950617/KF950618
			UAM42092	54.821389	-133.520833	KF950135,KF950361/KF950362, – / – ,KF950619/KF950620
			UAM42715	54.821389	-133.520833	KF950081, – / – , – / – , – / –
			UAM42719	54.821389	-133.520833	KF950082, – / – , – / – , – / –
		Alaska - Gravina Island	UAM70135	55.178333	-131.805833	KF950212, – / – , – / – , – / –
			UAM70137	55.178333	-131.805833	KF950137,KF950389/KF950390, – / – ,KF950649/KF950650
			UAM52744	55.333333	-131.743566	KF950202, – / – , – / – , – / –
			UAM52745	55.333333	-131.743566	KF950203, – / – , – / – , – / –
			UAM52746	55.333333	-131.743566	KF950204, – / – , – / – , – / –
		Alaska - Heceta Island	UAM23835	55.803056	-133.591389	KF950172,KF950339/KF950340, – / – ,KF950595/KF950596
			UAM23836	55.803056	-133.591389	KF950173, – / – , – / – , – / –
			UAM23837	55.803056	-133.591389	KF950174,KF950341/KF950342,KF950463/KF950464,KF950597/KF950598
			UAM23838	55.803056	-133.591389	KF950175, – / – , – / – , – / –
		Alaska - Kosciusko Island	UAM43254	55.918889	-133.685000	KF950192,KF950365/KF950366, – / – , – / –
			UAM43389	55.918889	-133.685000	KF950193, – / – , – / – , – / –
			UAM43406	55.918889	-133.685000	–, – / – , – / – ,KF950625/KF950626
			UAM43526	55.918889	-133.685000	KF950195, – / – , – / – , – / –
		Alaska - Kuiu Island	UAM43240	56.321389	-134.071667	–, – / – , – / – ,KF950623/KF950624
			UAM43396	56.321389	-134.071667	KF950194, – / – , – / – , – / –
			MSB148932	56.631367	-133.737167	KF950222,KF950259/KF950260,KF950411/KF950412,KF950519/KF950520
			MSB148945	56.631367	-133.737167	KF950223, – / – , – / – , – / –
		Alaska - Kupreanof Island	UAM20940	56.866667	-133.316667	KF950090, – / – , – / – , – / –
			UAM20941	56.866667	-133.316667	KF950148, – / – , – / – , – / –
			UAM20942	56.866667	-133.316667	KF950149,KF950319/KF950320, – / – ,KF950575/KF950576
			UAM23874	56.974830	-133.941160	KF950087, – / – , – / – , – / –
			UAM23875	56.974830	-133.941160	KF950176,KF950343/KF950344, – / – ,KF950599/KF950600
		Alaska - Lulu Island	UAM42712	55.439722	-133.455278	KF950190, – / – , – / – , – / –
			MSB221499	55.468500	-133.425800	–,KF950293/KF950294, – / – ,KF950551/KF950552
			MSB221504	55.468500	-133.425800	KF950237,KF950295/KF950296,KF950443/KF950444,KF950553/KF950554
			MSB221544	55.468500	-133.425800	–,KF950297/KF950298, – / – , – / –
			MSB221550	55.468500	-133.425800	KF950238, – / – , – / – , – / –
		Alaska - Mitkof Island	UAM31280	56.583333	-132.833333	KF950093,KF950347/KF950348, – / – , – / –
			UAM31281	56.583333	-132.833333	KF950181, – / – , – / – , – / –
			UAM74305	56.666667	-132.833333	KF950102, – / – , – / – , – / –

	UAM23174	56.733333	-132.966667	KF950104, – / – , – / – , – / –
Alaska - Noyes Island	UAM23652	55.451977	-133.659835	KF950160, – / – , – / – , – / –
	UAM23653	55.451977	-133.659835	KF950084,KF950331/KF950332, – / – ,KF950585/KF950586
	UAM23654	55.451977	-133.659835	KF950161, – / – , – / – , – / –
	UAM23674	55.451977	-133.659835	KF950162, – / – , – / – , – / –
	UAM23675	55.451977	-133.659835	KF950163, – / – , – / – ,KF950587/KF950588
Alaska - Prince of Wales Island	UAM23718	54.766667	-132.183333	KF950164, – / – , – / – , – / –
	UAM23719	54.766667	-132.183333	KF950165,KF950333/KF950334, – / – ,KF950589/KF950590
	UAM23720	54.766667	-132.183333	KF950166, – / – , – / – , – / –
	UAM23721	54.766667	-132.183333	KF950092, – / – , – / – , – / –
	UAM20443	55.833333	-133.150000	KF950142, – / – , – / – , – / –
	UAM20445	55.833333	-133.150000	KF950143, – / – , – / – , – / –
Alaska - Revillagigedo Island	UAM71472	55.489444	-131.598611	KF950213, – / – , – / – , – / –
	UAM23472	55.502382	-131.028099	KF950153, – / – , – / – , – / –
	UAM23473	55.502382	-131.028099	KF950154,KF950327/KF950328,KF950459/KF950460, – / –
	UAM23965	55.816667	-131.366667	KF950177, – / – , – / – , – / –
	UAM23967	55.816667	-131.366667	KF950178,/,/,KF950601/KF950602
Alaska - San Fernando Island	MSB221162	55.454640	-133.361020	KF950124,KF950287/KF950288,KF950437/KF950438,KF950545/KF950546
	UAM67523	55.473333	-133.389444	KF950210, – / – , – / – , – / –
	UAM67524	55.473333	-133.389444	KF950211, – / – , – / – , – / –
Alaska - Suemez Island	UAM23621	55.283333	-133.307199	KF950158, – / – , – / – , – / –
	UAM23622	55.283333	-133.307199	KF950159, – / – , – / – , – / –
	UAM24009	55.283333	-133.307199	KF950179,KF950345/KF950346, – / – ,KF950603/KF950604
Alaska - Warren Island	UAM31759	55.875000	-133.841667	KF950184, – / – , – / – , – / –
	UAM23409	55.875000	-133.841667	KF950091, – / – , – / – , – / –
	UAM31757	55.875000	-133.841667	KF950182,KF950351/KF950352,KF950467/KF950468,KF950609/KF950610
	UAM31760	55.875000	-133.841667	KF950185,KF950353/KF950354,KF950469/KF950470,KF950611/KF950612
	UAM31758	55.875000	-133.841667	KF950183, – / – , – / – , – / –
Alaska - Wrangell Island	UAM62279	56.318333	-132.286111	KF950207, – / – , – / – , – / –
	UAM22519	56.350000	-132.333333	–,KF950323/KF950324, – / – ,KF950579/KF950580
Alaska - Zarembo Island	UAM43246	56.333333	-132.833333	KF950191, – / – , – / – , – / –
	UAM20615	56.416667	-132.833333	KF950134,KF950309/KF950310, – / – ,KF950565/KF950566
	UAM20616	56.416667	-132.833333	KF950089, – / – , – / – , – / –
	UAM20617	56.416667	-132.833333	KF950144,KF950311/KF950312, – / – ,KF950567/KF950568
British Columbia - Bischof Island	HGSomo0202	52.582605	-131.564128	KF950139,KF950241/KF950242,KF950395/KF950396,KF950505/KF950506
British Columbia - Graham Island	UAM52610	52.366667	-132.208333	KF950110, – / – , – / – , – / –
	UAM52614	52.366667	-132.191667	KF950200,KF950373/KF950374,KF950483/KF950484, – / –
	UAM52616	52.366667	-132.191667	KF950201,KF950375/KF950376,KF950485/KF950486,KF950633/KF950634
	HGSomo0602	53.255084	-132.065841	KF950141,KF950245/KF950246,KF950397/KF950398,KF950507/KF950508
British Columbia - Moresby Island	HGSomo0402	52.343437	-131.433500	KF950140,KF950243/KF950244, – / – , – / –
Alaska - Cleveland Peninsula	UAM23763	55.750405	-132.183333	KF950088, – / – , – / – , – / –
	UAM23766	55.750405	-132.183333	KF950168,KF950337/KF950338, – / – ,KF950593/KF950594
	UAM23767	55.750405	-132.183333	KF950169, – / – , – / – , – / –
	UAM23768	55.750405	-132.183333	KF950170, – / – , – / – , – / –
	UAM23769	55.750405	-132.183333	KF950171, – / – , – / – , – / –
Alaska - Foggy Bay	UAM23411	54.983333	-130.960624	KF950151, – / – , – / – , – / –
	UAM23412	54.983333	-130.960624	KF950152,KF950325/KF950326, – / – ,KF950581/KF950582
	UAM23420	54.983333	-130.960624	KF950217, – / – , – / – , – / –
Alaska - Glacier Bay	UAM30461	58.466667	-135.850000	KF950107, – / – , – / – , – / –
Alaska - Juneau	MSB156996	58.343070	-134.639750	KF950229, – / – , – / – , – / –
	MSB149433	58.362037	-134.604783	KF950225,KF950263/KF950264,KF950415/KF950416,KF950523/KF950524

