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EXPLORING SIGNALS OF HISTORICAL DEMOGRAPHY IN BOREAL MAMMALS THROUGH INTEGRATION OF STATISTICAL CONSERVATION PHYLOGENETICS, TAXONOMY, AND COMPARATIVE PHYLOGEOGRAPHY

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by

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DISSERTATION

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EXPLORING SIGNALS OF HISTORICAL DEMOGRAPHY IN BOREAL MAMMALS THROUGH INTEGRATION OF STATISTICAL CONSERVATION PHYLOGENETICS, TAXONOMY, AND COMPARATIVE PHYLOGEOGRAPHY

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ABSTRACT

Understanding how diversity is partitioned across the landscape can provide perspectives related to the environmental processes that have influenced the evolutionary history of organisms. This main idea, often termed phylogeography, serves as the backdrop to my research where I explore three broad concepts including historical biogeography, cryptic diversity and ecology, and conservation phylogenetics. I address various questions in each of these concepts by using a set of mammals that are associated with montane and mesic environments of North America. More specifically, I focus on the jumping mice (Zapodidae) to test hypotheses that scale to the broader community. This approach allows for a more refined understanding and interpretation of how species have responded to geophysical changes of the past that may be useful for predicting how future environmental pressures may influence geographically oriented lineages. By integrating across multiple disciplines of population genetics, phylogenetics, phylogeography, distribution modeling, and paleoclimatology, I assess how environmental change has left an imprint on the genetics and ecology of various organisms. Signatures of the past are useful to forecast conservation issues of the future.

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INTRODUCTION

Systematics is undergoing a burgeoning resurgence (Wiley and Lieberman 2011) largely due to advancements in molecular sequencing technologies and novel phylogenetic reconstruction techniques that have provided unprecedented resolution in the study of evolutionary relationships (Edwards 2009; Hillis and Bull 1991; Knowles 2009; Knowles and Maddison 2002; Maddison 1997; Moritz and Hillis 1996). Consequently, intraspecific diversification, set within a broad geographic context, can now be explored in finer detail through phylogeographic studies (Avise 2000; Avise 2009; Hickerson et al. 2010). Frequently, historical biogeographic models are explored which are central to understanding how diversity is partitioned across the landscape (Riddle and Hafner 2007; Smith 2007; Wiens and Donoghue 2004). Increasingly integration of multiple forms of evidence (e.g. molecular phylogenies, fossils, and species distribution models – SDMs) are used to more finely delineate among alternative models (Carstens and Richards 2007) by explicitly testing phylogeographic hypotheses via statistical phylogeography (Knowles 2009), an approach developed over the last decade, but not without controversy (Beaumont et al. 2010; Templeton 2010). Statistical phylogeography, which is rooted in coalescent-based frameworks (Wakeley 2008), offers the necessary context to develop and test models of diversification and more clearly delineate among alternative evolutionary relationships.

Another emerging set of ideas focuses on the delimitation of species boundaries based largely on genetic information (Fujita *et al.* 2012), but bolstered by multiple forms of evidence within a general lineage context (de Queiroz 1998, 2007). Using only genetic information to describe geographic variation has been contentious (e.g., (Bauer et al. 2010; Fujita and Leache 2010; Leache and Fujita 2010), but approaches that integrate across genetic, morphological and ecological niche datasets may provide the most powerful means of assessing species boundaries (Fujita et al. 2012; Zhang et al. 2011) and developing a fully integrated taxonomy (Padial *et al.* 2010). An integrated taxonomy enhances our ability to explore processes of incipient diversification, rather than relying on the end products of diversification (e.g., identifying pre- and post-zygotic isolation mechanisms). Multiple, independently evolving loci, coupled with innovative methods of species-tree inference has fostered the identification of novel or cryptic species. Often lineages of organisms diverge at both genes and niches but may fail to be recognized by a morphologically-based taxonomy. Consequently, the general increase in the number of species has reinvigorated the call for consistency in taxonomy (Agapow et al. 2004; Isaac et al. 2004). However, others have argued that taxonomic consistency cannot be based on inaccurate phylogenetic understanding and can only be stabilized within an integrative context (Fujita et al. 2012; Padial et al. 2010).

In this dissertation, I test phylogenetic and phylogeographic hypotheses related to the evolution of North American zapodids. More specifically I assess historical biogeography, cryptic diversity and ecology, conservation phylogenetics within a broader phylogeographic and systematics context to better understand speciation within this group. Zapodids are widely distributed across North America and tend to inhabit regions characterized as cool and mesic or humid continental (Köppen climate type D - (Frey and Malaney 2009; Peel et al. 2007). Jumping mice habitats often coincide with riparian corridors, and especially mesic areas in montane regions in the dry climates of the interior west. Consequently, due to the isolation of montane regions and patchy distribution of riparian habitats, allopatric divergence is predicted to be common in jumping mice. Mammalian taxonomists (Holden and Musser 2005) recognize 4 species, the Woodland Jumping Mouse (*Napaeozapus insignis*), the Meadow Jumping Mouse (*Zapus hudsonius*), the Western Jumping Mouse (*Z. princeps*), and the Pacific Jumping Mouse (*Z. trinotatus*). Within the 4 species, 32 subspecies (Hall 1981; Krutzsch 1954) are recognized suggesting substantial geographic variation that can be assessed using phylogeographic hypothesis testing and, more broadly, an ideal system to better understand the roles of climate fluctuations in evolutionary diversification.

