

Phylogeographic structure in long-tailed voles (*Rodentia: Arvicolinae*) belies the complex Pleistocene history of isolation, divergence, and recolonization of Northwest North America's fauna

Yadéeh E. Sawyer & Joseph A. Cook

Department of Biology and Museum of Southwestern Biology, University of New Mexico, MSC03 2020, Albuquerque, New Mexico 87131-0001

Keywords

Microtus longicaudus, multilocus, Pacific Northwest, species distribution models, vole.

Correspondence

Yadéeh E. Sawyer, Department of Biology and Museum of Southwestern Biology, University of New Mexico, MSC03 2020, Albuquerque, NM 87131-0001.
Tel: +(505) 277 1358;
Fax: +1 (505) 277 0304;
E-mail: yadeehsawyer@gmail.com

Funding Information

Office of Graduate Studies, UNM, T&E Inc, National Science Foundation (Grant/Award Number: "DEB0731350", "DEB1258010") American Society of Mammalogists, USDA Forest Service (Tongass National Forest and PNW Forest Sciences Lab), Sitka Sound Science Center, Hertel and Gaudin families, UNM Graduate and Professional Student Association, Biology Graduate Student Association, UNM, Biology Department, UNM.

Received: 26 July 2016; Accepted: 1 August 2016

Ecology and Evolution 2016; **6**(18): 6633–6647

doi: 10.1002/ece3.2393

Introduction

Pleistocene glacial–interglacial cycles repeatedly affected divergence and speciation processes at high latitudes in both the Northern (Koch et al. 2006; Lee-Yaw et al. 2007; Godbout et al. 2008) and Southern Hemispheres (Lessa et al. 2010). In North America, the Laurentide and Cordilleran ice sheets extended far south during glacial phases (Dyke and Prest 1987; Roberts 1991; Carrara et al. 2007), resulting in major distributional changes in temperate

Abstract

Quaternary climate fluctuations restructured biodiversity across North American high latitudes through repeated episodes of range contraction, population isolation and divergence, and subsequent expansion. Identifying how species responded to changing environmental conditions not only allows us to explore the mode and tempo of evolution in northern taxa, but also provides a basis for forecasting future biotic response across the highly variable topography of western North America. Using a multilocus approach under a Bayesian coalescent framework, we investigated the phylogeography of a wide-ranging mammal, the long-tailed vole, *Microtus longicaudus*. We focused on populations along the North Pacific Coast to refine our understanding of diversification by exploring the potentially compounding roles of multiple glacial refugia and more recent fragmentation of an extensive coastal archipelago. Through a combination of genetic data and species distribution models (SDMs), we found that historical climate variability influenced contemporary genetic structure, with multiple isolated locations of persistence (refugia) producing multiple divergent lineages (Beringian or northern, southeast Alaska or coastal, and southern or continental) during glacial advances. These vole lineages all occur along the North Pacific Coast where the confluence of numerous independent lineages in other species has produced overlapping zones of secondary contact, collectively a suture zone. Finally, we detected high levels of neoendemism due to complex island geography that developed in the last 10,000 years with the rising sea levels of the Holocene.

and arctic species (Lyons 2003). As glaciers receded, deglaciated areas were recolonized by populations from refugia (Pielou 1991) and contemporary DNA footprints allow us to decipher the complex history of species movements following deglaciation (Hayes and Harrison 1992; Hewitt 2004; Marr et al. 2012). Populations that colonized de-glaciated regions have signatures of rapid population expansion (Hundertmark et al. 2002; Lessa et al. 2003; Walker et al. 2009), while refugial populations often reflect long-term stability (Rand 1954; Shafer et al. 2010;

Stewart et al. 2010). Reconstructing recolonization patterns, however, can be problematic (Godbout et al. 2008), especially in topographically complex regions or when sampling is limited, because of the potential for cryptic (unsampled) refugia (Shafer et al. 2010), distinctive modes of expansion (e.g., phalanx and pioneer-type expansion, Hewitt 1996, 2000), and even selective sweeps when inference is based on a single gene (Excoffier et al. 2009). Furthermore, genetic variation in some recolonized populations may be higher than expected due to admixture between multiple lineages following expansion from independent refugia (Petit et al. 2003; Marr et al. 2008). Admixture may be particularly complex in high-latitude archipelagos when colonizing populations arise from multiple island source populations (Crawford et al. 2001).

Across the broad expanse of northern North America, a few regions have emerged as sites of high lineage diversity because they are at the confluence of multiple recolonizing lineages (Cook and MacDonald 2013). We focus on one of these regions, the panhandle of southeast Alaska along the North Pacific Coast, where high levels of lineage diversity is being documented for a growing number of species, (e.g., Dawson et al. 2014). These divergent lineages are postulated to have persisted in different ice-free regions [Beringian, southern continental, or coastal (Pielou 1991; Loehr et al. 2006; Carrara et al. 2007)] with subsequent expansion into proximity (Conroy and Cook 2000; Demboski and Cook 2001). Southeast Alaska, a region with an extensive island archipelago and high levels of endemism (Cook and MacDonald 2001), has been colonized by multiple newly arrived species (Cook and MacDonald 2013). This region also experienced substantial habitat modification in the past 80 years due to commercial logging and other extractive industries (List 2000; Schoen and Dovichin 2007; Albert and Schoen 2013).

We explore how complex topography and dynamic geologic history conspired to shape contemporary lineage diversity in *Microtus longicaudus* (long-tailed vole), a species that spans more than 35 degrees latitude across western North America in montane and mesic herbaceous habitats (Smolen and Keller 1987; Lomolino et al. 1989). Previous work based on a single mitochondrial gene identified a series of geographically discrete lineages and a single area of secondary contact in southeast Alaska (Conroy and Cook 2000). Divergence among coastal (island) and continental clades was attributed to late Quaternary glacial–interglacial cycling by Conroy and Cook (2000) who suggested the island clade experienced recent expansion from a southeast Alaska refugium with subsequent low gene flow among islands. The northern clade reflected pre-last glacial maximum (LGM) isolation, while the

central and southern clades were the result of deeper (mid-Pleistocene) divergence.

By employing a multilocus approach and exploring historical climatic conditions predicted by species distribution models (SDM), we test previous phylogenetic hypotheses of lineage diversification across the broad range of *M. longicaudus* (e.g., Conroy and Cook 2000; Spaeth et al. 2009). We then revisit estimates of timing of divergence, refugial locations, and post-glacial colonization pathways through expanded geographic sampling. By focusing more intensively on the northwestern extent of the species' range, we first delimit the distribution and source of all lineages in the region. Second, through finer scale sampling, we begin to refine our understanding of the distributional edges of lineages to reveal areas of potential contact between distinct lineages and then test the hypothesis that these sites reflect postglacial (last 10,000 years) contact. Finally, through a combination of genetic data and species distribution models (SDMs), we examine the interplay between historical climate variability and contemporary fragmentation across an island archipelago to set the stage for detailed analyses of diversification and community assembly in this dynamic region.

Materials and Methods

Sampling and laboratory procedures

Museum specimens were obtained via fieldwork conducted annually since 1991. Frozen heart or liver tissues are archived at the Museum of Southwestern Biology ($n = 52$) and the University of Alaska Museum of the North ($n = 91$). Sampling now represents 46 localities spanning the geographic range of *M. longicaudus*. We focused most intensively on northwestern sampling to explore population structure across the Alexander Archipelago (AA) of southeast Alaska and identify the extent of contact between island and northern clades in southeast Alaska, with a higher sampling density near Haines ($n = 28$; Appendix S1; Fig. 1). Samples represented 11 of the 15 currently recognized subspecies of *M. longicaudus* (Fig. 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* (Appendix S1).