Northern		MSB156966	58.528400	-134.827167	KF950228,KF950271/KF950272,KF950423/KF950424,KF950531/KF950532
	Alaska - Misty Fjords	UAM33261	54.943611	-130.333611	KF950186, – / – , – / – , – / –
		UAM33262	54.943611	-130.333611	KF950187, – / – , – / – , – / –
		UAM23506	56.083333	-131.086460	KF950155, – / – , – / – , – / –
		UAM23560	56.083333	-131.086460	KF950156,KF950329/KF950330, – / – ,KF950583/KF950584
		UAM23564	56.083333	-131.086460	KF950157, – / – , – / – , – / –
	Alaska - Southeast	MSB193403	55.966500	-130.060100	KF950231,KF950279/KF950280,KF950431/KF950432,KF950539/KF950540
		MSB193469	55.966500	-130.060100	KF950232, – / – , – / – , – / –
		MSB193471	55.966500	-130.060100	KF950121,KF950283/KF950284,KF950435/KF950436,KF950543/KF950544
		MSB193665	55.966500	-130.060100	KF950233, – / – , – / – , – / –
		UAM20708	56.700000	-132.250000	KF950216,KF950315/KF950316,KF950455/KF950456,KF950571/KF950572
		UAM20709	56.700000	-132.250000	KF950146,KF950317/KF950318,KF950457/KF950458,KF950573/KF950574
		UAM20710	56.700000	-132.250000	KF950147, – / – , – / – , – / –
		UAM20951	56.700000	-132.250000	KF950150,KF950321/KF950322, – / – ,KF950577/KF950578
		UAM74397	57.366667	-133.466667	KF950214, – / – , – / – , – / –
	British Columbia - central	UAM52266	55.331944	-128.965278	KF950218,KF950371/KF950372,KF950481/KF950482,KF950631/KF950632
		UAM48717	55.331944	-128.965278	KF950096,KF950369/KF950370,KF950479/KF950480,KF950629/KF950630
	Washington	UAM67038	47.100000	-121.016667	KF950113, – / – , – / – , – / –
		MSB54615	47.371675	-123.547194	KF950138,KF950303/KF950304,KF950449/KF950450,KF950561/KF950562
	Alaska - Glacier Bay	UAM30462	59.069444	-138.348611	KF950108, – / – , – / – , – / –
	Alaska - Haines	UAM23661	59.150000	-135.350000	KF950105, – / – , – / – , – / –
		MSB193310	59.217640	-135.448180	KF950118,KF950275/KF950276,KF950427/KF950428,KF950535/KF950536
		MSB195074	59.245900	-135.175300	KF950234, – / – , – / – , – / –
		MSB193286	59.266710	-135.603360	KF950230, – / – , – / – , – / –
		MSB193394	59.266710	-135.603360	KF950119,KF950277/KF950278,KF950429/KF950430,KF950537/KF950538
		MSB193411	59.266710	-135.603360	KF950120,KF950281/KF950282,KF950433/KF950434,KF950541/KF950542
		MSB193298	59.294140	-135.696130	KF950117,KF950273/KF950274,KF950425/KF950426,KF950533/KF950534
		MSB195088	59.300100	-135.704200	KF950122, – / – , – / – , – / –
		MSB195092	59.300100	-135.704200	KF950123,KF950285/KF950286, – / – , – / –
		MSB146967	59.408383	-136.006867	KF950115,KF950257/KF950258,KF950409/KF950410,KF950517/KF950518
		UAM64434	59.623222	-136.089333	KF950099,KF950381/KF950382,KF950493/KF950494,KF950641/KF950642
		UAM64437	59.623222	-136.089333	KF950208,KF950383/KF950384,KF950495/KF950496,KF950643/KF950644
		UAM64444	59.623222	-136.089333	KF950209,KF950385/KF950386,KF950497/KF950498,KF950645/KF950646
	Alaska - interior	UAM31367	61.232778	-149.594444	KF950109,KF950349/KF950350,KF950465/KF950466,KF950607/KF950608
		UAM58449	65.166667	-143.550000	KF950206,KF950379/KF950380,KF950491/KF950492,KF950639/KF950640
		MSB143123	68.450000	-149.470000	KF950114,KF950251/KF950252,KF950403/KF950404,KF950513/KF950514
	Alaska - Juneau	UAM33266	58.533333	-133.683333	KF950094,KF950355/KF950356,KF950471/KF950472,KF950613/KF950614
	Alaska - Southeast	UAM76830	59.615833	-135.168333	KF950103,KF950393/KF950394,KF950503/KF950504,KF950653/KF950654
		UAM76828	59.616111	-135.138333	KF950215,KF950391/KF950392,KF950501/KF950502,KF950651/KF950652
	British Columbia - north	MSB155620	57.836800	-131.390100	KF950227,KF950267/KF950268,KF950419/KF950420,KF950527/KF950528
		UAM52753	57.865556	-131.284444	KF950205,KF950377/KF950378,KF950487/KF950488,KF950635/KF950636
	Montana	UAM66451	47.638000	-113.791200	KF950111, – / – , – / – , – / –
	Yukon - central	MSB145726	63.543100	-137.194800	KF950221,KF950255/KF950256,KF950407/KF950408, – / –
		MSB144475	63.841300	-135.461400	KF950220,KF950253/KF950254,KF950405/KF950406,KF950515/KF950516
	Yukon - south	UAM52756	60.838333	-137.329167	KF950098, – / – ,KF950489/KF950490,KF950637/KF950638
		MSB149318	61.200450	-133.046933	KF950224,KF950261/KF950262,KF950413/KF950414,KF950521/KF950522
		UAM66920	62.275954	-140.695895	KF950112, – / – , – / – , – / –
Southern	Utah	MSB77013	40.186140	-111.139530	KF950136,KF950307/KF950308,KF950453/KF950454,KF950563/KF950564
	Arizona	MSB47301	31.903300	-109.275000	KF950240,KF950301/KF950302,KF950447/KF950448,KF950559/KF950560
	Colorado	MSB76658	40.450000	-106.000000	KF950126,KF950305/KF950306,KF950451/KF950452, – / –
	New Mexico	MSB140765	35.800000	-106.500000	KF950219,KF950247/KF950248,KF950399/KF950400,KF950509/KF950510

Sorex cinereus		
	MSB143043	KF950085,KF950249/KF950250,KF950401/KF950402,KF950511/KF950512
	UAM34528	KF950127,KF950357/KF950358,KF950473/KF950474,KF950615/KF950616
	UAM36763	KF950128, – / – , – / – , – / –
	UAM30576	KF950086, – / – , – / – ,KF950605/KF950606
Sorex fumeus		
	MSB229215	KF950125,KF950299/KF950300,KF950445/KF950446,KF950555/KF950556
	UAM50145	KF950097, – / – , – / – , – / –
Sorex vagrans		
	MSB156348	KF950116,KF950269/KF950270,KF950421/KF950422,KF950529/KF950530
	MSB43638	KF950239, – / – , – / – ,KF950557/KF950558
	MSB155610	KF950226,KF950265/KF950266,KF950417/KF950418,KF950525/KF950526

Table 2. Primer list and PCR annealing temperatures. Primers used for amplification and sequencing mtDNA Cytochrome B (cyt*b*), and nuclear loci Alcohol Dehydrogenase 2 (ADH2), Apolipoprotein B (ApoB), Protein C-est-2 (ETS2), β-fibrinogen (FGB), interphotoreceptor retinoid-binding protein (IRBP), Recombination Activating Protein 1 (Rag1) and zona pellucida 3 (ZP3) for species indicated, including outgroups in each genus, with annealing temperatures (^{o}C) indicated in parentheses.

Species	Primer	Sequence (5'-3')	Reference
	cyt*b* (50)		
M. longicaudus	L14724		(Irwin *et al.* 1991; Kocher & White 1989)
	Vole 14		(Conroy & Cook 1999)
Peromyscus &	L14734		(Ohdachi et al. 2001)
S. monticolus	CytBRev		(Anderson and Yates 2000)
S. monticolus	**ADH2 (50)**		
	ADH2F		(Lyons *et al.* 1997)
	ADH2R		(Lyons *et al.* 1997)
S. monticolus	**ApoB (54.6)**		
	ApoBF		(Dubey *et al.* 2007)
	ApoBR		(Dubey *et al.* 2007)
M. longicaudus	**ETS2 (63)**		
	ETS2F		(Lyons *et al.* 1997)
	ETS2R		(Lyons *et al.* 1997)
M. longicaudus	**FGB (65)**		
	MSB_MFGBF	CGTTTGGATTGGCGGAGTGG	This study, modified from Matocq *et al* . (2007)
	MSB_MFGBR	GCACGTACGACAGGGACAACG	This study, modified from Matocq *et al* . (2007)
Peromyscus	**FGB (63)**		
	MSB_PFGBF	GCCGTTTGGATTGGCTGC	This study, modified from Matocq *et al* . (2007)
	MSB_PFGBR	CGACAGGGACAATGATGGC	This study, modified from Matocq *et al* . (2007)
S. monticolus	**FGB (63)**		
	MSB_SFGBF	GCCATCCTCTTTAGAACACTG	This study, modified from Matocq *et al* . (2007)
	MSB_SFGBR	CGATGGCTGGTAGGCGTCC	This study, modified from Matocq *et al* . (2007)
Peromysucs	**IRBP (60)**		
	MSB_PIRBPF	CCAGGAGGTACTGAGTGAGC	This study, modified from Stanhope *et al.* (1992)
	MSB_PIRBPR	GCTGAGTAGTCCATGCTAGC	This study, modified from Stanhope *et al.* (1992)
M. longicaudus	**Rag1 (60)**		
	MSB_Rag1F	GCAGTCTCCTTTAGTTCCAGAC	This study, modified from Steppan *et al* .(2004)
	MSB_Rag1R	CCAACAGGAACAACGTCAAGC	This study, modified from Steppan *et al* .(2004)
Peromyscus	**Zp3 (56)**		
	Z36FA		(Turner and Hoekstra 2006)
	Z37RA		(Turner and Hoekstra 2006)

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Table 3. Diversity indices, expansion statistics and models of evolution. n=haploid sample size; L=length of sequence; S=variable sites; Eta=#mutations; h=#haplotypes; Hd=haplotype diversity; π=nucleotide diversity; D=Tajima's D; Fs=Fu's FS; r=raggedness index; R2=Ramos-Osnin's R2; Model=model of evolution as selected by MODELTEST. Bold values are significant at p<0.05 (p<0.02 for FS). Refugia = refugial islands, Non-refugia = non refugial islands (see Table 4).