My dissertation presents three intergrated studies of zapodids that are based within an historical phylogenetic context to better explore the processes of diversification in a western North American montane associated mammal. Specifically, I use a statistical framework to assess alternative modes of incipient speciation by contrasting recent (Chapter 1) versus deep and persistent (Chapter 2) histories. In Chapter 3, I explore whether conservation practices for zapodids are based on a robust assessment of extant diversity and if they protect important processes and products of diversification. With these goals as background, I focus on assessing if the taxonomy accurately reflects phylogeographic variation within a multi-locus coalescent-based context using a species-tree. In the conclusions chapter, I propose an updated taxonomy using a hierarchical approach to species delimitation. Finally, jumping mice relationships are set within the broader context of North American boreal mammal biogeographic history using a comparative phylogeographic approach.

Overview

In the first chapter of my dissertation (Malaney et al. 2012), I tested alternative historical biogeographic hypotheses related to the diversification of a montane mammal endemic to the American Southwest. Specifically I used the parametric bootstrap based on sequence variation in two mitochondrial genes (cyt*b* and control region) to test alternative models of ancient vicariance, sequential colonization, or recent fragmentation as the most plausible scenario of regional divergence. Each scenario had been proposed as historical-biogeographic hypotheses for several southwestern montane-associated species, but with conflicting evidence for each. When coupled with SDMs and the fossil record, I revealed that the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) represents a neo-endemic that colonized eastward from the Edwards Plateau since the Late Pleistocene followed by recent fragmentation since the LGM. Further these efforts highlighted four conservation implications for this taxon: (1) *Z. h. luteus* is a monophyletic lineage on an independent evolutionary trajectory; (2) *Z. h. luteus* shared a recent common ancestor with *Z. h. pallidus* (not *Z. h. preblei*); (3) mtDNA does not reflect recent population declines; and (4) coalescent simulations and species distribution models reflect Holocene fragmentation.

In the second chapter, I focus on the montane regions of western North America and explore historical signals of persistent allopatric versus recent admixture (Knowles and Carstens 2007). Understanding how diversity is partitioned across the landscape can provide perspectives related to the environmental process that may have influenced evolutionary history and also provides an essential framework for conservation. Western North America has a diverse biota that is the product of complex evolutionary and environmental processes (Lomolino et al. 2006) and this region has experienced fluctuations tied to glacial cycling that may have left genetic imprints (Riddle and Hafner 2006). Significant intraspecific genetic variation in mammals across the west is also hypothesized to have been shaped by extreme topographic heterogeneity. Previous molecular investigations of western mammals provided novel views related to diversification, occasionally revealing unexpected genetic architectures (Alvarez-Castañeda and Patton 2004; Galbreath et al. 2010; Hornsby and Matocq 2011; Matocq 2002; Riddle et al. 2000). Documentation of geographic molecular variation in organisms, when combined with assessments of demography, historical biogeography, and niche variation, can provide insight into key questions related to climate change, post-Pleistocene colonization, habitat fragmentation, and possible future response to changing environments (Avise 2000; Avise 2009; Hickerson et al. 2010). In this chapter, I explore phylogeographic structure in the western jumping mouse (*Zapus princeps*) as a window into the biogeographic history of western North America. Specifically, I test alternative models of evolutionary history and then analyze spatial demography and niche divergence in this group.

The third chapter of my dissertation shifts from single marker (mtDNA) hypothesis tests into multi-locus coalescent-based assessments, but with a direct conservation application. This study points to the value of shifting conservation assessment from piecemeal appraisals of limited phylogenetic components (e.g. geographically proximal subspecies) to an expanded lineage-based assessment that places ecological and evolutionary divergence within a broader comparative framework. By using comprehensive sampling of taxonomic units across the geographic range of taxa, multiple genetic loci and the fossil record coupled with niche and population demographic assessments, I am better able assess conservation status. This assessment of zapodids highlights that conservation is often predicated on a weak understanding of taxonomic relationships and systematics coupled with biogeographic history should play a more central role in management actions.

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CHAPTER 1

THE BIOGEOGRAPHIC LEGACY OF AN IMPERILLED TAXON PROVIDES A FOUNDATION FOR ASSESSING LINEAGE DIVERSIFICATION, DEMOGRAPHY AND CONSERVATION GENETICS

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ABSTRACT

Aim

To test alternative biogeographic hypotheses related to the diversification of a montane mammal (*Zapus hudsonius luteus*) endemic to the American Southwest.

Location

Southwestern United States.

Methods

We used statistical phylogeographic analyses of mitochondrial DNA (1512 bp; two genes) from 93 individuals from 6 geographic regions to test diversification hypotheses. Species distribution models of climate and fossil records were integrated to assess contemporary and historical distributions and barriers to gene flow. We calculated dates of divergence and examined historical demography using coalescent simulations.

Results

We documented monophyly of *Z. h. luteus* represented by 19 segregated haplotypes. Predicted current distribution generally coincided with known localities while predicted paleodistributions suggested that this lineage was widespread throughout lower elevations of the American Southwest and on the Edwards Plateau (as documented by the fossil record). Population size did not change substantially during a westward shift in range that occurred in the last 100k generations. Results supported fragmentation of a common ancestor during the Holocene as the most plausible explanation for genetic structure.

Main conclusions

Monophyletic *Z. h. luteus* reflects fragmentation of a common ancestor with recent (Holocene) upslope colonization of disjunct montane areas. We refute the hypotheses of *in situ* divergence or origins from a Colorado Piedmont ancestor. Instead, westward colonization from the Edwards Plateau during the Wisconsin followed by Holocene fragmentation which serves as a generalized biogeographic hypothesis for species associated with mesic graminoid habitats in the American Southwest. Further exploration of these signatures using independent nuclear DNA is warranted. Key conservation implications: 1) *Z. h. luteus* is a monophyletic lineage on an independent evolutionary trajectory; 2) *Z. h. luteus* shared a recent common ancestor with *Z. h. pallidus* (not *Z. h. preblei*); 3) mtDNA does not reflect recent population declines; 4) coalescent simulations and species distribution models reflect Holocene fragmentation.