Genomic DNA was extracted using Omega Bio-Tek (Norcross, GA) E.Z.N.A. kits or salt extraction (Fleming and Cook 2002), with final concentrations adjusted to $50 \text{ ng } \mu\text{L}^{-1}$. We amplified mitochondrial (mtDNA) *cyt b* (767–1143 bp, $n = 118$) and nuclear (nuDNA) gene

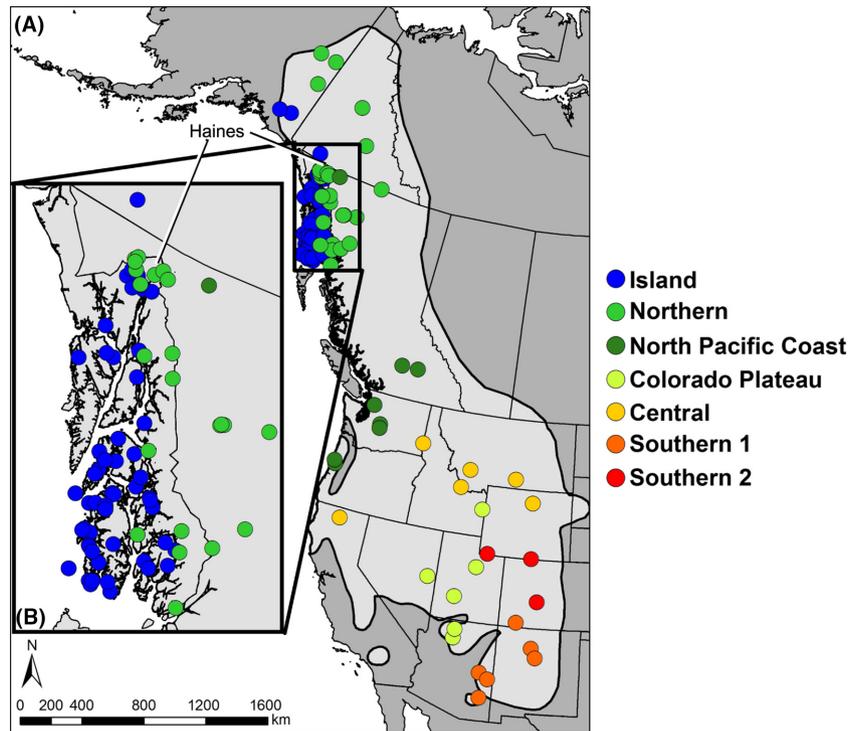


Figure 1. Current range of *M. longicaudus*. Light gray is the current range, black outlined regions. Dots are sampling locations colored by major *cyt b* clades (Fig. S1). (A) Entire range, (B) Haines and southeast Alaska.

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 S1). Polymerase chain reaction, sequencing, visualization, editing, and phasing procedures for alleles were detailed in Sawyer (2014). All sequences were deposited in GenBank (Appendix S1).

Phylogenetic analyses and estimation of divergence times

We used a multilocus approach to reconstruct species relationships (Maddison 1997; Carstens and Knowles 2007; Edwards et al. 2007). The species tree was estimated in *BEAST (Heled and 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. *A priori* groups were based on geographic populations, with individuals within northern populations assigned based on *cyt b*-supported clades (Appendix S1 – “locality”). Independent, unlinked loci (mtDNA and each nuDNA locus) were partitioned by gene and set to appropriate substitution models (Table S2) calculated in MODELTEST. An *a priori* uncorrelated lognormal relaxed clock was set for *cyt b* with a mutation rate of 4% Myr⁻¹ based on previous estimates ranging from 3 to 5% Myr⁻¹ (Conroy and Cook 1999; Brunhoff et al. 2003; Hope et al. 2013).

Utilizing a Bayesian uncorrelated relaxed clock assists in reducing errors associated with recent divergence and the lack of reliable calibration points (Drummond et al. 2006; Ho and Duchene 2014). 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. 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 and convergence onto the same tree was analyzed with the online software AWTY (Nylander et al. 2008). Three independent runs were checked for convergence in trace graphs then combined using LOGCOMBINER v1.7.5, with a 10% burn-in. Tree files were annotated in TREEANNOTATOR v1.7.5, and topologies were visualized in FIGTREE v1.4.0 (Rambaut 2009). Because we lacked reliable fossils for this species, we were unable to incorporate fossil calibration into either *cyt b* (Data S1) or species tree analyses.

Migration estimates

We used BAYESASS v3.0.3 (Wilson and Rannala 2003) to determine recent levels of gene flow among populations representing the major *cyt b* clades (designated with a 95% support for Bayesian and 70 for ML; Fig. S1) across

the islands of southeast Alaska, as well as among northern populations with secondary contact or in close geographic proximity. *BAYESASS* uses a nonequilibrium, multilocus Bayesian approach to estimate migration rates under a MCMC algorithm. We used phased multilocus data (mtDNA and nuDNA) 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 program guidelines.

Demographic analyses

To explore the signatures of stability and postglacial expansion for each well-supported major *cyt b* clade, we reconstructed extended Bayesian skyline plots (EBSP; mtDNA and nuDNA) and *cyt b* Bayesian skyline plots (Heled and Drummond 2008) implemented in *BEAST*. Colorado Plateau (COP) and North Pacific Coast (NPC) were omitted due to low sample sizes. Strict molecular clocks for all phased loci and appropriate models of evolution (Table S2) 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 and 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 (*H_d*), and nucleotide diversity (π)] for both mtDNA and nuDNA in *DNASP* 5.10.1 (Librado and Rozas 2009). Historical demographic change or selection potential were assessed through Tajima's *D* (1989), Fu's *F_s* (1997), and Ramos-Onsins and Rosas' *R₂* (Ramos-Onsins and Rozas 2002) with 10 thousand coalescent simulations. Selection potential was assessed through the HKA test (Hudson et al. 1987).

Species distribution models

We generated SDMs for *M. longicaudus* to identify regions of climate suitability across western North America, which were then tested with molecular data. Because we used relatively few southern samples, we did not 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 (~6 ka) and last glacial maximum (LGM; ~21 ka, <http://pmip2.lsce.ipsl.fr/>, Braconnot et al. 2007), and the last interglacial (LIG; ~120–140 ka). To avoid over-parameterization of the

model, we used *ENMTOOLS* (Warren et al. 2008, 2010) to eliminate highly correlated variables (Pearson correlation ≥ 0.75). Test layers were clipped to the extent of sampling, while projection layers were for western North America. Correlated bioclimatic variables were removed and only those judged to be the most important to *M. longicaudus* were retained for the final runs. Locality data were obtained from museum databases (e.g., ARCTOS <http://arctos.data-base.uaf.edu> and MaNIS <http://manisnet.org/>; Stein and Wieczorek 2004). Sites with large (>50 km) spatial errors were removed. Although genetic sampling was denser in the northern latitudes, that was not the case for SDMs (Fig. S2). To moderate spatial autocorrelation (Reddy and Davalos 2003), we reduced sample points to 50 km apart by removing intervening samples (Hope et al. 2011) for 149 final localities.

Species distribution models were constructed for each time period using *MAXENT* v3.3.3k (Elith et al. 2006; Phillips et al. 2006; Phillips and Dudik 2008). Basic assumptions were as follows: no topographic change has occurred, niche conservatism (Wiens and Graham 2005), environmental data adequately predict 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 bioclimatic variables 1 (annual mean temperature), 6 (min temperature of coldest month), 7 (temperature annual range), 9 (mean temperature of driest quarter), and 11 (mean temperature of coldest quarter) and were performed using cross-validation across 10 runs, with a random test percentage of 25%, regularization parameter of 5 (e.g., Hope et al. 2011; Warren and Seifert 2011), and 1000 iterations; all other values were default. Models were tested for performance using the randomization feature in *ENMTOOLS*. 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) using the raster calculator. Minimum threshold values for climate suitability were the low median threshold values over all replicates (Pearson et al. 2007). These models were assessed with respect to potential refugial locations as identified by Sawyer (2014).

Results

Phylogenetic analysis

The multilocus species tree identified just a single well-supported clade (island and northern together; Fig. 2), while other clades identified based on mtDNA alone (Conroy and Cook, 2000; this study) were only moderately supported. Nuclear haplotypes (Fig. S3) generally were either

lineage specific or shared across many individuals. Shared alleles were not dependent on geographic proximity, suggesting the lower resolution found in the species tree compared to the more geographically structured mtDNA tree may result from incomplete lineage sorting, rather than admixture (Toews and Brelsford 2012).

We found stronger geographic structure within the faster evolving *cyt b* across the range of *M. longicaudus* (Fig. 1 and Fig. S1), but all phylogenies were consistent with four geographic groups: (1) southern, comprised of two lineages (S1: Colorado and Wyoming; S2: New Mexico, Colorado, and Arizona); (2) central (California, Idaho, Montana, and Wyoming); (3) COP (Arizona into Idaho); and (4) northwest, consisting of NPC (British Columbia, Oregon, and Washington), northern (eastcentral Alaska, through Yukon and British Columbia), and island (southcentral Alaska, southern Yukon, and southeast Alaska). Two mainland southeast Alaska locations, Haines and Juneau, have representatives of both northern and island clades.

Both northern and island clades showed substantial internal structure, with many geographically restricted lineages identified (Fig. 2 and Fig. S1).

Genetic diversity, demographic analyses and current levels of gene flow

Nuclear loci had varying levels of allelic diversity (Table S2), with ETS2 the most geographically structured. No selection was detected in HKA tests for all loci. Ramos-Onsín and Rozas R_2 values were significant for all loci. We inferred demographic history based on degree of genetic variation, significance of expansion statistics (Table S2), and both *cyt b* skyline plots and EBSPs (Fig. 3). Populations that experienced recent expansion generally have low H_d , while high H_d and π are indicative of long-term stability, and low H_d and high π suggest population bottlenecks. Levels of variation across all loci (mtDNA and nuDNA), although generated independently, were assessed for consistency across loci. The genetic signature of the island clade is consistent with a founder event that then experienced rapid growth, with high *cyt b* H_d a result of genetic drift in the small, fragmented populations of the archipelago. The northern clade signature is also consistent with reduced ancestral population size followed by rapid expansion, while the central clade was historically stable. The southern clade represents a glacially stable population that may have experienced a bottleneck (this signature only in the *cyt b* data). Small sample sizes for the NPC and COP clades preclude inference.