Species	Group	Gene	n	L	S	h	Hd	π	D	Fs (p<.02)	R2	Model of Evolution
M. longicaudus	All Samples	Cytb	140	1143	174	100	0.992	0.01423	**-0.08804**	**-0.61525**	**0.08687**	TrN+I+G
		ETS2	63	733								GTR+I+G
		FGB	79	600								HKY+G
		Rag1	70	963								HKY
	No Outgroups	Cytb	136	1143	128	96	0.992	0.01037	**-0.09456**	**-0.57918**	**0.08725**	
		ETS2	61	733	14	14	0.477	0.002	-0.04807	**-0.1418**	**0.09083**	
		FGB	77	600	18	19	0.371	0.00094	**-0.00791**	**-0.18466**	**0.09204**	
		Rag1	68	963	9	10	0.182	0.00023	**-0.00041**	**-0.10372**	**0.09885**	
	Island	Cytb	86	1143	73	57	0.984	0.00519	**-0.09551**	**-0.29755**	**0.09479**	HKY+I+G
		ETS2	35	733	9	5	0.138	0.00061	**-0.0251**	0.00678	**0.11424**	HKY+I+G
		FGB	42	600	7	8	0.182	0.00033	**-0.0096**	**-0.01618**	**0.11433**	HKY+I
		Rag1	39	963	3	4	0.124	0.00013	**-0.00142**	**-0.00572**	**0.11697**	TrN
	Refugia	Cytb	36	1143	34	19	0.948	0.0052	-0.10885	-0.10906	**0.1141**	HKY+G
		ETS2	24	733	2	3	0.163	0.00024	**-0.01231**	**0.20236**	**0.1708**	HKY
		FGB	30	600	4	3	0.297	0.00132	-0.02833	0.08965	**0.13912**	HKY
		Rag1	28	963	2	3	0.489	0.00055	-0.02278	0.14512	**0.14835**	HKY
	Non-refugia	Cytb	50	1143	54	40	0.986	0.00555	**-0.09545**	**-0.20269**	**0.10568**	TrN+I
		ETS2	46	733	11	3	0.127	0.00123	**-0.03223**	0.04974	**0.12001**	HKY
		FGB	54	600	6	7	0.244	0.00044	**-0.00255**	**0.07172**	**0.12803**	TrN+I
		Rag1	50	963	2	3	0.117	0.00012	**-0.00293**	0.09541	**0.13511**	TrN
Peromyscus	All Samples	Cytb	192	1143	209	107	0.984	0.01224	**-0.09268**	**-0.69546**	**0.08185**	GTR+I+G
		FGB	109	479	26	19	0.24	0.00098	**-0..02871**	**-0.29886**	**0.08599**	HKY
		IRBP	99	421	9	9	0.381	0.00116	**-0.00929**	**-0.24871**	**0.08744**	HKY
		Zp3	112	314	11	14	0.233	0.00094	**-0.01977**	**-0.25383**	**0.08864**	HKY+I
	No Outgroups	Cytb	190	1143	145	109	0.984	0.01042	**-0.07315**	**-0.55263**	**0.08163**	
		FGB	107	479	21	18	0.228	0.00078	-0.01356	**-0.22712**	**0.08829**	
		IRBP	96	421	9	9	0.391	0.0012	**-0.03044**	**-0.21412**	**0.08876**	
		Zp3	109	314	9	12	0.223	0.00087	**-0.015**	**-0.24393**	**0.08962**	

P. keeni	Island	Cytb	155	1143	89	80	0.978	0.00459	**-0.0772**	-0.31143	**0.08483**	GTR+I+G
		FGB	75	479	2	3	0.065	0.00014	-0.10294	-0.40733	**0.08532**	TrN+I
		IRBP	63	421	4	5	0.391	0.00107	-0.02635	-0.12602	**0.09724**	HKY+I
		Zp3	76	314	8	9	0.199	0.00089	-0.01263	**-0.17179**	**0.09829**	HKY+I
	Refugia	Cytb	47	1143	42	29	0.97	0.00463	**-0.08343**	**-0.15405**	**0.4077**	HKY+I
		FGB	40	479	4	5	0.395	0.0009	-0.01661	0.11807	**0.13538**	TrN
		IRBP	32	421	4	5	0.571	0.00171	-0.01988	0.11493	**0.13758**	HKY
		Zp3	42	314	6	4	0.603	0.0066	-0.07205	-0.0308	**0.11389**	TrN+I
	Non-refugia	Cytb	108	1143	100	68	0.984	0.00613	**-0.08062**	**-0.3738**	**0.09076**	GTR+I+G
		FGB	110	479	0	1	0	0	-	-	-	HKY
		IRBP	94	421	4	7	0.665	0.00224	-0.02728	-0.09094	**0.09908**	HKY+I
		Zp3	110	314	8	9	0.254	0.00111	**-0.0272**	**-0.08196**	**0.10334**	HKY+I
S. monticolus	All Samples	Cytb	158	1140	138	58	0.87	0.01483	**-0.08163**	-0.67266	**0.08461**	GTR+I+G
		ADH2	77	281	2	3	0.076	0.00028	-0.08555	-0.41299	**0.08496**	HKY
		ApoB	55	500	30	12	0.62	0.00611	**-0.08992**	-0.1969	**0.09157**	HKY
		FGB	75	589	13	9	0.117	0.00058	**-0.01859**	**-0.12373**	**0.09643**	HKY+I+G
	No Outgroups	Cytb	148	1140	71	51	0.852	0.00905	-0.10863	**-0.50509**	**0.08594**	
		ADH2	72	281	2	3	0.055	0.00025	-0.10054	-0.3663	**0.08607**	
		ApoB	50	500	5	5	0.541	0.00317	-0.05092	-0.13439	**0.09457**	
		FGB	68	589	4	4	0.044	0.00011	**-0.08883**	-0.37778	**0.08677**	
	Island	Cytb	115	1140	38	31	0.764	0.00151	**-0.06231**	**-0.15173**	**0.09154**	HKY+I+G
		ADH2	48	281	1	2	0.041	0.00015	-0.07474	-0.21871	**0.09318**	HKY+I
		ApoB	26	500	5	4	0.338	0.00155	-0.04454	0.02484	**0.1175**	HKY
		FGB	46	589	5	5	0.146	0.00032	**-0.00623**	**-0.03408**	**0.11045**	HKY+I
	Refugia	Cytb	34	1140	25	16	0.913	0.00341	-0.08419	**-0.02008**	**0.1172**	GTR+I
		ADH2	30	281	0	1	0	0	-	-	-	JC
		ApoB	18	500	2	3	0.392	0.00084	-0.01306	0.22258	**0.17967**	HKY
		FGB	30	589	3	4	0.251	0.00046	**-0.01126**	**0.14274**	**0.15434**	HKY
	Non-refugia	Cytb	81	1140	35	26	0.751	0.00146	**-0.04799**	**-0.09461**	0.09909	HKY+G
		ADH2	66	281	1	2	0.6	0.00022	-0.07799	-0.33319	**0.0999**	HKY+I
		ApoB	34	500	3	2	0.299	0.0018	-0.03143	0.08012	**0.13118**	HKY
		FGB	62	589	4	4	0.182	0.00041	**-0.01448**	0.02697	**0.12298**	HKY+I

Table 4. Locality information and abbreviations. Refugia = potential refugial islands and hypothesized island groups = island and adjacent mainland populations based on paleo-shoreline reconstruction and LGM glacial cover. –= not included in the analyses that require the given information. Localities included in the Shimodaira-Hasegawa tests are indicated with asterisk.

Region	**Location**	**Refugia**	**Hypothesized island group**	**Areaha**	**Distance (km)**
Alaskan Islands	Admiralty (ADM)*	no	Inner Northern	431,309	5
	Baker (BKR)*	no	Middle and Outer Southern	13,512	13
	Baranof (BNF)	no	Outer Northern	424,016	6
	Chichagof (CGF)*	yes	Outer Northern	545,317	5
	Coronation (CRN)*	yes	Coronation	9,120	11
	Dall (DAL)*	yes	Middle and Outer Southern	65,869	7
	Etolin (ETN)*	no	Middle and Outer Southern	88,995	2
	Forrester (FRS)*	yes	Forrester	1,013	34
	Gravina (GRV)*	no	Inner Southern	23,307	3
	Heceta (HEC)*	no	Middle and Outer Southern	18,916	9
	Kosciusko (KSC)*	no	Middle and Outer Southern	48,259	7
	Kuiu (KUI)*	no	Middle and Outer Southern	193,455	3
	Kupreanof (KRF)*	no	Middle and Outer Southern	282,415	2
	Lulu (LUL)*	yes	Middle and Outer Southern	6,022	11
	Mary (MRY)	no	–	1,763	8
	Mitkof (MIT)*	no	Middle and Outer Southern	54,753	1
	Noyes (NYS)*	yes	Middle and Outer Southern	12,836	13
	Orr (ORI)	–	–	–	–
	Prince of Wales (POW)*	no	Middle and Outer Southern	578,202	6
	Revillagigedio (REV)*	no	Inner Southern	302,659	2
	San Fernando (SNF)*	no	Middle and Outer Southern	8,782	11
	Suemez (SMZ)*	yes	Middle and Outer Southern	15,200	7
	Sukkwan (SWN)	–	–	–	–
	Tuxekan (TXN)	no	–	8,523	7
	Warren (WRN)	yes	Middle and Outer Southern	5,067	11
	Wrangell (WRG)*	no	Middle and Outer Southern	56,948	1
	Zarembo (ZRB)*	no	Middle and Outer Southern	47,263	5
British Columbian Islands	Bischof (BSF)	–	–	–	–
	Graham (GRM)	–	–	–	–
	Hotsprings (HTS)	–	–	–	–
	Moresby (MRB)	–	–	–	–
	Ramsay (RMS)	–	–	–	–
	Vancouver (VCR)	–	–	–	–
Mainland	British Columbia (BC)	no	–		
	Mainland Southeast Alaska (MLSE)	no	–		
	Northern mainalnd Southeast (NMLSE)	no	–		
	Interior Alaska, Yukon and White Pass (North)	no	–		
	Cleveland Peninsula (CP/MLCP)*	–	Inner Southern	–	–
	Foggy Bay (FB/MLFB)*	–	Middle and Outer Southern	–	–
	Glacier Bay (GB/MLGB)*	–	Outer Northern	–	–
	Haines (HNS/MLHNS)*	–	–	–	–
	Interior Alaska (IAK/MLS)	–	–	–	–
	Juneau (JNO/MLJNO)*	–	Inner Northern	–	–
	Klukwan (KLU/MLKLU)	–	–	–	–
	Misty Fjords (MFD/MLMFD)*	–	Inner Southern	–	–
	Southeast Central (SEC AK/MLSEC)*	–	–	–	–
	Southeast North (SEN AK/MLSEN)	–	–	–	–
	Southeast South (SES AK/MLSES)	–	–	–	–
	Skagway (SKW/MLSKW)	–	–	–	–
	Taiya River (TYR/MLTYR)	–	–	–	–
	White Pass (WP/MLWP)	–	–	–	–
	British Columbia - Central (BCC)*	–	–	–	–
	British Columbia - North (BCN)	–	–	–	–
	British Columbia - South (BCS)	–	–	–	–
	Washington (WA)	–	–	–	–
	Yukon Territory - Central (YTC)	–	–	–	–
	Yukon Territory - South (YTS)*	–	–	–	–