Keywords American Southwest, coalescent parametric bootstrap, species distribution modelling, fossils, montane biogeography, *Zapus hudsonius luteus.*

INTRODUCTION

Climate oscillations that change local environmental conditions often cause species distributions to shift, expand or contract along latitudinal or elevational gradients (Hewitt, 2001, 2004). Whenever species track fluctuating environmental conditions, populations may experience alternating periods of either isolation or connectivity (Hewitt, 1996; Wiens, 2004; Wiens & Graham, 2005). Genetic signatures often reflect the response of organisms to changing environments. These signatures may reveal episodes of range shifts (e.g. expansion), admixture of previously isolated populations, or range contraction sustaining population divergence. Teasing apart the influence of complex historical processes has proven difficult, but statistical phylogeography enhances our ability to test specific hypotheses related to the evolution and biogeography of organisms (Knowles, 2009).

Climate change during the Pleistocene is hypothesized to have shaped the distributions, divergence patterns, and historical demography of species in western North America. Cooler, mesic conditions extended to lower elevations and latitudes during glacial periods, but subsequently retreated upslope and to higher latitudes during warmer and more xeric interglacial periods. Cyclic glacial/inter-glacial episodes were repeated >20 times during the Pleistocene culminating in the diversification of North American terrestrial mammals via the Rancholabrean faunal events (Bell *et al.*, 2004). These processes sequentially led to complex historical patterns revealed by distinctive genetic signatures. For example, longhorn beetles (genus *Moneilema*) and jumping spiders (genus *Habronattus*) exhibit a genetic signature of divergence on isolated Madrean sky islands in the Southwest (Maddison & McMahon, 2000; Masta, 2000; Smith & Farrell, 2005). Southwestern canyon tree frogs (*Hyla arenicolor*) have deep divergence but repeated episodes of hybridization with closely related taxa (Barber, 1999; Bryson *et al.*, 2010; Klymus *et al.*, 2010). Mountain snails (*Oreohelix* sp.) show signatures of long-term isolation, possibly through multiple glacial cycles (Weaver *et al.*, 2006), while montane salamanders (*Plethodon ouachitae*) show structure developed through a stepping stone dispersal along an east-west axis (Shepard & Burbrink, 2008). Finally, montane grasshoppers (*Melanoplus* sp.) were isolated on mountains but subsequent expansion during interglacials led to complex, admixed signatures (Knowles, 2001b, a; Knowles *et al.*, 2007). Thus, genetic signatures reflect diverse histories ranging from deep and structured to ephemeral and stochastic. An alternative possibility is that populations persisted in isolation during glacial cooling and then tracked changing environments into new regions with warming and drying conditions. This alternative vicariance hypothesis for the American Southwest (Findley, 1969; Patterson, 1980; Frey *et al.*, 2007) has yet to be empirically tested using phylogeographic methods. The sky islands of the North American Southwest are rich reservoirs of biological diversity (Merriam, 1890), that long have been the focus of naturalists and served as the empirical foundation for various hypotheses on origins, diversification, and biogeographic history of the biota of the region (Brown, 1971). This system is ideal for exploring population genetic variation within the context of paleo-environmental fragmentation.

The mammalian fauna of the mountains of the American Southwest is an assemblage of primarily Cordilleran and Boreo-Cordilleran species of northern origins (Armstrong, 1972), although a minority of the assemblage also includes representatives from elsewhere (Patterson, 1989). There has been debate whether the processes that produced these assemblages were the result of vicariance (isolation) of prior widespread pluvial communities (Findley, 1969; Patterson, 1980; Sullivan, 1994; Ditto & Frey, 2007; Frey *et al.*, 2007) or postglacial colonization (immigration and mixing, Davis *et al.*, 1988; Lomolino *et al.*, 1989; Lomolino & Davis, 1997). Not previously considered is the possibility that mesic grasslands to the east of this region provided a source for colonization of high elevation mesic sites during the Holocene. These scenarios form the basis of three alternative hypotheses of historical biogeography that are expected to produce unique demographic signatures reflected in the DNA as detected using calculations of the coalescent. Integration of information from current and historical distributions based on independent data, such as fossils and species distribution models (SDMs), can further support alternative hypotheses. The first hypothesis (i.e., ancient vicariance - AV) of long-term isolation of communities reflects sustained segregation through alternating climate cycles associated with multiple pluvial and interglacial periods (Findley, 1969; Brunsfeld *et al.*, 2001). The second hypothesis (i.e., sequential colonization - SC) is colonization via a stepping stone process from a northern source (Davis *et al.*, 1988; Lomolino *et al.*, 1989; Lomolino & Davis, 1997). The third hypothesis (i.e., recent fragmentation - RF) is a single recent vicariant event corresponding to the current interglacial in which fragmentation of more widespread pluvial communities has occurred since the Wisconsin (McDonald & Brown, 1992; Hafner, 1993; Patterson, 1999; Smith & Brown, 2002; Frey *et al.*, 2007).

Ample fossil evidence suggests that several species that today are associated with mesic grasslands in the eastern US, had a wider distribution further west during the Pleistocene (Harris & Findley, 1964; Harris, 1970; Findley *et al.*, 1975; Harris, 1990;

Hafner, 1993; Harris, 1993; Lear & Harris, 2007). Fossils provide an important direct link (albeit often incomplete) to historical distributions. New approaches in phylogeography that combine coalescent-based analyses of historical demography with species distribution modelling and direct fossil evidence allow formal tests regarding how contemporary faunas were assembled including rates of migration, divergence history (timing and patterns), and demographic changes. Genetic signatures thus allow tests among three alternative historical biogeographic hypotheses.