The mean of three runs for the Bayesian estimates of migration indicated low levels of gene flow between major

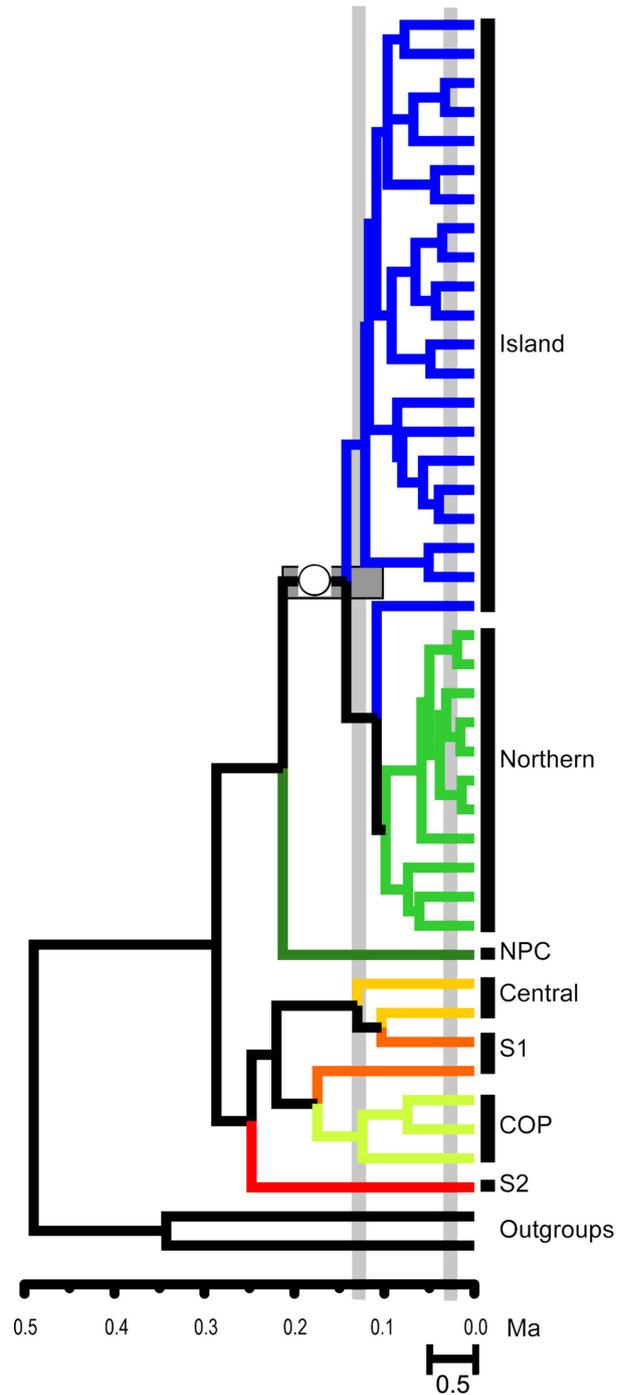


Figure 2. Phased multilocus Bayesian Species Tree. Posterior probabilities of ≥ 0.95 are represented with open circles on branches. Horizontal gray bars represent divergence date estimates and vertical bars indicate approximate time for the LIG and LGM. NPC = North Pacific Coast; COP = Colorado Plateau; S1 & S2 = southern clades.

cyt b clades within northern regions of secondary contact (Table 1), with the island clade the most genetically isolated. Gene flow (proportion of migrants derived from

other populations) among geographically proximate representatives of distinct clades was highest from populations in the northern clade (Haines and Juneau) into the Haines population of the island clade (0.009–0.012; Fig. S4; Table S5). The island clade contained populations with a very small proportion of mainland migrants (<0.0187 between any island/adjacent mainland pair; Table S6).

Divergence times and alternate models of glacial refugia and postglacial recolonization

The multilocus estimation places the north/island clade TMRCA before the LIG (142 ka; Table S7; Cyt *b* estimates – Data S1).

Strong predictive ability of SDMs is indicated with AUC values >0.80 (Warren et al. 2008). SDMs in this study had predictive performances with a mean AUC value of 0.834 (standard deviation 0.04) for the training and test data and performed significantly better than random. The LIG SDM suggests *M. longicaudus* was restricted to coastal or extreme southern locations at this time, with a subsequent increase in climate suitability for the LGM in interior western North America, allowing northward and eastward movement. By the mid-Holocene, climate conditions were suitable to cover most of the current range of *M. longicaudus*. Because SDMs are conservative (i.e., limited by a minimum threshold value) and relatively few northern continental localities were included, the full northern range currently occupied was not predicted in the models (Fig. 4).

Discussion

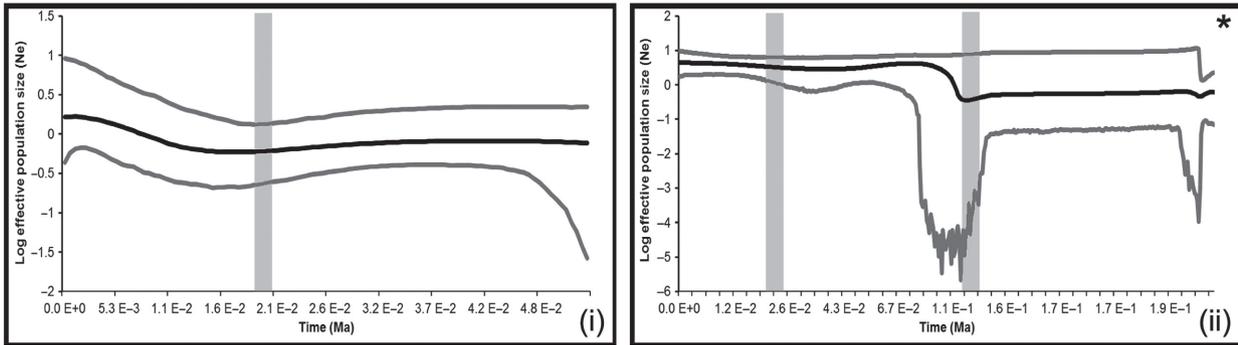
Deciphering the dynamic history of a region sets the stage for interpreting how contemporary environmental change (e.g., deforestation, climate change) may impact species and ultimately ecosystems. In the case of coastal Alaska, our understanding of diversity, island biogeography, and community assembly across the vast Alexander Archipelago was predicated on the hypothesis that the region was entirely glaciated until about 12,000 years ago, and this suggested a narrow timeframe for colonization and diversification of the contemporary biota (Klein 1964). Subsequent phylogeographic (Cook et al. 2006; Shafer et al. 2010), geological (Carrara et al. 2007; Ager

et al. 2010), and paleontological (Heaton and Grady 2003, 2007) investigations have revealed complex histories including deeper, in situ persistence and divergence for many species along the coast that were later followed by waves of colonization westward through the coast range from other ice-age refugia (Cook and MacDonald 2013).

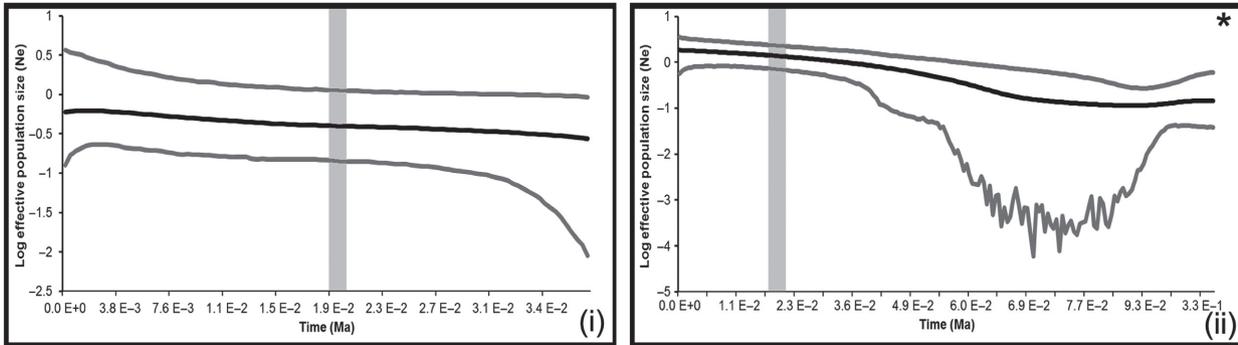
Through the use of multilocus phylogenetics and SDMs, we explored how historical climatic events structured genetic variation in a common rodent across northwestern North America and then focused more intently on subsequent diversification across the islands of southeast Alaska. Sources for postglacial colonization of these northern latitudes typically were located in either southern ice-free regions (northward; e.g., Stone et al. 2002) or Beringia (southward; e.g., Eddingsaas et al. 2004). Because populations of taxa in the higher latitude deglaciated regions are hypothesized to be relatively homogenous due to recent northward expansion while southern source populations should retain signatures of long-term persistence and deeper divergence (Hewitt 2000; Lessa et al. 2003; Malaney and Cook 2013), we expected to find similar genetic signatures for *M. longicaudus*. Instead, we uncovered substantial structure in coastal Alaska, with admixture in some mainland populations that reflected complex histories of origin. Contemporary coastal mainland populations are derived from historically persistent (coastal refugial) populations in Southeast Alaska (Carrara et al. 2007) or derived from recent westward colonizers that arrived from one or more refugial sources outside of the region. Contemporary island populations in contrast are derived only from populations that persisted in or near the region (i.e., coastal refugium) and each of these insular populations subsequently has begun to diverge independently (neoendemics). We emphasize persistence “in or near the region” because the precise location of a LGM coastal refugium or series of refugia, when sea levels were up to 165 m lower, has not been identified. Intraspecific variability in this species at the far northwestern edge of its range mirrors to some extent the history of several other species studied to date, indicating that contemporary species in the region may be admixed as a result of contact between distinctive persistent and colonizing lineages. Similarly, contemporary communities in the region are a composite of both persistent and recently colonized species that arrived from multiple geographic sources (Cook et al. 2001, 2006). This dynamic