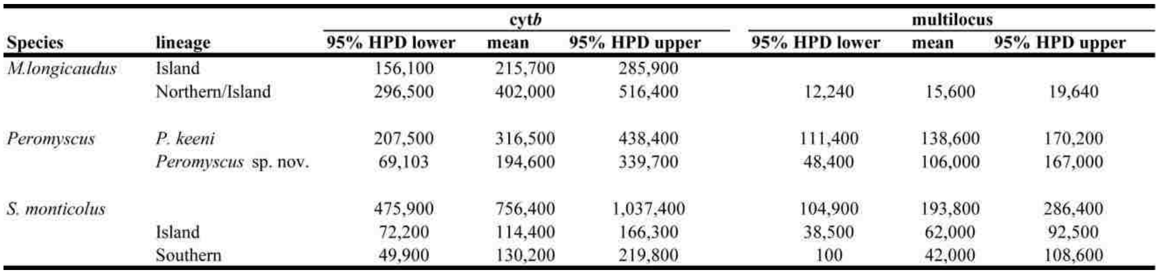
Table 5. Between group net genetic divergences among major cyt *b* lineages of *M. longicaudus*, *Peromyscus* and *S. monticolus*. The number of base differences per site from estimation of net average between groups of sequences is shown. Standard error estimate(s) are shown above the diagonal. All ambiguous positions were removed for each sequence pair. Evolutionary analyses were conducted in MEGA5.

M. longicaudus	Central	Colorado Plateau	Island	Northern	North Pacific Coast	Southern	*M. pennsylvanicus*	*M. montanus*
Central		0.40%	0.40%	0.40%	0.40%	0.50%	0.80%	0.80%
Colorado Plateau	2.50%		1.30%	0.30%	1.00%	0.50%	0.80%	0.80%
Island	2.40%	0.30%		0.30%	0.30%	0.50%	0.80%	0.70%
Northern	2.50%	1.30%	1.20%		0.90%	0.50%	0.80%	0.70%
North Pacific Coast	2.30%	0.30%	1.20%	0.20%		0.50%	0.80%	0.80%
Southern	3.40%	3.60%	3.70%	3.80%	3.70%		9.90%	7.80%
M. pennsylvanicus	9.90%	9.30%	10.20%	10.10%	9.90%	0.80%		0.60%
M. montanus	8.50%	8.30%	8.60%	8.90%	9.00%	0.70%	4.70%	

Peromyscus	*Peromyscus* sp. nov.	*P. keeni*	*P. maniculatus* - East	*P. maniculatus* - West	*P. maniculatus* - Southwest	*P. leucopus*	*P. melanotis*
Peromyscus sp. nov.		0.50%	0.50%	0.50%	0.50%	0.90%	1.00%
P. keeni	3.60%		0.50%	0.50%	0.40%	0.80%	1.00%
P. maniculatus - East	4.00%	3.80%		0.40%	0.50%	9.20%	1.00%
P. maniculatus - West	3.50%	3.80%	3.20%		0.50%	9.90%	13.30%
P. maniculatus - Southwest	3.50%	2.30%	3.20%	3.10%		9.40%	12.70%
P. leucopus	10.70%	10.00%	0.80%	0.90%	0.90%		1.10%
P. melanotis	13.40%	13.30%	12.90%	1.00%	1.00%	14.00%	

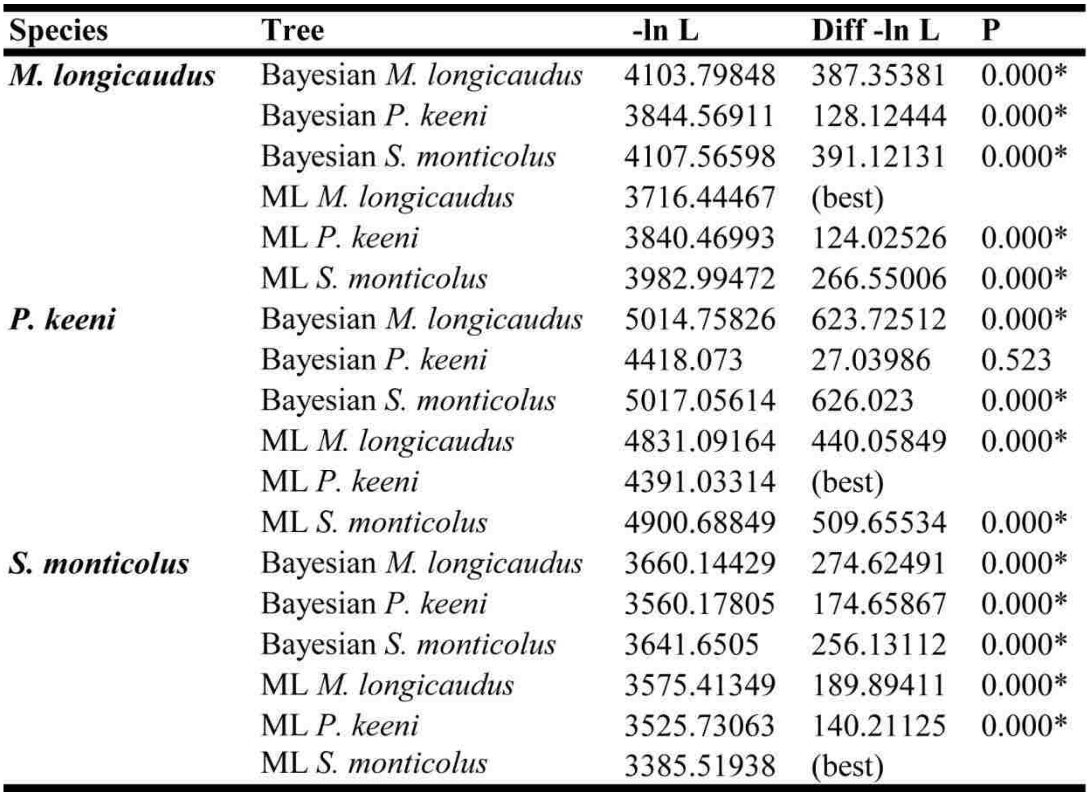
S. monticolus	Island	Northern	Southern	*S. cinereus*	*S. fumeus*	*S. vagrans*
Island		0.50%	0.60%	0.70%	0.80%	0.60%
Northern	4.80%		0.40%	0.70%	0.80%	0.60%
Southern	5.40%	1.70%		9.50%	8.90%	4.60%
S. cinereus	9.10%	8.80%	0.70%		0.70%	0.70%
S. fumeus	8.40%	9.00%	0.80%	8.40%		0.80%
S. vagrans	5.90%	5.30%	0.50%	8.30%	8.70%	

Table 6. Divergence date estimates for the island lineages of *M. longicaudus*, *P. keeni* and *S. monticolus* based on both cyt *b* and phased multi-locus analysis.



		cyt*b*			multilocus		
Species	**lineage**	**95% HPD lower**	**mean**	**95% HPD upper**	**95% HPD lower**	**mean**	**95% HPD upper**
M.longicaudus	Island	156,100	215,700	285,900			
	Northern/Island	296,500	402,000	516,400	12,240	15,600	19,640
Peromyscus	*P. keeni*	207,500	316,500	438,400	111,400	138,600	170,200
	Peromyscus sp. nov.	69,103	194,600	339,700	48,400	106,000	167,000
S. monticolus		475,900	756,400	1,037,400	104,900	193,800	286,400
	Island	72,200	114,400	166,300	38,500	62,000	92,500
	Southern	49,900	130,200	219,800	100	42,000	108,600

Table 7. Cyt *b* Shimodaira and Hasegawa tests for *M. longicaudus*, *P. keeni* and *S. monticolus* for both Bayesian and Maximum Likelihood trees. *=significant p-value at α≤0.05.