The New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) is a morphologically and genetically distinctive mammal restricted to riparian habitats in the southwestern United States (Miller, 1911; Hafner *et al.*, 1981; Morrison, 1992; King *et al.*, 2006; Frey & Malaney, 2009). Originally described as a distinct species, *Z. luteus*, based on unique pelage and cranial morphology (Miller, 1911), it was reclassified as a subspecies of *Z. princeps* (Krutzsch, 1954) and later as a subspecies of *Z. hudsonius* (Hafner *et al.*, 1981). Genetic studies identified three fixed allozyme alleles in comparisons with other subspecies of *Z. hudsonius* (Hafner *et al.*, 1981). Reciprocal monophyly of mtDNA haplotypes (Ramey *et al.*, 2005; King *et al.*, 2006; Vignieri *et al.*, 2006) further suggests that *Z. h. luteus* may warrant status as an independent species.

Zapus h. luteus has been extirpated from most historical locations due to degradation of riparian habitats primarily as a function of livestock grazing (Frey & Malaney, 2009) and in December 2007, was listed as a candidate for protection under the federal Endangered Species Act. Current conservation status for the subspecies includes “Endangered” on the state list for New Mexico and “Threatened” in Arizona. The species has a Natural Heritage conservation status of “Globally Rare” and "Critically Imperiled

(S1)” in Arizona, Colorado, and New Mexico. Although the IUCN Red List of Threatened Species (http://www.iucnredlist.org/apps/redlist) lists *Z. h. luteus* as “Lower Risk, Near Threatened (LR, NT)”, that listing was based on an earlier assessment that recommended further study (Yensen *et al.*, 1998). Subsequently, molecular genetic analyses have led to a better appreciation of genetic distinctiveness of the taxon (Ramey *et al.*, 2005; King *et al.*, 2006; Vignieri *et al.*, 2006).
Further, comprehensive field surveys and ecological studies have revealed dramatic declines in distribution and abundance of the taxon due to ongoing severe threats of drought, catastrophic wildfires, and harmful land management practices, which together warrant a change in listing to "Critically Endangered (CR)" (IUCN, 2001; Frey & Malaney, 2009).

In general, *Z. hudsonius* (Findley *et al.*, 1975; Hall, 1981; Frey & Malaney, 2009) is found in habitats identified as humid continental (Köppen climate type D)(Peel *et al.*, 2007; Frey & Malaney, 2009) but these habitats are highly restricted in the dry climates of the interior west. Consequently, at its southwestern margin this species is restricted to riparian corridors with cool, mesic habitats. Disjunct populations of *Z. h. luteus* are known from the San Juan, Jemez, Sangre de Cristo, Sacramento, and White mountains. However, unlike other montane specialists in the region *Z. h. luteus* also occurs in low-elevation riparian habitats along major rivers (Fig. 1), including the Rio Grande and principal tributaries of the San Juan River (Findley *et al.*, 1975; Hoffmeister, 1986; Hafner, 1993; Frey & Malaney, 2009).

Hafner and colleagues (Hafner *et al.*, 1981; Hafner, 1993) hypothesized that *Z. hudsonius* colonized the American Southwest either southward from the Colorado

Piedmont or westward from the Edwards Plateau, during glacial maxima when cool, mesic grasslands existed across central and southern New Mexico and further northeast and east. Westward colonization is supported by late Wisconsin fossils of *Z. hudsonius* from central Texas (Dalquest *et al.*, 1969; Hafner, 1993) and early Holocene subfossils in southwestern New Mexico (Scarbrough, 1986), indicating a broad potential distribution throughout the lowlands east of current *Z. h. luteus* distribution.

Our goal is to test alternative biogeographic hypotheses of diversification with statistical phylogeography by integrating coalescent-based modelling (Richards *et al.*, 2007; Buckley, 2009; Franklin, 2010), fossil evidence, and SDMs. Specifically, we test models of spatiotemporal diversification for *Z. h. luteus* linking low elevation populations with montane congeners of the American Southwest. First, we test whether each geographically isolated population is a distinct evolutionary unit. Second, we assess whether contemporary or historical barriers to gene flow can be identified based on SDMs. We estimate dates of divergence and then use coalescent simulations to test if divergence is consistent with paleodistribution models and Late Pleistocene fossils. Fourth, we use coalescent simulations to test three alternative hypotheses of historical biogeography. Finally, we explore historical demography for *Z. h. luteus* to tease apart the effects of fluctuating climate on historical population size (N_E) and to assess landscape genetic diversity. We conclude by summarizing empirical and simulated data that refute alternative colonization or *in situ* diversification hypotheses and establish a management framework for the conservation of *Z. h. luteus* (Richardson & Whittaker, 2010; Scoble & Lowe, 2010).

METHODS

DNA extraction, PCR and sequencing

We obtained mitochondrial DNA sequences from 93 *Z. h. luteus* representing 22 localities and 6 spatially distinct geographic regions (Fig. 1, Appendix S1) to address phylogeographic questions and explore historical demographic parameters that influence conservation efforts. We sequenced a fragment of the mitochondrial control region (CR – 372 bp) and the complete cytochrome *b* gene (cyt *b* – 1140 bp). Genomic DNA was extracted from frozen (-80ºC) or ethanol (95% EtoH) preserved heart or liver tissue using Qiagen DNeasy Kit extraction protocols (QIAGEN, Inc.). We used CR primers L15926 and H16498 and cyt *b* primers L14398A and H15634A (King *et al.*, 2006) for all PCR reactions which contained 2 µl of ~50ng/µl of template DNA, 1.25 µl of primer (10mM), 0.5 µl of dNTP's (10 mM), 2 µl $MgCl_2$ (25 mM), 2 µl of 10x polymerase reaction buffer, 0.08 µl of *Taq* polymerase (Applied Biosystems, Foster City, CA) and adjusted to a final volume of 25 µl with ddH20. Thermal-cycling profile followed: 180 s at 94ºC; 30 cycles of 60 s at 94ºC, 60 s at 50ºC, and 120 s at 72ºC.