Figure 3. Cyt *b* Bayesian skyline plots (i) and EBSPs (ii) for the major cyt *b* clade populations: (A) island, (B) northern, (C) central, and (D) southern, excluding NPC and COP. EBSP central line indicates mean change in effective population size through time, with upper and lower lines showing the 95% posterior density. Significant population size change in EBSPs are indicated with asterisks. The x-axis right-to-left from past (TMRCA) to present and is scaled in millions of years and the y-axis is the log effective population size scaled by generation time. Vertical gray bars indicate the LIG (when applicable, right) and LGM (left) for reference.

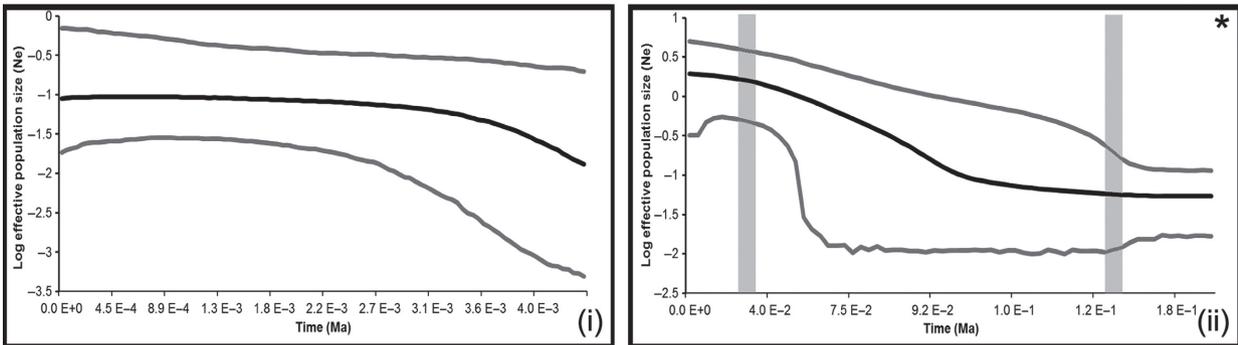
(A) *M. longicaudus* - Island



(B) *M. longicaudus* - Northern



(C) *M. longicaudus* - Central



(D) *M. longicaudus* - South

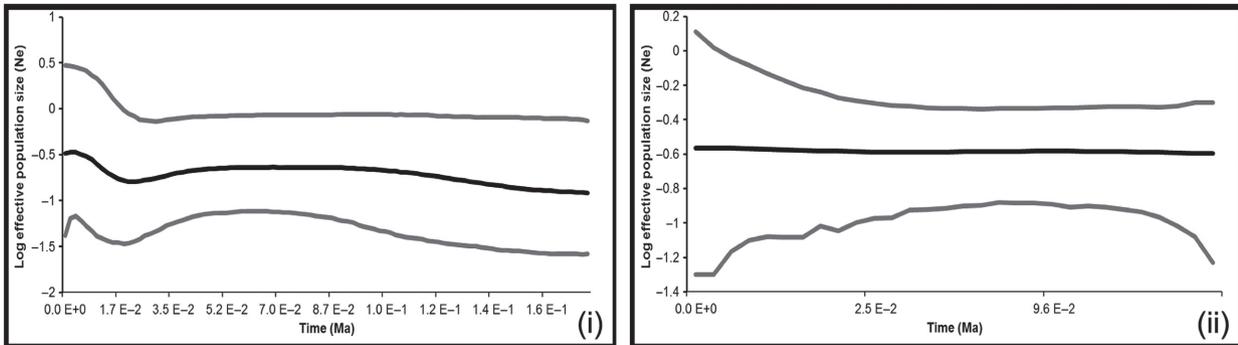


Table 1. Major *cytb* clade in regions of northern secondary contact. Bayesian migration estimates determined in *BAYESASS*. Nonmigrants within each population are indicated in bold along the diagonal. Values are the proportion of migrant genes donated from source populations (columns) into sink populations (rows).

From...	Migration rates into...		
	Island	Northern	NPC
Island	0.988	0.007	0.005
Northern	0.019	0.970	0.011
NPC	0.050	0.156	0.795

perspective on assembly where species and communities may have multiple origins has broad implications ranging from new perspectives on the island biogeography of the archipelago, to revising conservation plans for this highly

fragmented and heavily altered landscape and to establishing the history and critical roles of parasites in wildlife and zoonotic pathogens in humans in the region.

Biogeographic drivers of isolation, glacial refugia, and postglacial recolonization

This more detailed view of the phylogeography of *M. longicaudus* refines our understanding of divergence within southeast Alaska and largely corroborates earlier continental-scale work that revealed patterns of differentiation based on more restricted geographic and genetic sampling (Conroy and Cook 2000; Spaeth et al. 2009), but there are notable discrepancies. Spaeth et al. (2009) focused on the Greater Yellowstone Ecosystem, identifying postglacial subfossils representing both the northern and

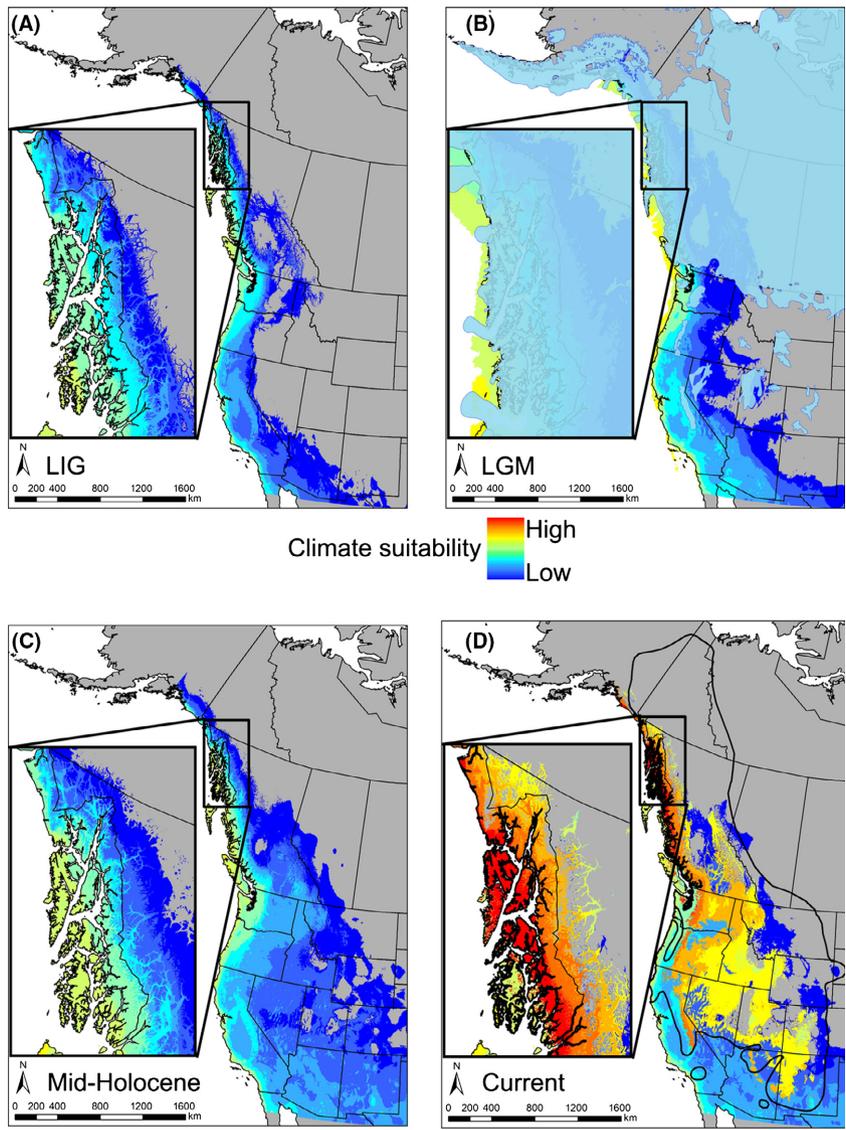


Figure 4. SDM output. (A) LIG (~125 ka), (B) LGM (~20 ka), (C) mid-Holocene (~6 ka), and (D) current time periods. The thick black line in (D) is the current range for *M. longicaudus*. The solid blue coloring in (B) is glacial ice cover. SDM climate suitability at each time period is limited by minimum median threshold values over all replicates. Because the SDMs are conservative, not all current localities are predicted in the models.

central clades within Yellowstone (Fig. 5). Our expanded assessment detected substantial spatial and temporal patterns of genetic differentiation across the entire range of *M. longicaudus*, not previously identified by either Conroy and Cook (2000) or Spaeth et al. (2009).