Species	**Tree**	**-ln L**	**Diff -ln L**	**P**
M. longicaudus	Bayesian *M. longicaudus*	4103.79848	387.35381	0.000*
	Bayesian *P. keeni*	3844.56911	128.12444	0.000*
	Bayesian *S. monticolus*	4107.56598	391.12131	0.000*
	ML *M. longicaudus*	3716.44467	(best)	
	ML *P. keeni*	3840.46993	124.02526	0.000*
	ML *S. monticolus*	3982.99472	266.55006	0.000*
P. keeni	Bayesian *M. longicaudus*	5014.75826	623.72512	0.000*
	Bayesian *P. keeni*	4418.073	27.03986	0.523
	Bayesian *S. monticolus*	5017.05614	626.023	0.000*
	ML *M. longicaudus*	4831.09164	440.05849	0.000*
	ML *P. keeni*	4391.03314	(best)	
	ML *S. monticolus*	4900.68849	509.65534	0.000*
S. monticolus	Bayesian *M. longicaudus*	3660.14429	274.62491	0.000*
	Bayesian *P. keeni*	3560.17805	174.65867	0.000*
	Bayesian *S. monticolus*	3641.6505	256.13112	0.000*
	ML *M. longicaudus*	3575.41349	189.89411	0.000*
	ML *P. keeni*	3525.73063	140.21125	0.000*
	ML *S. monticolus*	3385.51938	(best)	

Table 8. Regression analysis for *M. longicaudus*, *P. keeni* and *S. monticolus* cyt *b* genetic variation (*S*, *h*, *Hd* and *π*) tested against log island size and log isolation. Significant at α≤0.05 Holm-Bonferroni corrected p-values (p') are in bold.

Species	Topographical Feature	Genetic feature	adjusted R^2	df	ss	ms	f	p' value
M. longicaudus	area	*S*	0.437	1.000	197.510	197.510	14.204	**0.010**
		h	0.515	1.000	25.147	25.147	19.041	**0.004**
		Hd	0.441	1.000	0.645	0.645	14.387	**0.010**
		π	0.499	1.000	0.000	0.000	17.941	**0.004**
	isolation	*S*	0.175	1.000	93.729	93.729	4.596	0.143
		h	0.139	1.000	8.768	8.768	3.740	0.143
		Hd	0.098	1.000	0.205	0.205	2.837	0.143
		π	0.311	1.000	0.000	0.000	8.687	**0.038**
P. keeni	area	*S*	0.239	1.000	392.737	392.737	9.488	**0.034**
		h	0.135	1.000	31.571	31.571	5.225	0.153
		Hd	0.032	1.000	0.081	0.081	1.900	0.540
		π	0.125	1.000	0.000	0.000	4.869	0.153
	isolation	*S*	0.229	1.000	378.907	378.907	9.038	**0.035**
		h	0.384	1.000	76.714	76.714	17.814	**0.002**
		Hd	0.003	1.000	0.047	0.047	1.076	0.618
		π	0.000	1.000	0.000	0.000	1.011	0.618
S. monticolus	area	*S*	0.223	1.000	58.349	58.349	7.012	0.108
		h	0.084	1.000	8.250	8.250	2.919	0.412
		Hd	-0.042	1.000	0.012	0.012	0.162	1.000
		π	0.050	1.000	0.000	0.000	2.095	0.490
	isolation	*S*	0.238	1.000	61.744	61.744	7.575	0.098
		h	0.105	1.000	9.550	9.550	3.459	0.389
		Hd	-0.049	1.000	0.002	0.002	0.022	1.000
		π	0.121	1.000	0.000	0.000	3.893	0.375

Table 9. Between group net genetic divergences of cyt *b* among refugial and non-refugial Southeast Alaskan populations lineages of *M. longicaudus*, *P. keeni* and *S. monticolus*. The number of base differences per site from estimation of net average between groups of sequences is shown. Standard error estimate(s) are shown above the diagonal. All ambiguous positions were removed for each sequence pair. Evolutionary analyses were conducted in MEGA5.

M. longicaudus		non-refugia																	refugia	
		MLJNO	REV	MLHNS	MLS	MLSEC	MLSEN	MLGB	ORI	KRF	KSC	KUI	MIT	POW	WRG	ZRB	SWN	TXN	CRN	FST
non-refugia	MLJNO		0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.20%	0.30%	0.30%	0.30%
	REV	0.90%		0.20%	0.30%	0.20%	0.30%	0.30%	0.30%	0.20%	0.30%	0.20%	0.30%	0.20%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%
	MLHNS	0.30%	0.40%		0.20%	0.00%	0.10%	0.20%	0.10%	0.10%	0.00%	0.10%	0.00%	0.10%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%
	MLS	0.50%	0.80%	0.40%		0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%
	MLSEC	0.40%	0.50%	0.10%	0.50%		0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%
	MLSEN	0.60%	0.70%	0.20%	0.70%	0.40%		0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%
	MLGB	1.00%	1.30%	0.40%	0.70%	0.70%	0.80%		0.40%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.40%	0.40%	0.30%
	ORI	1.10%	1.20%	0.10%	0.50%	0.50%	0.40%	1.50%		0.30%	0.10%	0.20%	0.30%	0.20%	0.30%	0.30%	0.30%	0.30%	0.40%	0.30%
	KRF	0.50%	0.70%	0.00%	0.20%	0.30%	0.30%	0.80%	0.80%		0.20%	0.10%	0.20%	0.10%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%
	KSC	0.90%	1.00%	0.00%	0.30%	0.30%	0.20%	1.30%	0.20%	0.70%		0.20%	0.30%	0.10%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%
	KUI	0.40%	0.60%	0.00%	0.30%	0.20%	0.20%	0.80%	0.80%	0.20%	0.60%		0.20%	0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%
	MIT	0.60%	0.80%	0.00%	0.40%	0.30%	0.30%	1.00%	1.00%	0.40%	0.80%	0.40%		0.10%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%
	POW	0.40%	0.70%	0.00%	0.40%	0.30%	0.30%	0.90%	0.60%	0.30%	0.50%	0.30%	0.40%		0.20%	0.20%	0.20%	0.10%	0.20%	0.20%
	WRG	0.90%	1.00%	0.60%	1.00%	0.80%	0.90%	1.30%	1.30%	0.70%	1.00%	0.60%	0.80%	0.80%		0.20%	0.30%	0.30%	0.30%	0.30%
	ZRB	0.70%	0.80%	0.20%	0.60%	0.40%	0.50%	1.10%	1.00%	0.50%	0.90%	0.30%	0.60%	0.50%	0.70%		0.30%	0.30%	0.30%	0.20%
	SWN	0.70%	0.90%	0.10%	0.50%	0.40%	0.40%	1.10%	1.00%	0.50%	0.90%	0.40%	0.60%	0.50%	0.90%	0.70%		0.30%	0.30%	0.30%
	TXN	1.00%	1.30%	0.50%	0.90%	0.80%	0.80%	1.60%	1.50%	0.90%	1.30%	0.80%	1.00%	0.40%	1.30%	1.10%	1.10%		0.30%	0.30%
	YTS	1.00%	1.00%	0.40%	0.80%	0.70%	0.50%	1.40%	1.30%	0.80%	1.10%	0.70%	0.70%	0.80%	1.00%	0.90%	1.00%	1.40%	1.40%	1.20%
refugia	CRN	1.00%	1.20%	0.50%	0.90%	0.80%	0.80%	1.40%	1.50%	0.80%	1.20%	0.80%	1.00%	0.70%	1.30%	1.10%	1.10%	1.20%		0.30%
	FST	0.80%	1.10%	0.40%	0.80%	0.60%	0.70%	1.30%	1.10%	0.70%	1.00%	0.60%	0.80%	0.70%	1.20%	0.90%	0.90%	1.20%	1.10%	
	CGF	0.50%	0.70%	0.10%	0.50%	0.20%	0.40%	0.80%	0.60%	0.30%	0.50%	0.20%	0.30%	0.30%	0.70%	0.40%	0.40%	0.80%	0.80%	0.70%
	DAL	0.60%	0.80%	0.10%	0.50%	0.20%	0.40%	1.10%	0.90%	0.40%	0.70%	0.40%	0.60%	0.40%	0.80%	0.60%	0.60%	1.00%	1.00%	0.80%
	LUL	0.60%	0.70%	0.20%	0.60%	0.30%	0.40%	0.80%	0.60%	0.30%	0.40%	0.20%	0.30%	0.30%	0.80%	0.40%	0.40%	0.80%	0.80%	0.70%
	NYS	0.60%	0.60%	0.20%	0.50%	0.40%	0.50%	1.00%	0.80%	0.40%	0.60%	0.30%	0.40%	0.40%	0.80%	0.50%	0.60%	1.00%	0.80%	0.70%
	SMZ	0.70%	0.80%	0.30%	0.60%	0.40%	0.50%	1.10%	0.90%	0.50%	0.70%	0.40%	0.60%	0.50%	0.90%	0.60%	0.70%	1.10%	0.90%	0.90%
	WRN	0.50%	0.60%	0.20%	0.50%	0.20%	0.40%	0.90%	0.80%	0.30%	0.60%	0.30%	0.40%	0.30%	0.60%	0.30%	0.50%	0.90%	0.90%	0.70%

CGF	DAL	LUL	NYS	SMZ	WRN	YTS	MLJNO	non-refugia
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	REV	
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	MLHNS	
0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	MLS	
0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.30%	MLSEC	
0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	MLSEN	
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	MLGB	
0.20%	0.30%	0.20%	0.30%	0.30%	0.30%	0.30%	ORI	
0.20%	0.30%	0.20%	0.20%	0.30%	0.20%	0.30%	KRF	
0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	KSC	
0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.30%	KUI	
0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	MIT	
0.10%	0.20%	0.10%	0.20%	0.20%	0.20%	0.30%	POW	
0.10%	0.20%	0.20%	0.10%	0.20%	0.10%	0.20%	WRG	
0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	ZRB	
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	SWN	
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	TXN	
0.20%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	YTS	
0.70%	0.90%	0.70%	0.80%	0.90%	0.70%		CRN	refugia
0.20%	0.30%	0.20%	0.20%	0.30%	0.20%	0.30%	FST	
0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.30%	CGF	
	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	DAL	
0.30%		0.20%	0.20%	0.20%	0.20%	0.30%	LUL	
0.30%	0.40%		0.20%	0.20%	0.20%	0.20%	NYS	
0.40%	0.50%	0.40%		0.20%	0.20%	0.20%	SMZ	
0.40%	0.60%	0.50%	0.60%		0.20%	0.30%	WRN	
0.30%	0.40%	0.40%	0.40%	0.50%		0.20%		