Bi-directional sequencing reactions used the BIGDYE Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA) and with an automated sequencer (Model 3130, Applied Biosystems, Inc., Foster City, California) using the original primers plus cyt*b*IF2 and cyt*b*IR2 internal primers for the cyt *b* gene (King *et al.*, 2006). Sequences were cleaned with ethanol precipitation and edited with SEQUENCHER ver. 4.5 (GeneCodes) and compared to a reference sequence (GenBank No. AF119262; *Z. trinotatus*). Sequences were aligned using MUSCLE ver. 3.7 (Edgar, 2004) available at the

European Bioinformatics Institute web services (http://www.ebi.ac.uk/Tools/webservices/) and validated by eye. Individual genes were deposited in GenBank (JN546435 - JN546538; Appendix 1). Sixteen *Z. h. luteus* and 8 individuals from related subspecies (two of each: *Z. h. campestris, Z. h. intermedius, Z. h. pallidus, Z. h. preblei*) were obtained from GenBank (Appendix S1).

Phylogeography

We evaluated phylogenetic heterogeneity using the partition homogeneity test in PAUP* ver. 4.0b10 (Swofford, 2002). Given the lack of significant differences between these linked markers, all subsequent phylogeographic analyses were completed with a concatenated dataset with two non-independent data partitions (CR – non-coding and cyt *b* – coding). Phylogenies for *Z. h. luteus* were compared to closely related subspecies to identify the most recent common ancestor (MRCA, Appendix S1, Fig. 2; (Ramey *et al.*, 2005; King *et al.*, 2006). Phylogenetic inference was based on Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian inference (Posterior probability - PP). MODELTEST ver. 3.7 (Posada & Crandall, 1998) estimated the best-fit model of nucleotide substitution by the Akaike Information Criterion (AIC) resulting in a general-time reversible plus gamma (GTR + Γ) used in character state analyses. All phylogeny reconstructions were conducted using the University of Alaska Fairbanks Life Science Informatics Portal (http://biotech.inbre.alaska.edu/portal/). Trees from MP, ML, and PP were comparable with the most credible inferences of relationships confined to nodes of nonparametric bootstrap support (MP, ML) or posterior probability (PP) values (Hillis & Bull, 1993; Felsenstein, 2004).

For phylogeny reconstruction, we performed maximum parsimony analyses using PAUP* ver. 4.0b10 (Swofford, 2002), through heuristic searches using 1,000 random addition sequence replicates involving tree bisection-reconnection (TBR) branch swapping. Transitions and transversions were treated equally and gaps were treated as a 5th state. We assessed statistical support for clades with nonparametric bootstrap analysis (Felsenstein, 1985) using 1,000 bootstrap replicates, each with 100 random addition sequence replicates and TBR branch swapping.

Maximum likelihood topologies and associated support were obtained with GARLI ver. 0.960 (Zwickl, 2006) using parameter estimates from MODELTEST. Support was evaluated using 1,000 bootstrap replicates (Felsenstein, 1985). Bayesian inference was implemented in MRBAYES ver. 3.1.2 (Huelsenbeck & Ronquist, 2005). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) sampling was performed using four chains run for 1,000,000 generations, with default parameters and sampling every 1000th generation. Three independent searches were performed to ensure convergence for each analysis.

NETWORK ver. 4.2 (http://www.fluxus-technology.com) was used to generate a median joining network representing the genealogical relationships among haplotypes of *Z. h. luteus* because incipient speciation may violate methods used in phylogenetic reconstructions (Posada & Crandall, 2002). Haplotype (h) and nucleotide (π) diversity and mean pairwise nucleotide differences (K) were calculated in DNASP ver. 5.10.00 (Librado & Rozas, 2009). We used Analysis of Molecular Variance (AMOVA) to identify variation within and between distinct geographic regions of *Z. h. luteus*. Results of AMOVA were compared to original geographic regions (Fig. 1).

Species Distribution Modelling

We downloaded raster coverage's for 19 bioclimatic variables from the WorldClim database (http//www.worldclim.org) for contemporary and last glacial maximum (LGM) at 30 arc-seconds resolution (Hijmans *et al.*, 2005). We followed modelling procedures from previous studies (Waltari *et al.*, 2007; Waltari & Guralnick, 2009), and reduced the dataset to the eleven most biologically meaningful and uncorrelated coverages for North America (Rissler & Apodaca, 2007). Localities for *Z. h. luteus* were obtained from original field-collected GPS coordinates or georeferencing through a review of field notes and other information associated with museum specimens. Localities for the sister taxon, *Z. h. pallidus,* were downloaded from MANIS (8 Jan 2010). Localities with >0.5km^2 uncertainty were discarded resulting in 92 *Z. h. luteus*, and 60 *Z. h. pallidus* localities (Fig. 3).