The multilocus estimate for TMRCA of *M. longicaudus* is before the LIG (about 290 ka, Fig. 2), but is shallower than single-locus estimates from previous studies (340 ± 70 ka, Conroy and Cook 2000). Difficulty in establishing these estimates may reflect our inability to adequately calibrate trees with fossils and thus account for rate decay (Ho et al. 2005). Contrasting with the pre-LIG mtDNA estimates of divergence (Fig. S3), the shallower fossil dates are extending only to the Wisconsinan glaciation in Idaho, Wyoming, Colorado, and New Mexico (Schultz and Howard 1935; Anderson 1968; Harris

1970; Hager 1972; Walker 1982; White et al. 1984) and postglacial locations in Alberta and British Columbia (Harrington 2011b). The absence of older fossils, especially at the northern extent of their range where we suspect refugial persistence (Guthrie 1968; Youngman 1975), may reflect poor preservation, lack of exploration of the region, or simply the difficulty of distinguishing vole fossil teeth (Harrington 2011a). If the earlier DNA-derived estimate for initiation of separation (290 ka) is correct, then divergence among major lineages of *M. longicaudus* was likely reinforced through late-Pleistocene cycles of glacial isolation, as indicated by the SDMs (Fig. 4). Southern clades apparently experienced longer-term stability and isolation, while the strongly supported, yet shallow structure among most northern clades is due to recent (Holocene) range expansion.

Our findings are consistent with the hypothesis that long-tailed voles persisted in a southeast Alaska coastal refugium (island clade) during the LGM, followed by expansion onto the islands and mainland and then recent isolation on multiple islands as sea levels rose (Fig. 5). Heaton and Grady (2007) found abundant *M. longicaudus* fossils from On Your Knees Cave (49-PET-408) on Prince of Wales Island (Fig. 5) 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 and Grady 2003), which suggests rapid recolonization shortly after the LGM. The number of coastal refugial sites occupied by *M. longicaudus* should be further explored because SDMs and multilocus genetic signatures suggest the possibility that *M. longicaudus* persisted in up to three refugia within the AA. Fossil support for refugial locations in the AA may prove problematic, however, as much of the coast exposed during the LGM is now under up to 165 m of water (Carlson 2007; Shugar et al. 2014).

Lack of connectivity between insular populations produced extensive interisland structure, with populations on 13 of the 19 islands displaying island-specific haplotypes and significant mtDNA divergence (see also Sawyer 2014). Gene flow among island populations in the AA was inhibited due to sea-level rise during the early Holocene (c. 14–8 ka bathymetric reconstruction, Baichtal and Carlson 2010). Also, within the AA, *M. longicaudus* is the only vole that occurs on most of the islands (Baranoff island is a curious exception). On the mainland of southeast Alaska, this vole is syntopic with two congeners, *M. oeconomus* (root vole) and *M. pennsylvanicus* (meadow vole); however, the phylogeographic histories of those two species remain poorly understood in the region. Both species are thought to be Holocene colonizers of

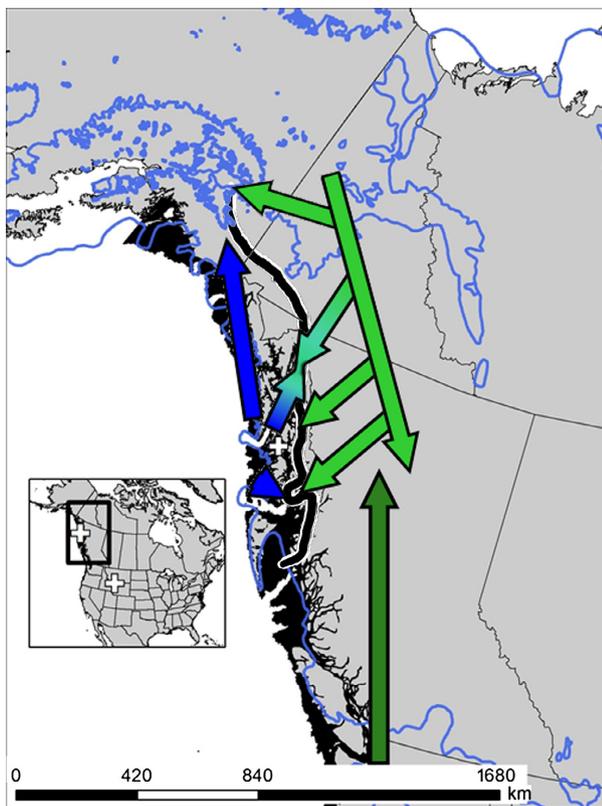


Figure 5. Proposed postglacial colonization routes (arrows) for *M. longicaudus* based on genetic signatures and SDMs. Plus (+) = fossil (SE Alaska)/subfossil (Yellowstone) locations and arrow colors correspond to current *cyt b* lineages: dark green = North Pacific Coast, green = northern, and blue = island. Northern and island clade refugial locations and postglacial colonization with location of geographic proximity indicated with the thick black line and secondary contact with converging arrows. Blue line indicates extent of glacial ice, and solid black coastal regions are exposed continental shelf at the LGM.

southeast that originated outside of the coastal region (Cook and MacDonald 2013). With regard to other potentially closely associated species, the phylogeography of the ermine (*Mustela erminea*), a vole specialist predator (Verts and Carraway 1998), has been explored. Three distinctive lineages of ermine, one endemic (island) and two originating outside the region (Beringian and southern) also have been identified in southeast Alaska (ermine; Fleming and Cook 2002; MacDonald and Cook 2007; Dawson et al. 2014), although there is limited spatial correspondence between the long-tailed vole and ermine lineages at finer spatial scales within southeast Alaska. The island lineage of *M. longicaudus*, for example, co-occurs with all three major clades (continental, Beringian, and island) of ermine. Hence, although the broader regional patterns of lineage divergence due to persistence in multiple glacial refugia are shared among this predator and its prey, idiosyncratic differences due to distinct colonization abilities, lineage persistence, or random events are evident on individual islands and on the mainland in southeast Alaska. These limited examples point to the need for more detailed comparative assessments with other taxa, such as plants and associated arthropods, across this complex landscape.

The island and northern clades of *M. longicaudus* have at least two points of secondary contact on the mainland (Haines and Juneau) and the multiple sites of geographic proximity southward along the mainland coast of southeast Alaska indicate the possibility of additional locations of contact between distinctive lineages (Fig. 4). Island individuals likely followed glacial retreat through multiple colonization pathways (Fig. 5) to recolonize the adjacent mainland while sea levels were low, while northern individuals apparently colonized the mainland rapidly through river corridors extending through the coast range after ice sheets receded. Detailed assessment of mainland sites based on increased sampling density is needed to interpret the expansion from the east, a process noted for other mammals (Cook and MacDonald 2013). This region of contact along the coast may reflect a generalized suture zone, where processes of introgression are similar to those detected in coastal populations of red-backed voles of the genus *Myodes* (Runck et al. 2009) and montane shrews, *Sorex monticolus* (Demboski and Cook 2001; Sawyer 2014). Contrary to previous suggestions that the northern clade of long-tailed voles expanded along a single interior route from south of the ice (Conroy and Cook 2000), we hypothesize that the northern clade persisted in Beringia and recently expanded southward into previously glaciated regions of southern Alaska, Yukon, and northern British Columbia (Fig. 5) as noted in moose, wolverine, ermine, and other species (MacDonald

and Cook 2007). Two points that are potentially inconsistent with this conclusion are (1) lack of verifiable pre-Holocene fossils of long-tailed voles in Beringia, and (2) SDMs do not predict suitable environments north of the ice for long-tailed vole persistence during the LGM. We also recognize the possibility that with increased sampling across Yukon and British Columbia, either a more southern distribution of the northern clade may be detected, increasing the possibility of a southern (vs. Beringian) origin for this clade, or climatic niche suitability with a more northern range may be detected, supporting the Beringian origin for this clade. High levels of intralinear genetic diversity, net genetic distance among other clades, and the restriction of the range of this clade to high latitudes, however, are consistent with persistence in a northern refugium. Additionally, the species tree indicates a close association of the island and northern clades, suggesting a northern origin. Numerous paleontological as well as phylogeographic studies that identified genetic signatures point toward the persistence of many species in an eastern Beringia refugium during glacial periods, but clearly, there is a need for expanded analyses to further refine our understanding of these northern communities during the LGM (Fleming and Cook 2002; Stamford and Taylor 2004; Sawyer 2014).