P. keeni		non-refugia																		
		BCC	BCN	BCS	HTS	ADM	MLJNO	GRV	MLCP	MLMFD	REV	MLHNS	MLKLU	MLSEC	MLSKW	MLWP	MRY	MLGB	ETN	KRF
non-refugia	BCC		0.00%	0.20%	0.30%	0.20%	0.00%	0.00%	0.00%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.20%	0.00%	0.00%
	BCN	0.00%		0.20%	0.20%	0.20%	0.00%	0.20%	0.00%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.20%	0.00%	0.10%
	BCS	0.30%	0.40%		0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.30%	0.30%	0.20%	0.20%
	HTS	0.90%	0.90%	1.30%		0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.20%	0.30%
	ADM	0.50%	0.50%	0.90%	0.90%		0.20%	0.30%	0.20%	0.30%	0.20%	0.10%	0.20%	0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%
	MLJNO	0.00%	0.00%	0.50%	0.90%	0.50%		0.20%	0.00%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.20%	0.00%	0.10%
	GRV	0.00%	0.60%	0.60%	1.40%	1.00%	0.60%		0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.30%	0.30%	0.20%	0.20%
	MLCP	0.00%	0.00%	0.50%	1.00%	0.50%	0.10%	0.50%		0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.20%	0.00%	0.10%
	MLMFD	0.30%	0.30%	0.80%	1.30%	0.80%	0.40%	0.90%	0.10%		0.20%	0.20%	0.20%	0.10%	0.30%	0.20%	0.30%	0.30%	0.10%	0.20%
	REV	0.20%	0.30%	0.70%	1.20%	0.70%	0.20%	0.80%	0.30%	0.60%		0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%
	MLHNS	0.10%	0.20%	0.50%	0.70%	0.30%	0.20%	0.60%	0.20%	0.50%	0.40%		0.00%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.10%
	MLKLU	0.30%	0.40%	0.70%	1.10%	0.70%	0.40%	0.70%	0.30%	0.70%	0.60%	0.10%		0.10%	0.10%	0.20%	0.30%	0.20%	0.10%	0.20%
	MLSEC	0.00%	0.10%	0.30%	1.00%	0.50%	0.10%	0.40%	0.10%	0.30%	0.30%	0.20%	0.40%		0.20%	0.10%	0.20%	0.20%	0.10%	0.10%
	MLSKW	0.60%	0.70%	1.00%	1.60%	1.10%	0.70%	1.00%	0.60%	1.00%	0.90%	0.40%	0.20%	0.70%		0.20%	0.30%	0.20%	0.20%	0.20%
	MLWP	0.10%	0.20%	0.60%	1.10%	0.70%	0.20%	0.70%	0.20%	0.50%	0.40%	0.30%	0.50%	0.20%	0.80%		0.20%	0.20%	0.10%	0.20%
	MRY	0.50%	0.60%	1.00%	1.40%	1.00%	0.60%	1.10%	0.60%	0.90%	0.60%	0.70%	0.90%	0.60%	1.20%	0.70%		0.30%	0.20%	0.20%
	MLGB	0.30%	0.40%	0.80%	1.30%	0.80%	0.40%	0.90%	0.40%	0.70%	0.60%	0.30%	0.40%	0.40%	0.60%	0.50%	0.90%		0.20%	0.20%
	ETN	0.00%	0.00%	0.40%	0.90%	0.50%	0.00%	0.50%	0.00%	0.30%	0.20%	0.20%	0.30%	0.10%	0.60%	0.10%	0.50%	0.30%		0.10%
	KRF	0.10%	0.20%	0.40%	1.10%	0.60%	0.20%	0.50%	0.20%	0.50%	0.40%	0.30%	0.50%	0.10%	0.60%	0.30%	0.70%	0.50%	0.20%	
	KSC	0.10%	0.00%	0.60%	1.00%	0.70%	0.20%	0.70%	0.20%	0.30%	0.40%	0.30%	0.50%	0.20%	0.80%	0.40%	0.70%	0.50%	0.20%	0.30%
	KUI	0.40%	0.40%	0.80%	1.20%	0.90%	0.40%	0.90%	0.40%	0.80%	0.60%	0.60%	0.70%	0.50%	1.00%	0.60%	0.80%	0.80%	0.40%	0.60%
	MIT	0.10%	0.20%	0.50%	1.00%	0.60%	0.20%	0.70%	0.20%	0.50%	0.30%	0.30%	0.50%	0.20%	0.80%	0.30%	0.70%	0.50%	0.10%	0.30%
	MLFB	0.50%	0.60%	0.90%	1.50%	1.00%	0.60%	1.10%	0.60%	0.90%	0.50%	0.70%	0.90%	0.60%	1.20%	0.60%	0.00%	0.90%	0.50%	0.70%
	POW	0.10%	0.10%	0.50%	0.90%	0.60%	0.10%	0.70%	0.20%	0.50%	0.30%	0.20%	0.50%	0.20%	0.80%	0.20%	0.70%	0.50%	0.10%	0.30%
	SNF	0.20%	0.20%	0.60%	1.10%	0.70%	0.20%	0.70%	0.20%	0.50%	0.40%	0.30%	0.50%	0.20%	0.80%	0.40%	0.70%	0.50%	0.10%	0.30%
	WRG	0.10%	0.10%	0.50%	0.90%	0.50%	0.10%	0.60%	0.10%	0.40%	0.30%	0.20%	0.40%	0.10%	0.70%	0.30%	0.60%	0.40%	0.10%	0.20%
	ZRB	0.40%	0.50%	0.80%	1.20%	0.80%	0.40%	0.90%	0.50%	0.80%	0.70%	0.50%	0.80%	0.30%	1.10%	0.60%	1.00%	0.80%	0.40%	0.60%
	RMS	0.60%	0.70%	1.00%	1.10%	0.60%	0.70%	1.00%	0.70%	0.90%	0.90%	0.50%	0.90%	0.70%	1.30%	0.90%	1.20%	1.00%	0.70%	0.80%
	VCR	0.50%	0.70%	0.90%	1.20%	0.70%	0.70%	1.20%	0.70%	0.90%	0.70%	0.50%	0.80%	0.60%	1.20%	0.70%	1.20%	1.00%	0.60%	0.70%
	WA	0.60%	0.60%	1.10%	1.30%	0.70%	0.60%	1.10%	0.70%	1.00%	0.80%	0.60%	0.90%	0.60%	1.30%	0.80%	1.10%	1.00%	0.60%	0.70%
	YTS	0.30%	0.30%	0.80%	1.10%	0.80%	0.40%	0.90%	0.40%	0.70%	0.60%	0.50%	0.70%	0.40%	1.00%	0.20%	0.90%	0.70%	0.30%	0.50%
refugia	CRN	0.20%	0.20%	0.60%	1.10%	0.70%	0.20%	0.70%	0.20%	0.50%	0.40%	0.30%	0.50%	0.20%	0.80%	0.40%	0.70%	0.50%	0.10%	0.30%
	FST	0.20%	0.20%	0.60%	1.10%	0.70%	0.20%	0.70%	0.20%	0.50%	0.40%	0.30%	0.50%	0.20%	0.80%	0.30%	0.70%	0.50%	0.10%	0.30%
	BNF	0.60%	0.60%	1.00%	1.00%	0.20%	0.60%	1.10%	0.70%	0.90%	0.80%	0.40%	0.80%	0.70%	1.20%	0.80%	1.10%	1.00%	0.60%	0.70%
	CGF	0.40%	0.40%	0.90%	0.80%	0.10%	0.50%	1.00%	0.50%	0.70%	0.70%	0.20%	0.70%	0.50%	1.10%	0.70%	1.00%	0.80%	0.40%	0.60%
	BKR	0.10%	0.10%	0.50%	0.90%	0.50%	0.10%	0.60%	0.20%	0.50%	0.40%	0.20%	0.40%	0.20%	0.70%	0.30%	0.60%	0.50%	0.10%	0.30%
	DAL	0.20%	0.20%	0.60%	1.10%	0.70%	0.20%	0.70%	0.30%	0.60%	0.40%	0.40%	0.50%	0.30%	0.80%	0.30%	0.70%	0.60%	0.20%	0.40%
	HEC	0.20%	0.40%	0.60%	1.30%	0.80%	0.40%	0.70%	0.30%	0.50%	0.60%	0.50%	0.70%	0.20%	1.00%	0.50%	0.90%	0.70%	0.30%	0.30%
	LUL	0.40%	0.40%	0.80%	1.30%	0.80%	0.40%	0.90%	0.40%	0.70%	0.60%	0.50%	0.70%	0.40%	1.00%	0.50%	0.90%	0.70%	0.30%	0.50%
	NYS	0.20%	0.30%	0.70%	1.20%	0.70%	0.30%	0.60%	0.20%	0.60%	0.50%	0.30%	0.50%	0.40%	0.60%	0.40%	0.80%	0.60%	0.30%	0.40%
	SMZ	0.00%	0.10%	0.40%	0.90%	0.60%	0.10%	0.50%	0.10%	0.40%	0.30%	0.20%	0.40%	0.10%	0.70%	0.20%	0.60%	0.40%	0.00%	0.10%
	WRN	0.40%	0.40%	0.80%	1.10%	0.90%	0.40%	0.90%	0.50%	0.70%	0.60%	0.50%	0.70%	0.50%	1.00%	0.60%	0.90%	0.70%	0.40%	0.60%