We constructed SDMs for both contemporary and paleodistributions (at LGM) for both *Z. h. luteus* and *Z. h. pallidus* and the combined distribution of *Z. h. luteus/pallidus* using the default settings in the program MAXENT ver. 3.3.3a (Elith *et al.*, 2006; Phillips *et al.*, 2006). We ran 20 replicates with 20th percentile training presence criteria and depicted the results using the point-wise bootstrap mean of the models. Localities represent the known distribution for *Z. h. luteu*s and *Z. h. pallidus* to identify the variables constituting the fundamental niche of each individually (Hutchinson, 1957; Soberon & Peterson, 2005; Holt, 2009; Soberon, 2010) and the combined potential paleodistribution was used to identify potential overlap between lineages. A threshold value of 0.70 was used to interpret predicted distributions and structure *a priori* hypotheses for coalescent simulations to establish divergence patterns at the LGM. Basic assumptions of SDMs include niche conservatism (Wiens & Graham, 2005), environmental data adequate to generate predictions of a species' distribution (Kozak *et al.*, 2008; McCormack *et al.*, 2010), and adequate records of occurrence that encapsulate the species niche (Pearson *et al.*, 2007).

Timing of Divergence

Fossil deposits in South Dakota, Nebraska, and Kansas, identify the most recent common ancestor for *Z. hudsonius* (*Z. sandersi*) in the middle Pleistocene ~1.0 Myra (Kurtén & Anderson, 1980). We chose a conservative divergence point of 1.0 Myr BP for *Z. hudsonius* from *Z. sandersi* and calculations of molecular sequence evolution was 3.14% per Myr (95%CI = 1.70% & 4.58%). A Bayesian coalescent approach implemented in BEAST ver. 1.5.3 was used to estimate the timing of divergence (Drummond & Rambaut, 2007). The GTR+ Γ model of evolution with four rate categories was used with priors of an uncorrelated lognormal tree, constant population size, and an assumed relaxed lognormal clock scaled to 100 ky BP (Drummond *et al.*, 2006). All other parameter settings were default. Analyses estimated tree shape and divergence dates for nodes and sampled every 1000 iterations for 50 million generations with 10% of the initial samples discarded as burn-in. Results were analyzed in TRACER ver. 1.5 (Drummond & Rambaut, 2007) to check for appropriately large Effective Sample Size (ESS) values, convergence of results, and performance of operators.

Coalescent Simulations

Coalescent simulations were conducted to test specific historical biogeographic hypotheses (AV, SC, RF) with MESQUITE ver. 2.7 (Maddison & Maddison, 2009) using a likelihood based or frequentist approach (Knowles & Maddison, 2002; Hickerson *et al.*, 2010) versus estimating parameters not directly related to our questions (Beaumont *et al.*, 2002). Gene matrices were simulated with 1,000 replicates for each hypothesis using ancestral $N_{E(f)}$ (84,395) from our estimate of the parameter θw, one-year generation time, and divergence estimate for *Z. h. luteus/pallidus* (17.5 kya) obtained in BEAST. We evaluated the validity of these models by using upper and lower confidence intervals (90%) of θw (Knowles *et al.*, 2007).

We constructed genealogies from each matrix in PAUP* heuristic parsimony searches with 10 random addition replicates, tree bisection-reconnection branch swapping and max-trees set to 100. Each search produced a majority-rule consensus tree from which we calculated *s* (Slatkin & Maddison, 1989), a measure of discord between the reconstructed gene tree and the assignment of individuals into separate lineages. When lineage assignment is treated as a character that is mapped parsimoniously onto the gene tree, *s* is the number of observed character state changes. Higher values of *s* for a specific locus indicate that sequences are paraphyletic with respect to their lineage association, a possible indication of either gene flow or incomplete lineage sorting. The test statistic of empirical data was compared against simulated data and considered to be significant (two-tailed) if the empirical values occur outside of the 90% CI generated via simulation tests.

Our θ estimates (effective population size scaled to the neutral mutation rate) were calibrated to recent fossil dates (100 kyr BP) using the equation $\theta = 4N_{E(f)}\mu$, assuming $\mu = 3.14$ substitutions per Myr calculated in BEAST. Scaled branch widths of θ were used for each of the biogeographic hypotheses.

Historical demography

Historical demography was reconstructed with Bayesian Skyline Plots (BSP; (Drummond *et al.*, 2005) as implemented in BEAST which estimates θ through time and does not require a specified demographic model (e.g. constant size, exponential growth, logistic growth, or expansive growth). We used the same parameters as timing of divergence and applied five grouped coalescent intervals (*m*).

Finally, we tested for non-neutral mutational changes with Tajima's *D* (Tajima, 1989), Fu's F_S (Fu, 1997), which were calculated in DNASP ver. 5.10 (Librado & Rozas, 2009) and significance was tested with 10,000 coalescent simulations. For these historical demographic analyses, we used a reduced dataset of 56 individuals representing coding region (cyt *b*) of sequence data as these tests are sensitive to synonymous versus non-synonymous changes and missing data.

Landscape genetics

We tested the null hypotheses of no population differentiation among all sampled sites ($F_{ST} = 0$) using 10,000 permutations in ARLEQUIN. To examine the relationship between geographic distance and genetic distance we performed Mantel tests and interpolation of genetic landscape shape using Alleles in Space (AIS, (Miller, 2005).

RESULTS

DNA extraction, PCR and sequencing

Using the concatenated dataset of 1514 bp (i.e., 1512 plus 2 insertions), we documented 19 haplotypes, with 36 variable sites of which 17 were parsimony informative for *Z. h. luteus* (Table 1). We re-sequenced 8 individuals for CR given differences reported between Ramey *et al.* (2005) and King *et al.* (2006) datasets and added sequences from cyt *b* for these individuals. We further compared CR & cyt *b* sequences with King *et al.* (2006) for 13 individuals. We documented no discordance with either dataset downloaded from GenBank when compared to our *Z. h. luteus* sequences but identified and then corrected errors in reporting museum catalogue numbers and localities (Appendix S1).