Species distribution models are consistent with persistence of *M. longicaudus* along the coast of Oregon and Washington (NPC clade) during glacial advances. The central and southern clades were 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, was found to occur northward into Utah and potentially contacts both the S2 subclade and central clade.

Contemporary genetic structure and current levels of gene flow

Deciphering signatures of incomplete lineage sorting versus secondary admixture is critical for interpreting how historical climate shaped contemporary distributions and genetic structure. Shallow divergence between northern and island populations near Haines may reflect recent (Holocene) secondary contact or incomplete lineage sorting. Future studies should incorporate more intensive sampling of individuals, especially in suspected contact zones, and expanded genomic coverage to explore potential admixture (Qu et al. 2012).

The distribution of major clades in *M. longicaudus* is generally inconsistent with subspecific designations (Fig. 1; Hall 1981). For example, Forrester and Coronation are identified as independent lineages, but these

islands were previously placed in a single subspecies, *M. l. coronarius* (MacDonald and Cook 2009). All major clades span multiple subspecies of *M. longicaudus*, while several subspecies also include multiple clades. A reassessment of subspecies, originally based on morphological variation, is warranted.

Segregation of the northern/island clade from the NPC, COP, central, and southern clades is reflected in both the species tree (Fig. 2) and migration estimates (Table 1). The lack of support for deeper nodes may be a result of the relatively dense sampling for the northern/island clade. Compared to the northern clade, lower levels of gene flow from the island clade into the Haines area likely reflect physical barriers to movement (i.e., ocean straits, extant glaciers). Genetic exchange among island populations also is now limited, a finding that points to the possibility that these insular biotas are evolving independently and further reinforcing the urgency of managing this archipelago on an island by island basis, given that the AA comprises the largest federally managed forest in the United States, the Tongass National Forest (6.8 million ha).

Conclusions

Understanding the interplay between topography and historical climate change on both the distribution of contemporary species and the structure of genetic variation within these species sets, a powerful stage for forecasting and mitigating biotic responses to changing conditions. At a regional scale along the long-tailed vole's boundary in the Pacific northwest, significant structure reflects their dynamic expansion from multiple refugia concomitant with the contraction of glacial cover and as influenced by rising sea levels and isostatic rebound that played out over the complex topography of Pacific coastal North America. Similar processes of isolation and complex colonization along the North Pacific Coast were recently identified for this vole's primary predator, the ermine (Dawson et al. 2014). Our expanded view of molecular variation on 19 islands across the AA identifies the deeper signature of persistence in a coastal refugium that was the source for continental admixed populations and insular populations that are subsequently diverging, largely independently. Further work should focus on how species on individual islands will respond to changing environmental conditions, including a series of anthropogenic stressors (Hannon et al. 2010; Cook and MacDonald 2013) and rising sea levels. Recovering ancient DNA from the extensive fossil record from the region (>3000 specimens; T. H. Heaton, pers. comm.) would significantly extend our comprehension of temporal genetic variability (Miller et al. 2012) in this dynamic region.

Acknowledgments

We thank the Cuervo laboratory for both technical support and comments on this manuscript and D. Banks-Richardson, S. Thompson, W. Kanagy, and A. Chavez for laboratory assistance. We also acknowledge the efforts of personnel associated with the fieldwork and museum curation at the University of New Mexico's (UNM) Museum of Southwestern Biology and the University of Alaska's Museum of the North. We acknowledge technical support from UNM Department of Biology's Molecular Biology Facility and University of Alaska, Fairbanks Life Science Informatics Facility. We thank the Hertel and Gaudin families, UNM Graduate and Professional Student Association, the Biology Graduate Student Association, the Biology Department, and the Office of Graduate at the University of New Mexico. We also thank T&E Inc, the American Society of Mammalogists, USDA Forest Service (Tongass National Forest and PNW Forest Sciences Lab), National Science Foundation (DEB1258010), Sitka Sound Science Center, and Undergraduate Opportunities (UnO) program (DEB0731350) for support of this work.

Data accessibility

Sample locations with museum numbers, latitude and longitude, major *cyt b* clade, and associated GenBank accession numbers are uploaded as online supplemental material in Appendix S1. PCR conditions are provided as Supporting information in Table S1.

Conflict of Interest

None declared.

References

- Ager, T. A., P. E. Carrara, J. L. Smith, V. Anne, and J. Johnson. 2010. Postglacial vegetation history of Mitkof Island, Alexander Archipelago, Southeastern Alaska. *Quatern. Res.* 73:259–268.
- Albert, D. M., and J. W. Schoen. 2013. Use of historical logging patterns to identify disproportionately logged ecosystems within temperate rainforests of Southeastern Alaska. *Conserv. Biol.* 27:774–784.
- Anderson, E. 1968. Fauna of the little box elder cave, converse county, Wyoming. *The Carnivora. Univ. Colorado* 6:1–59.
- Baichtal, J. F., and R. J. Carlson. 2010. Development of a model to predict the location of Early-Holocene habitation sites along the western coast of Prince of Wales Island and the Outer Islands, Southeast Alaska. *Curr. Res. Pleistocene* 27:64–67.
- Braconnot, P., B. Otto-Bliesner, S. Harrison, S. Jousaume, J.-Y. Peterchmitt, A. Abe-Ouchi, et al. 2007. Results of PMIP2 coupled simulations of the Mid-Holocene and Last