											refugia													
KSC	KUI	MIT	MLFB	POW	SNF	WRG	ZRB	RMS	VCR	WA	CRN	FST	BNF	CGF	BKR	DAL	yesHEC	yesLUL	yesNYS	yesSMZ	yesWRN	YTS	BCC	non-refugia
0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	BCN	
0.00%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.00%	0.20%	0.20%	BCS	
0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	HTS	
0.30%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	ADM	
0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	MLJNO	
0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.00%	0.20%	0.20%	GRV	
0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	MLCP	
0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	MLMFD	
0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	REV	
0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	MLHNS	
0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	MLKLU	
0.20%	0.20%	0.20%	0.30%	0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	MLSEC	
0.20%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.10%	0.20%	0.20%	MLSKW	
0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	MLWP	
0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.10%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.10%	MRY	
0.30%	0.30%	0.20%	0.00%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	MLGB	
0.20%	0.30%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	ETN	
0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.00%	0.20%	0.20%	KRF	
0.20%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	KSC	
	0.20%	0.20%	0.30%	0.10%	0.10%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	KUI	
0.60%		0.20%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	0.20%	0.10%	0.20%	0.30%	MIT	
0.30%	0.50%		0.20%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	MLFB	
0.70%	0.90%	0.60%		0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	POW	
0.30%	0.50%	0.30%	0.60%		0.00%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	SNF	
0.40%	0.60%	0.30%	0.70%	0.00%		0.10%	0.20%	0.20%	0.30%	0.30%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	WRG	
0.30%	0.50%	0.20%	0.60%	0.20%	0.30%		0.20%	0.20%	0.30%	0.20%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	ZRB	
0.60%	0.90%	0.50%	1.00%	0.50%	0.60%	0.30%		0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	RMS	
0.70%	1.10%	0.80%	1.20%	0.70%	0.80%	0.80%	0.80%		0.20%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	VCR	
0.80%	0.80%	0.60%	1.00%	0.60%	0.80%	0.70%	0.80%	0.80%		0.30%	0.30%	0.30%	0.20%	0.20%	0.20%	0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	WA	
0.70%	0.80%	0.80%	1.10%	0.70%	0.80%	0.70%	1.00%	1.00%	0.80%		0.30%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.20%	0.30%	0.30%	YTS	
0.50%	0.80%	0.50%	0.90%	0.40%	0.50%	0.40%	0.80%	0.90%	0.90%	1.00%	0.50%	0.50%	1.00%	0.80%	0.50%	0.60%	0.70%	0.70%	0.60%	0.40%	0.50%		CRN	refugia
0.40%	0.60%	0.30%	0.70%	0.30%	0.30%	0.30%	0.50%	0.90%	0.80%	0.80%		0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	FST	
0.40%	0.60%	0.30%	0.70%	0.30%	0.30%	0.30%	0.60%	0.80%	0.80%	0.80%	0.40%		0.20%	0.20%	0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	BNF	
0.80%	1.00%	0.70%	1.10%	0.60%	0.80%	0.60%	0.80%	0.60%	0.80%	0.90%	0.80%	0.80%		0.10%	0.20%	0.20%	0.30%	0.30%	0.20%	0.20%	0.30%	0.30%	CGF	
0.60%	0.90%	0.60%	1.00%	0.60%	0.60%	0.50%	0.80%	0.60%	0.70%	0.80%	0.60%	0.60%	0.20%		0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	0.30%	0.30%	BKR	
0.30%	0.40%	0.20%	0.60%	0.20%	0.30%	0.20%	0.30%	0.60%	0.50%	0.60%	0.30%	0.30%	0.50%	0.50%		0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	DAL	
0.40%	0.60%	0.40%	0.70%	0.30%	0.40%	0.30%	0.70%	0.90%	0.70%	0.80%	0.40%	0.40%	0.80%	0.70%	0.30%		0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	HEC	
0.50%	0.80%	0.50%	0.90%	0.50%	0.50%	0.40%	0.70%	0.90%	0.90%	1.00%	0.50%	0.50%	1.00%	0.70%	0.50%	0.60%		0.20%	0.20%	0.20%	0.30%	0.30%	LUL	
0.50%	0.80%	0.50%	0.90%	0.10%	0.10%	0.40%	0.80%	1.00%	1.00%	1.00%	0.50%	0.50%	0.90%	0.80%	0.50%	0.60%	0.70%		0.20%	0.10%	0.10%	0.20%	NYS	
0.50%	0.70%	0.40%	0.80%	0.30%	0.30%	0.40%	0.70%	0.90%	0.80%	0.90%	0.50%	0.50%	0.80%	0.70%	0.40%	0.50%	0.60%	0.50%		0.10%	0.20%	0.20%	SMZ	
0.20%	0.40%	0.20%	0.60%	0.10%	0.20%	0.20%	0.50%	0.70%	0.50%	0.60%	0.20%	0.20%	0.60%	0.50%	0.20%	0.30%	0.30%	0.30%	0.20%		0.20%	0.20%	WRN	
0.60%	0.80%	0.50%	0.90%	0.10%	0.20%	0.50%	0.80%	1.00%	1.00%	0.90%	0.60%	0.60%	1.00%	0.80%	0.50%	0.60%	0.80%	0.20%	0.50%	0.30%		0.20%		

S. monticolus		non-refugia																		
		BCC	BSF	GRM	ADM	MLJNO	GRV	MLCP	MLMFD	REV	MLSEC	MLSES	MRB	MLGB	ETN	KRF	KSC	KUI	MIT	MLFB
non-refugia	BCC		0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%
	BSF	0.20%		0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%
	GRM	0.10%	0.10%		0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.20%	0.20%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	ADM	0.20%	0.20%	0.10%		0.00%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%
	MLJNO	0.20%	0.20%	0.10%	0.00%		0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.10%	0.10%	0.10%
	GRV	0.10%	0.10%	0.00%	0.10%	0.10%		0.00%	0.00%	0.10%	0.00%	0.00%	0.20%	0.10%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	MLCP	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%		0.00%	0.10%	0.00%	0.00%	0.20%	0.10%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	MLMFD	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%		0.10%	0.00%	0.00%	0.20%	0.20%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	REV	0.10%	0.20%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%		0.10%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%
	MLSEC	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%		0.00%	0.20%	0.20%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	MLSES	0.00%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%		0.20%	0.20%	0.10%	0.10%	0.10%	0.00%	0.00%	0.00%
	MRB	0.30%	0.40%	0.30%	0.40%	0.40%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%		0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%
	MLGB	0.30%	0.40%	0.20%	0.40%	0.40%	0.20%	0.20%	0.30%	0.30%	0.30%	0.30%	0.50%		0.20%	0.10%	0.20%	0.20%	0.20%	0.20%
	ETN	0.20%	0.30%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.40%	0.40%		0.10%	0.20%	0.10%	0.10%	0.10%
	KRF	0.10%	0.20%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.30%	0.10%	0.20%		0.10%	0.10%	0.10%	0.10%
	KSC	0.20%	0.30%	0.20%	0.30%	0.30%	0.20%	0.20%	0.20%	0.20%	0.20%	0.10%	0.40%	0.30%	0.40%	0.20%		0.10%	0.10%	0.10%
	KUI	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.10%	0.00%	0.10%	0.00%	0.00%	0.30%	0.20%	0.20%	0.10%	0.20%		0.00%	0.00%
	MIT	0.10%	0.10%	0.00%	0.10%	0.20%	0.00%	0.10%	0.10%	0.10%	0.10%	0.10%	0.30%	0.30%	0.20%	0.10%	0.10%	0.10%		0.00%
	MLFB	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.30%	0.20%	0.20%	0.10%	0.20%	0.00%	0.00%	
	POW	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.30%	0.20%	0.20%	0.10%	0.10%	0.00%	0.00%	0.00%
	SNF	0.40%	0.50%	0.40%	0.50%	0.60%	0.40%	0.50%	0.40%	0.50%	0.40%	0.40%	0.70%	0.40%	0.60%	0.40%	0.50%	0.50%	0.30%	0.50%
	WRG	0.50%	0.50%	0.40%	0.50%	0.50%	0.50%	0.50%	0.50%	0.50%	0.40%	0.30%	0.70%	0.60%	0.60%	0.50%	0.60%	0.50%	0.50%	0.40%
	ZRB	0.10%	0.20%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.40%	0.30%	0.30%	0.10%	0.10%	0.10%	0.10%	0.10%
	WA	0.00%	0.10%	-0.10%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.20%	0.30%	0.10%	0.00%	0.00%	-0.10%	0.00%	0.00%
refugia	CRN	0.10%	0.20%	0.10%	0.20%	0.20%	0.00%	0.00%	0.00%	0.10%	0.10%	0.10%	0.30%	0.30%	0.20%	0.00%	0.20%	0.10%	0.10%	0.00%
	FST	0.40%	0.40%	0.30%	0.20%	0.20%	0.30%	0.30%	0.30%	0.40%	0.30%	0.30%	0.50%	0.60%	0.50%	0.40%	0.30%	0.30%	0.30%	0.30%
	BKR	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.10%	0.00%	0.10%	0.00%	0.00%	0.30%	0.30%	0.20%	0.10%	0.20%	0.00%	0.10%	0.00%
	DAL	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.10%	0.00%	0.10%	0.00%	0.00%	0.30%	0.30%	0.20%	0.10%	0.10%	0.00%	0.00%	0.00%
	HEC	0.20%	0.40%	0.30%	0.40%	0.40%	0.30%	0.30%	0.30%	0.30%	0.30%	0.30%	0.50%	0.50%	0.40%	0.30%	0.40%	0.30%	0.30%	0.30%
	LUL	0.10%	0.20%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.00%	0.10%	0.40%	0.30%	0.30%	0.10%	0.30%	0.10%	0.10%	0.10%
	NYS	0.40%	0.50%	0.30%	0.50%	0.50%	0.40%	0.40%	0.40%	0.40%	0.40%	0.30%	0.60%	0.50%	0.50%	0.40%	0.50%	0.30%	0.30%	0.40%
	SMZ	0.10%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.30%	0.30%	0.20%	0.10%	0.20%	0.00%	0.10%	0.00%
	WRN	0.10%	0.20%	0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.40%	0.30%	0.30%	0.10%	0.30%	0.10%	0.10%	0.00%