Phylogeography

Zapus h. luteus was monophyletic but showed little geographic structure (Fig. 2). Tree topologies were consistent across methods MP, ML, and PP. Median joining network (Fig. 4) identified a common haplotype in the Jemez Mountains (Hap 1) that is shared with the Sacramento Mountains and upper Rio Grande. The most divergent haplotype (Hap 12) differs by 8 mutations and occurs in the Sangre de Cristo Mountains. The tree topologies identified *Z. h. pallidus* as sister taxon to *Z. h. luteus* (Fig. 2). This agrees with previous findings by Ramey *et al.* (2005; based on mtDNA sequence and nuclear microsatellites), shared characteristic haplotypes (Vignieri *et al.*, 2006), and more extensive mtDNA sequence and nuclear microsatellite data (King *et al.*, 2006).

Species Distribution Modelling

Distribution models performed well (i.e., AUC > 0.95) with variables of annual mean temperature (Bio1) and precipitation of the driest month (Bio15) contributing most to the model (Bio1 – 45.2%, Bio15 – 11.0%, Bio17 – 9.1%, Bio7 – 8.0%, Bio9 – 7.6%, Bio8 – 7.0%, others <5.0%). Annual mean temperature was the most informative variable alone based on the jackknife test of variable importance. In general, this model accurately predicted the location of 4 of 6 known regions (Jemez, Sangre de Cristo, White, Sacramento). However, the model failed to predict occupied areas along major low-elevation rivers in arid areas (i.e., lower Rio Grande, San Juan River tributaries), perhaps because suitable microclimate in these river systems is extremely limited (Fig. 3). In addition, the model predicted suitable climate in several areas where *Z. h. luteus* is not known to occur such as the Mogollon Mountains and Black Range in southwestern New Mexico.

The LGM model predicted wider (compared to current) potential paleodistributions for *Z. h. luteus* (Fig. 3). Most of this predicted distribution is outside the currently occupied range. Fossils for this lineage of *Z. hudsonius* are available from Hall, Schulze, and Zesch caves on the Edwards Plateau (Fig. 3; (Dalquest *et al.*, 1969; Hafner, 1993; Sagebiel, 2010), and from Tonk Creek in the North-central plains (Pfau, 1994), all of which date to the late Wisconsin. Scarbrough (1986) identified fossil teeth of *Z. hudsonius* from Bat Cave, Plains of San Augustin (= Agustín) in southwestern New Mexico that date to the early Holocene (approximately 8000y BP; Harris, 1990). Additional older fossils are available for *Zapus* sp. in Kansas and Oklahoma dating from the Middle Pleistocene into the Pliocene (Krutzsch, 1954; Hibbard, 1956; Klingener, 1963). Finally, there are several Holocene and Pleistocene faunas throughout the American Southwest where *Zapus* are absent (Kurtén & Anderson, 1980; Harris, 1990).

Timing of Divergence

The MRCA of *Z. h. luteus* dates to the Late Pleistocene 17.5kyr BP (95% CI, 3.0 – 38.7kyr BP) which diverged from the most recent common ancestor of *Z. h. pallidus* roughly 25kyr BP (95%CI, 7.1 – 62.4kyr BP) from an average mutation rate of 3.14% (95% CI, 1.71% – 4.58%) per million years. We calculated $\Theta w = 0.0053$ resulting in an ancestral N_E of 84,395.

Coalescent Simulations

The recently fragmented ancestor hypothesis could not be rejected and alternative hypotheses (AV and SC) of diversification were rejected. These results are based on the observed value of Slatkin and Maddison's *s* as compared to simulated values ($s = 56$; Fig. 2; Slatkin and Maddison, 1989).

Historical demography

All coalescent calculations of neutrality failed to reject the null hypothesis of static demography (Table 2). *Zapus h. luteus* populations were static for the last 175k years but began increasing roughly 25kyr BP, or at the LGM and entering into the current interglacial (i.e., early Holocene; all ESS values > 300; Fig. 4). That period coincides with the split of *Z. h. luteus/pallidus* (Fig. 2). A slight increase in effective population size from the late Pleistocene through the Holocene corresponds to the range shifts documented between the paleodistribution and the contemporary distribution of *Z. h.*

luteus (Fig. 3). We do not detect a significant signature of population demographic expansion using these techniques.

Landscape Genetics

Results of AMOVA revealed that 66% of the variation is within populations of *Z. h. luteus* with a lower than expected fixation index (F_{ST} = .3394, P < 0.01) for *Z. h. luteus*. The correlation of genetic distance to geographic distance was low (r = 0.034) with little chance of observing values greater (*P* = 0.4396) or less (*P* = 0.5614). Barriers to gene flow, based on landscape shape interpolation, exist in the northern distribution of *Z. h. luteus* (Fig. 4).

DISCUSSION

Biogeographic History

Based on an array of independent evidence including phylogeny, coalescent simulations, SDMs, and fossils, the recently fragmented ancestor model was supported. We rejected alternative models of sequential colonization and the ancient vicariance with persistent isolation. The ancestor of *Z. h. luteus* occurred on the Edwards Plateau and eastern edge of the Southern Plains during the LGM, a conclusion supported by both SDMs and direct fossil evidence. We postulate that the ancestor then shifted distribution westward as it tracked warming climate of the Holocene, eventually resulting in vicariance into multiple populations as it retreated to mesic riparian refugia in mountains or along major rivers. Given the close association of *Z. h. luteus* with riparian areas (Frey & Malaney, 2009), we hypothesize the use of river systems (e.g., the Rio Grande or Pecos River) or ancient lake shores (Plains of San Agustín) as colonization routes due to the dense herbaceous cover required and these areas coincide with the potential distributions at LGM. The only fossils of *Z. hudsonius* from the American Southwest are those from the Plains of San Agustín in southwestern New Mexico, which are dated to the Holocene (8000kyr BP). The appearance of *Z. hudsonius* fossils at this time and place suggests the early Holocene colonization of New Mexico, because this species is absent from multiple earlier fossil deposits in this region (Kurtén & Anderson, 1980; Scarbrough, 1986; Harris, 1990). We detected signatures of recent fragmentation and shifting distributions to higher elevations but failed to detect a strong signature of demographic expansion. The Bayesian skyline plot showed that effective population size remained constant for several thousand generations. Further, there was no departure from neutrality typically indicative of populations experiencing rapid demographic change (Lessa *et al.*, 2003; Lessa *et al.*, 2010). Consequently, we conclude *Z. h. luteus* shifted distribution since the LGM with minor historical fluctuations in population size, and have only recently (i.e., last 10kyr) been fragmented to their current distributions.