- Glacial Maximum – Part 1: experiments and large-scale features. *Clim. Past* 3:261–277.
- Brunhoff, C., K. E. Galbreath, V. B. Fedorov, J. A. Cook, and M. Jaarola. 2003. Holarctic phylogeography of the root vole (*Microtus oeconomus*): implications for late Quaternary biogeography of high latitudes. *Mol. Ecol.* 12:957–968.
- Carlson, R. J. 2007. Current models for the human colonization of the Americas: the evidence from Southeast Alaska. Cambridge University, England.
- Carrara, P. E., T. A. Ager, and J. F. Baichtal. 2007. Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. *Can. J. Earth Sci.* 44:229–244.
- Carstens, B. C., and L. L. Knowles. 2007. Estimating species phylogeny from gene-tree probabilities despite incomplete lineage sorting: an example from *Melanoplus* grasshoppers. *Syst. Biol.* 56:400–411.
- Conroy, C. J., and J. A. Cook. 1999. MtDNA evidence for repeated pulses of speciation within Arvicolinae and Murid rodents. *J. Mamm. Evol.* 6:221–245.
- Conroy, C. J., and J. A. Cook. 2000. Phylogeography of a post-glacial colonizer: *Microtus longicaudus* (Rodentia: Muridae). *Mol. Ecol.* 9:165–175.
- Cook, J. A., and S. O. MacDonald. 2001. Should endemism be a focus of conservation efforts along the North Pacific Coast of North America. *Biol. Conserv.* 97:207–213.
- Cook, J. A., and S. O. MacDonald. 2013. *Island Life: Coming to Grips with the Insular Nature of Southeast Alaska and Adjoining Coastal British Columbia*, Illustrated ed. University of Washington Press, Washington.
- Cook, J. A., A. L. Bidlack, C. J. Conroy, J. R. Demboski, M. A. Fleming, A. M. Runck, et al. 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska. *Biol. Conserv.* 97:215–227.
- Cook, J. A., N. G. Dawson, and S. O. MacDonald. 2006. Conservation of highly fragmented systems: the north temperate Alexander Archipelago. *Biol. Conserv.* 133:1–15.
- Crawford, D. J., E. Ruiz, T. F. Stuessy, E. Tepe, P. Aqueveque, F. Gonzalez, et al. 2001. Allozyme diversity in endemic flowering plant species of the Juan Fernandez Archipelago, Chile: Ecological and historical factors with implications for conservation. *Am. J. Bot.* 88:2195–2203.
- Dawson, N. G., A. G. Hope, S. L. Talbot, and J. A. Cook. 2014. A multilocus evaluation of ermine (*Mustela erminea*) across the Holarctic, testing hypotheses of Pleistocene diversification in response to climate change. *J. Biogeogr.* 41:464–475.
- Demboski, J. R., and J. A. Cook. 2001. Phylogeography of the dusky shrew, *Sorex monticolus* (Insectivora, Soricidae): insight into deep and shallow history in northwestern North America. *Mol. Ecol.* 10:1227–1240.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4:699–710.
- Dyke, A. S., and V. K. Prest. 1987. Late Wisconsinan and holocene history of the laurentide ice sheet. *Géog. Phys. Quatern.* 42:237–263.
- Eddingsaas, A. A., B. K. Jacobsen, E. P. Lessa, and J. A. Cook. 2004. Evolutionary history of the arctic ground squirrel (*Spermophilus parryii*) in Nearctic Beringia. *J. Mammal.* 85:601–610.
- Edwards, S. V., L. Liu, and D. K. Pearl. 2007. High-resolution species trees without concatenation. *Proc. Natl Acad. Sci. USA* 104:5936–5941.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Excoffier, L., M. Foll, and R. J. Petit. 2009. Genetic consequences of range expansions. *Annu. Rev. Ecol. Evol. Syst.* 40:481–501.
- Fleming, M. A., and J. A. Cook. 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. *Mol. Ecol.* 11:795–807.
- Fu, Y. X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* 147:915–925.
- Godbout, J., A. Fazekas, C. H. Newton, F. C. Yeh, and J. Bousquet. 2008. Glacial vicariance in the Pacific Northwest: evidence from a lodgepole pine mitochondrial DNA minisatellite for multiple genetically distinct and widely separated refugia. *Mol. Ecol.* 17:2463–2475.
- Guthrie, R. D. 1968. Paleocology of a late Pleistocene small mammal community from interior Alaska. *Arctic* 21: 223–244.
- Hager, M. W. 1972. A late Wisconsin recent vertebrate fauna from the Chimney-Rock animal trap Larimer county Colorado. *Contrib. Geol. Univ. Wyoming* 11:63–71.
- Hall, E. R. 1981. *The mammals of North America*, Vol. 2: Pp. 601–1181. John Wiley & Sons, New York.
- Hannon, P. E., D. V. D'Amore, D. T. Witter, and M. B. Lamb. 2010. Influence of forest canopy and snow on microclimate in a declining yellow-cedar forest of Southeast Alaska. *Northwest Sci.* 84:73–87.
- Harrington, C. R. 2011a. Pleistocene vertebrates of the Yukon Territory. *Quatern. Sci. Rev.* 30:2341–2354.
- Harrington, C. R. 2011b. Quaternary cave faunas of Canada: a review of the vertebrate remains. *J. Caves Karst Stud.* 73:162–180.
- Harris, A. H. 1970. Dry Cave mammalian fauna and late pluvial conditions in southeastern New Mexico. *Tex. J. Sci.* 22:3–27.
- Hayes, J. P., and R. G. Harrison. 1992. Variation in mitochondrial DNA and the biogeographic history of woodrats (*Neotoma*) of the eastern United States. *Syst. Biol.* 41:331–344.
- Heaton, T. H., and F. Grady (2003) The Late Wisconsin vertebrate history of Prince of Wales Island, southeast

- Alaska, Pp. 17–53 in *Ice Age cave faunas of North America* (eds B. W. Schubert, J. I. Mead and R. W. Graham), Indiana University Press, Indiana.
- Heaton, T. H., and F. Grady. 2007. The vertebrate fossil record of On Your Knees Cave, Prince of Wales Island, Southeast Alaska. *Quat. Int.* 167–168:160.
- Heled, J., and A. J. Drummond. 2008. Bayesian inference of population size history from multiple loci. *BMC Evol. Biol.* 8:289–303.
- Heled, J., and A. J. Drummond. 2010. Bayesian inference of species trees from multilocus data. *Mol. Biol. Evol.* 27:570–580.
- Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* 58:247–276.
- Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- Hewitt, G. M. 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philos. Trans. R. Soc. B Biol. Sci.* 359:183–195.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25:1965–1978.
- Ho, S. Y. W., and S. Duchene. 2014. Molecular-clock methods for estimating evolutionary rates and timescales. *Mol. Ecol.* 23:5947–5965.
- Ho, S. Y. W., M. J. Phillips, A. Cooper, and A. J. Drummond. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Mol. Biol. Evol.* 22:1561–1568.
- Hope, A. G., E. Waltari, V. B. Fedorov, A. V. Goropashnaya, S. L. Talbot, J. A. Cook. 2011. Persistence and diversification of the Holarctic shrew, *Sorex tundrensis* (Family Soricidae), in response to climate change. *Mol. Ecol.* 20:4346–4370.
- Hope, A. G., N. Takebayashi, K. E. Galbreath, S. L. Talbot, and J. A. Cook. 2013. Temporal, spatial and ecological dynamics of speciation among amph-Beringian small mammals. *J. Biogeogr.* 40:415–429.
- Hudson, R. R., M. Kreitman, and M. Aguade. 1987. A test of neutral molecular evolution based on nucleotide data. *Genetics* 116:153–159.
- Hundertmark, K. J., G. F. Shields, I. G. Udina, R.T. Bowyer, A. A. Danilkin, C. C. Schwartz. 2002. Mitochondrial phylogeography of moose (*Alces alces*): Late Pleistocene divergence and population expansion. *Mol. Phylogenet. Evol.* 22:375–387.
- Klein, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. *J. Mammal.* 45:226–235.
- Koch, M. A., C. Kiefer, D. Ehrlich, J. Vogel, C. Brochmann, K. Mummenhoff. 2006. Three times out of Asia Minor: the phylogeography of *Arabis alpina* L. (Brassicaceae). *Mol. Ecol.* 15:825–839.
- Kozak, K. H., C. H. Graham, and J. J. Wiens. 2008. Integrating GIS-based environmental data into evolutionary biology. *Trends Ecol. Evol.* 23:141–148.
- Lee-Yaw, J. A., J. T. Irwin, and D. M. Green. 2007. Postglacial range expansion from northern refugia by the wood frog, *Rana sylvatica*. *Mol. Ecol.* 17:867–884.
- Lessa, E. P., J. A. Cook, and J. L. Patton. 2003. Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proc. Natl Acad. Sci. USA* 100:10331–10334.
- Lessa, E. P., G. D'Elia, and U. F. J. Pardinias. 2010. Genetic footprints of late Quaternary climate change in the diversity of Patagonian-Fuegian rodents. *Mol. Ecol.* 19:3031–3037.
- Librado, P., and J. Rozas. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25:1451–1452.
- Lim, H. C., and F. H. Sheldon. 2011. Multilocus analysis of the evolutionary dynamics of rainforest bird populations in Southeast Asia. *Mol. Ecol.* 20:3414–3438.
- List, P. C.. 2000. *Environmental ethics and forestry: a reader*. Temple University Press, Philadelphia.
- Loehr, J., K. Worley, A. Grapputo, J. Carey, A. Veitch, D. W. Coltman. 2006. Evidence for cryptic glacial refugia from North American mountain sheep mitochondrial DNA. *J. Evol. Biol.* 19:419–430.
- Lomolino, M. V., J. H. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American southwest. *Ecology* 70:180–194.
- Lyons, S. K. 2003. A quantitative assessment of the range shifts of Pleistocene mammals. *J. Mammal.* 84:385–402.
- MacDonald, S. O., and J. A. Cook. 2007. Mammals and amphibians of southeast Alaska. *Spec. Publ. Mus. Southwest. Biol.* 8:1–191, i–vii.
- MacDonald, S. O., and J. A. Cook. 2009. *Recent mammals of Alaska*. Pp. 1–387. University of Alaska Press, Fairbanks.
- Maddison, W. P. 1997. Gene trees in species trees. *Syst. Biol.* 46:523–536.
- Malaney, J. L., and J. A. Cook. 2013. Using biogeographical history to inform conservation: the case of Preble's meadow jumping mouse. *Mol. Ecol.* 22:6000–6017.
- Marr, K. L., G. A. Allen, and R. J. Hebda. 2008. Refugia in the Cordilleran ice sheet of western North America: chloroplast DNA diversity in the Arctic-alpine plant *Oxyria digyna*. *J. Biogeogr.* 35:1323–1334.
- Marr, K. L., G. A. Allen, R. J. Hebda, and L. J. McCormick. 2012. Phylogeographical patterns in the widespread arctic-alpine plant *Bistorta vivipara* (Polygonaceae) with emphasis on western North America. *J. Biogeogr.* 40:847–856.
- McCormack, J. E., A. J. Zellmer, and L. L. Knowles. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation: Insights from tests with niche models. *Evolution* 64:1231–1244.
- Miller, W., S. C. Schuster, A. J. Welch, A. Ratana, O. C. Bedoya-Reina, F. Zhao, et al. 2012. Polar and brown bear genomes reveal ancient admixture and demographic