					refugia										
POW	SNF	WRG	ZRB	WA	CRN	FST	BKR	DAL	HEC	LUL	NYS	SMZ	WRN	BCC	non-refugia
0.10%	0.10%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	BSF	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	GRM	
0.00%	0.20%	0.20%	0.10%	0.00%	0.10%	0.20%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	ADM	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	MLJNO	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	GRV	
0.00%	0.20%	0.20%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	MLCP	
0.00%	0.20%	0.20%	0.10%	0.10%	0.10%	0.10%	0.00%	0.00%	0.10%	0.10%	0.10%	0.00%	0.10%	MLMFD	
0.00%	0.20%	0.20%	0.10%	0.00%	0.00%	0.20%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	REV	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	MLSEC	
0.00%	0.20%	0.20%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	MLSES	
0.00%	0.20%	0.20%	0.10%	0.00%	0.10%	0.20%	0.00%	0.00%	0.10%	0.10%	0.20%	0.00%	0.10%	MRB	
0.20%	0.20%	0.30%	0.20%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	0.20%	0.20%	0.20%	MLGB	
0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	ETN	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	KRF	
0.10%	0.20%	0.20%	0.10%	0.10%	0.10%	0.20%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	KSC	
0.10%	0.20%	0.20%	0.10%	0.00%	0.10%	0.20%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.20%	KUI	
0.00%	0.20%	0.20%	0.10%	0.00%	0.10%	0.10%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	MIT	
0.00%	0.10%	0.20%	0.00%	0.00%	0.10%	0.20%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	MLFB	
0.00%	0.20%	0.20%	0.10%	0.00%	0.00%	0.10%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.00%	POW	
	0.20%	0.20%	0.10%	0.00%	0.10%	0.20%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	SNF	
0.40%		0.30%	0.10%	0.10%	0.20%	0.20%	0.20%	0.10%	0.20%	0.20%	0.30%	0.20%	0.20%	WRG	
0.40%	0.90%		0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.20%	0.30%	0.20%	0.20%	ZRB	
0.10%	0.40%	0.50%		0.10%	0.10%	0.20%	0.10%	0.00%	0.20%	0.10%	0.20%	0.10%	0.10%	WA	
-0.10%	0.10%	0.30%	0.00%		0.10%	0.20%	0.00%	0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	CRN	refugia
0.10%	0.30%	0.50%	0.10%	0.10%		0.20%	0.10%	0.10%	0.20%	0.10%	0.20%	0.10%	0.10%	FST	
0.30%	0.60%	0.70%	0.40%	0.30%	0.40%		0.10%	0.20%	0.20%	0.20%	0.20%	0.10%	0.20%	BKR	
0.00%	0.50%	0.40%	0.10%	0.00%	0.10%	0.30%		0.00%	0.20%	0.10%	0.20%	0.00%	0.10%	DAL	
0.00%	0.30%	0.40%	0.10%	0.00%	0.10%	0.30%	0.00%		0.20%	0.10%	0.20%	0.00%	0.10%	HEC	
0.30%	0.70%	0.70%	0.40%	0.30%	0.30%	0.60%	0.30%	0.30%		0.20%	0.20%	0.20%	0.20%	LUL	
0.10%	0.50%	0.50%	0.20%	0.00%	0.10%	0.40%	0.10%	0.10%	0.30%		0.20%	0.10%	0.10%	NYS	
0.40%	0.80%	0.80%	0.40%	0.20%	0.30%	0.40%	0.40%	0.30%	0.60%	0.40%		0.10%	0.20%	SMZ	
0.00%	0.50%	0.40%	0.10%	0.00%	0.10%	0.20%	0.00%	0.00%	0.30%	0.10%	0.30%		0.10%	WRN	
0.10%	0.50%	0.50%	0.20%	0.00%	0.10%	0.40%	0.10%	0.10%	0.40%	0.20%	0.40%	0.10%			

CHAPTER 5

Conclusion

Glacial-interglacial oscillation over the past 2.5 million years has promoted both speciation and intraspecies diversification. Species range, geographic features (e.g., mountains, fragmented habitat), and historical climate all play a part in contemporary population dynamics. Segregation of conspecific populations as a result of historic climatic fluctuations, and enhanced by geographic barriers, results in local adaptation which further promotes diversification upon post-glacial contact (Demboski & Cook 2001; Galbreath *et al.* 2009). Contact of divergent lineages in high latitudes is a rarity and often goes undocumented. Likewise, complex interplay of varying degrees of connectivity across such islands can result in endemic lineages.

With the use of genetics and GIS techniques, it is possible to tease apart species history leading to diversification and often uncover previously unrecognized variation or endemics (Lucid & Cook 2007; Weksler *et al.* 2010). Non-refugial populations generally show signs of rapid expansion with reduced genetic variation and minimal diversification when compared to refugial populations (Hewitt 2004; Lessa *et al.* 2003; Marr *et al.* 2012). Genetic differences across island inhabitants, with limited connectivity and smaller effective population sizes can be a result of either cryptic refugia or rapid genetic drift (Adler 1992; Dobzhansky 1963; Whittaker 1998), either resulting in high levels of endemism.

Previous work on *Microtus longicaudus*, *Peromyscus keeni* and *Sorex monticolus* was based on a single mitochondrial maker and focused on describing observed phylogeographic variation, rather than identifying the drivers of said variation.

Additionally, sampling was limited in scope for both across the entire range of each species and within Southeast Alaska. My dissertation work used this foundational research as a basis for hypothesis testing and the identification of evolutionary drivers of diversification in these three small mammals. Chapters 2 and 3 highlight the complexity and identify idiosyncratic responses to glacial variation and subsequent colonization and contact. Chapter 4 highlights the interwoven relationship between physical island characteristics and past flux of connectivity.

Although chapter 2 found “typical” post-glacial colonization patterns in *M. longicaudus* across western North America with regards to southern genetic diversity, northern genetic diversity, the number of refugia, and location of secondary contact were far from ordinary. Pleistocene climate variability was the primary driver of the observed variation; however geographic features, such as mountain ranges, played a significant role in colonization pathways and current lineage range limitations. Through the use of SDMs, genetic diversity, signals of demographic change, and phylogeographic relationships, four major locations were identified for glacial persistence of *M. longicaudus*: 1) southern continental, 2) southern coastal, 3) northern coastal refugia in Southeast Alaska, and 4) Beringia in south-central Yukon. Most major lineage diversification began prior to the last interglacial. The Northern and Island lineages, although distinctive based on mtDNA, share nuclear alleles as a result of incomplete lineage sorting, rather than introgression, hybridization or current gene flow.

Global discovery rates of non-marine mammals are estimated at about 10%, with only one species between 1993 and 2009 in high latitudes (Ceballos & Ehrlich 2009). Chapter 3 found strong genetic support for the formal description of a new *Peromyscus* in central and southern Yukon (revision in preparation). Additionally, this species appears to have persisted in cryptic northern refugia and remains geographically limited, with geographic proximity to its congeners, *P. keeni*, which occupied coastal refugia throughout the glacial cycles of the Pleistocene, and *P. maniculatus* from western North America. The persistence of *Peromyscus* in unglaciated regions south and north of the ice and in northern coastal refugia is highly uncommon, especially for North America restricted taxa.

The signatures of northern coastal refugia was explored in chapter 4. Disentangling confounding signals of coastal refugia and island biogeographic patters proved challenging, but *M. longicaudus*, *P. keeni* and *S. monticolus* have endemic lineages in the Alexander Archipelago, regardless of the driving force. The dynamics of this high latitude island system emphasize the importance of understanding both individual species response and community composition prior to implementing regional management plans. Life history characteristics, intraspecific genetic variation and gene flow, and SDMs each provide independent lines of evidence as to the effects of historical climate and island connectivity for each species across this fragmented habitat. Predictions of future climate change coupled with current levels of endemism and migration provide a starting point for defensive management of such a unique system as the Tongass National Forest.

The questions now become: What are the dynamics among other populations of *M. longicaudus* that have experienced post-glacial secondary contact? And, how does that contribute to our understanding of southern refugial taxa? What do bacular and karyotypic analysis suggest about the Yukon *Peromyscus*? And, what are the population level dynamics among the paraphyletic lineages of *P. maniculatus*? Across the Alexander Archipelago, what major biogeographic breaks can be identified using multilocus data? Finally, can population level markers (e.g., microsatellites, SNP analyses) more specifically identify refugial locations? More generally, we can also revisit our methods for subspecies identification to better reflect species history, rather than single gene or phenotypic patterns.

Climate change and conservation are terms that have gained momentum over the last few decades, but for good reason. Effects of anthropogenic habitat modification and shifting climate patterns can already be observed in many taxa, bringing the need for predictive and flexible conservation strategies to the forefront of biology. Understanding how and where a species or lineage came from can help us determine where it might go. Through the unification of fields both within biology (e.g., molecular techniques, ecological studies) and independently (e.g., computer science, economics), we can be better equipped to handle the uncertainty that lies ahead.

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