- footprints of past climate change. *Proc. Natl Acad. Sci. USA* 109:E2382–E2390.
- Nylander, J. A. A., J. C. Wilgenbusch, D. L. Warren, and D. L. Swofford. 2008. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581–583.
- Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34:102–117.
- Petit, R. J., I. Aguinalgalde, J. L. de Beaulieu, C. Bittkau, S. Brewer, R. Cheddadi, et al. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. *Science* 300:1563–1565.
- Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190:231–259.
- Pielou, E. 1991. *After the Ice age: the return of life to glaciated North America*. University of Chicago Press, Chicago.
- Qu, Y. H., R. Y. Zhang, Q. Quan, G. Song, S. H. Li, F. Lei. 2012. Incomplete lineage sorting or secondary admixture: disentangling historical divergence from recent gene flow in the Vinous-throated parrotbill (*Paradoxornis webbianus*). *Mol. Ecol.* 21:6117–6133.
- Rambaut, A., and A. J. Drummond. 2007. Tracer v1.5. <http://beast.bio.ed.ac.uk/Tracer> (accessed 23 April 2012).
- Rambaut, A. 2009. FigTree v1.4.0. <http://tree.bio.ed.ac.uk/software/figtree/> (accessed 5 December 2012).
- Ramos-Onsins, S. E., and J. Rozas. 2002. Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.* 19:2092–2100.
- Rand, A. L. 1954. The ice age and mammal speciation in North America. *Arctic* 7:31–35.
- Reddy, S., and L. M. Davalos. 2003. Geographical sampling bias and its implications for conservation priorities in Africa. *J. Biogeogr.* 30:1719–1727.
- Roberts, B. L. 1991. Modeling the Cordilleran ice-sheet. *Geogr. Phys. Et Quatern.* 45:287–299.
- Runck, A. M., M. D. Matocq, and J. A. Cook. 2009. Historic hybridization and persistence of a novel mito-nuclear combination in red-backed voles (genus *Myodes*). *BMC Evol. Biol.* 9:114.
- Sawyer, Y. 2014. *Living on the edge: a comparative phylogeographic study of refugial and insular fragmentation*. University of New Mexico, New Mexico.
- Schoen, J. W., and E. Dovichin, eds. 2007. *The coastal forests and mountains Ecoregion of Southeastern Alaska and the Tongass National Forest: A conservation assessment and resource synthesis*. Audubon Alaska and the Nature Conservancy, Anchorage, Alaska.
- Schultz, C. B., and E. B. Howard. 1935. The fauna of burnet cave, Guadalupe mountains, New Mexico. *Proc. Natl. Acad. Sci.* 87:273–298.
- Shafer, A. B. A., C. I. Cullingham, S. D. Cote, and D. W. Coltman. 2010. Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America. *Mol. Ecol.* 19:4589–4621.
- Shugar, D. H., I. J. Walker, O. B. Lian, J. B. R. Eamera, C. Neudorf, et al. 2014. Post-glacial sea-level change along the Pacific coast of North America. *Quatern. Sci. Rev.* 97:170–192.
- Smolen, M. J., and B. L. Keller. 1987. *Microtus longicaudus*. *Mamm. Spec.* 271:1–7.
- Spaeth, P. A., M. van Tuinen, Y. L. Chan, D. Terca, and E. A. Hadly. 2009. Phylogeography of *Microtus longicaudus* in the tectonically and glacially dynamic central Rocky Mountains. *J. Mammal.* 90:571–584.
- Stamford, M. D., and E. B. Taylor. 2004. Phylogeographical lineages of Arctic grayling (*Thymallus arcticus*) in North America: divergence, origins and affinities with Eurasian *Thymallus*. *Mol. Ecol.* 13:1533–1549.
- Stein, B. R., and J. Wiecek. 2004. Mammals of the world: Manis as an example of data integration in a distributed network environment. *Biodiv. Inform.* 1:14–22.
- Stewart, J. R., A. M. Lister, I. Barnes, and L. Dalen. 2010. Refugia revisited: individualistic responses of species in space and time. *Proc. R. Soc. B Biol. Sci.* 277:661–671.
- Stone, K. D., R. W. Flynn, and J. A. Cook. 2002. Post-glacial colonization of northwestern North America by the forest-associated American marten (*Martes americana*, Mammalia: Carnivora: Mustelidae). *Mol. Ecol.* 11:2049–2063.
- Tajima, F. 1989. Statistical-method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123:585–595.
- Toews, D. P. L., and A. Brelsford. 2012. The biogeography of mitochondrial and nuclear discordance in animals. *Mol. Ecol.* 21:3907–3930.
- Verts, B. J., and L. N. Carraway. 1998. *Land mammals of Oregon*. University of California Press, California.
- Walker, M. J., A. K. Stockman, P. E. Marek, and J. E. Bond. 2009. Pleistocene glacial refugia across the Appalachian Mountains and coastal plain in the millipede genus *Narceus*: evidence from population genetic, phylogeographic, and paleoclimatic data. *BMC Evol. Biol.* 9:25–35.
- Walker, N. 1982. Early Holocene vertebrate fauna. Pp. 274–308 in G. C. Frison and D. J. Stanford, eds. *The Agate Basin Site: a record of the paleoindian occupation of the northwestern High Plains*. Academic Press, New York.
- Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21:335–342.
- Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism:

quantitative approaches to niche evolution. *Evolution* 62:2868–2883.

- Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33:607–611.
- White, J. A., H. G. McDonald, E. Anderson, and J. M. Soiset. 1984. Lava blisters as carnivore traps. Pp. 241–256 in H. H. Genoways and M. R. Dawson, eds. *Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday*. Carnegie Museum of Natural History, Pittsburgh, PA.
- Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36:519–539.
- Wilson, G. A., and B. Rannala. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163:1177–1191.
- Youngman, P. M. 1975. Mammals of the Yukon territory, Canada. *Natl. Mus. Nat. Sci. Publ. Zool.*, 10:1–192.

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Specimens examined.

Figure S1. Dated Bayesian *cytb* trees.

Figure S2. Sampling localities for species distribution models.

Figure S3. 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.

Figure S4. Phased nuclear haplotype distribution in Northern and Island clades of *M. longicaudus*.

Table S1. Primer list and PCR annealing temperatures.

Table S2. Diversity indices, expansion statistics and models of evolution.

Table S3. Between group net genetic distance.

Table S4. Locality abbreviations.

Table S5. Island and Northern *cytb* clade populations near the geographic regions of contact (Haines and Juneau, Alaska).

Table S6. Bayesian migration estimates for Southeast Alaska populations determined in BAYESASS for *M. longicaudus*.

Table S7. *Cyt b* and phased multilocus divergence date estimates.

Data S1. *Cyt b* data - Methods and Results.

Microtus longicaudus

- 1 Appendix I. Specimens examined. Major *cytb* clade C=Central, I=Island, and N=Northern. Museum number acronyms are MSB=
 2 Museum of Southwestern Biology; UAM=University of Alaska Museum of the North, Fairbanks. GenBank numbers correspond to
 3 *cytb*, and each allele for ETS2, FGB, and Rag1, respectively, – = not applicable. GenBank sequences in bold were obtained from other
 4 studies. Outgroup sequences for FGB and *M. montanus* sequences for ETS2 and Rag 1 were not generated

cyt b clade	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	

Microtus longicaudus

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

Microtus longicaudus

			,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, -/-, -/-, -/-

Microtus longicaudus

		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
		UAM72153	56.318	-132.286	KF948541, -/-, -/-, -/-
		UAM97289	55.344	-131.498	KF948575, -/-, -/-, -/-
	Alaska - Juneau	MSB156999	58.343	-134.640	KF948550, KF948653/KF948654, KF948803/KF948804, KF948995/KF948996
	Alaska - southeast	UAM74134	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
	Yukon - south	UAM34297	60.400	-137.050	AF187228 , KF948725/KF948726, KF948915/KF948916, KF949089/KF949090
		UAM34298	60.400	-137.050	AF187229 , KF948727/KF948728, KF948917/KF948918, KF949091/KF949092
Northern (N)	Alaska - Glacier Bay	UAM34593	65.228	-144.500	AF187190 , -/-, -/-, -/-
		UAM34594	65.228	-144.500	AF187189 , -/-, KF948919/KF948920, -/-
	Alaska - Haines	MSB195109	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

Microtus longicaudus

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, -/-

Microtus longicaudus

	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 , -/-, -/-, -/-
<i>M. montanus</i>	MSB121523				KF948532, -/-, -/-, -/-
<i>M. montanus</i>					AF119280 , -/-, -/-, -/-
<i>M. pennsylvanicus</i>	MSB110998				KF948531, -/-, -/-, -/-
<i>M. pennsylvanicus</i>	MSB149290				- , KF948649/KF948650, -/-, -/-
<i>M. pennsylvanicus</i>					AF119279 , -/-, -/-, -/-

Microtus longicaudus

M.
pennsylvanicus

-, -/-, -/-, **AY241463**/-

5