Hafner *et al.* (1981) suggested that the ancestor of *Z. h. luteus* instead occurred in the north (inferring close relationship with *Z. h. preblei*, which is the geographically closest conspecific populations to *Z. h. luteus*). These ancestors were hypothesized to have colonized Arizona and southern New Mexico during pluvial maxima via southward movement through the plains east of the Southern Rocky Mountains. Hafner *et al.* (1981) cited prior studies (Harris & Findley, 1964; Harris, 1970; Harris *et al.*, 1973) that suggested broad occurrence of cool, moist-grasslands throughout central and southern New Mexico as supporting evidence. However, upon discovery that LGM fossils of *Zapus* from the Edwards Plateau were *Z. hudsonius* rather than *Z. princeps*, Hafner (1993) modified this scenario to suggest that *Z. hudsonius* spread south and west to colonize the American Southwest. In doing so, he also refuted the earlier paleo-reconstruction hypothesis that the flora and fauna of the Edwards Plateau were continuously distributed across the High Plains to the Rocky Mountains through alpine meadow habitat (Dalquest *et al.*, 1969). Thus, Hafner (1993) concluded that the flora and fauna of the Edwards Plateau resulted from eastern grassland influence, rather than western boreal influences. Our study provides broad support for Hafner's (1993) conclusions, but refutes the earlier southward colonization model of Hafner *et al.* (1981). First, and in agreement with previous studies (Ramey *et al.*, 2005; King *et al.*, 2006; Vignieri *et al.*, 2006), *Z. h. luteus* is most closely related to *Z. h. pallidus*, not *Z. h.*

preblei. Secondly, there are no fossils to suggest either a *Z. h. luteus/preblei* ancestor on the Colorado Piedmont or an *in situ* lineage of *Z. h. luteus* in the American Southwest before the Holocene. The fossil record is consistent with a *Z. h. luteus/pallidus* ancestral lineage. Finally, divergence of *Z. h. luteus* and *Z. h. pallidus* coincided with the LGM when the recent ancestor of *Z. h. luteus* colonized north-westward during the warm, arid phase of the Holocene (Harris, 1990), while the *Z. h. pallidus* lineage shifted north and east. It seems likely that the phylogeographic history of *Z. h. luteus* may apply to other species that occur in the American Southwest but that have northeastern affinities (e.g., southern redbelly dace [*Phoxinus erythrogaster*], meadow vole [*Microtus pennsylvanicus*]).

Potential current distributions for *Z. h. luteus* were predicted from several areas (e.g. Mogollon Mountains and Black Range) where there are no records (Findley *et al.*, 1975; Hafner *et al.*, 1981; Morrison, 1992; Frey & Malaney, 2009; Frey, 2010). Three possibilities emerge: 1) these regions were colonized and subsequently went extinct (Findley, 1969; Patterson, 1980), 2) populations currently exist but have yet to be documented (Udvardy, 1969; Frey, 2009), or 3) colonization never occurred (Lomolino, 1993; Lomolino & Davis, 1997). Holocene fossils of *Z. hudsonius* from the Plains of San Agustín located near the northern edge of the Mogollon Mountain-Black Range massive and the edge of Pleistocene Lake San Agustín (Scarbrough, 1986) suggest *Z. h. luteus* was extirpated from this region.

Vicariance and Dispersal

Minimal genealogical structuring (Fig. 2) across the spatially disjunct populations of *Z. h. luteus* in the southwestern United States reflects a shallow demographic history without demographic expansion or contemporary gene flow (Excoffier *et al.*, 2009). Frey's (1994) cladistic analysis of allozyme data uncovered an unresolved polytomy and she concluded that *Z. h. luteus* diverged as a result of vicariance through the peripheral isolates model of speciation. Understanding the timing of these processes is critical because some of the patterns we documented, including low structure, shared haplotypes, no isolation by distance, and non-significant population increase, could alternatively be interpreted as signatures of recent gene flow. However, our explicit tests of hypotheses of historical biogeography demonstrate that there is no gene flow among currently isolated regions.

Brown (1971) hypothesized that boreal mammals in the Great Basin were island-bound Pleistocene relicts that are now survivors of more widespread ancestors, a paradigm which has persisted, albeit strongly challenged, for nearly four decades. Subsequent researchers have suggested many boreal species are capable of traversing the intervening desert habitats with high success (Davis & Dunford, 1987; Lawlor, 1998; Floyd *et al.*, 2005) thereby allowing persistent gene flow among islands. Timing of original establishment (extinction driven), or alternatively, timing of immigration among islands (colonization driven), is of critical importance in making sound conclusions about historical biogeography and conservation (DeChaine & Martin, 2006; Shepard & Burbrink, 2008, 2009). Indeed, there may be little genetic divergence among recently isolated regions because the coalescent process takes time and may be locally discordant (Rosenberg & Nordborg, 2002). But, concluding there is ongoing gene flow without entertaining alternatives can be problematic (Knowles, 2009; Beaumont *et al.*, 2010). Colonization-driven processes would exhibit different signatures than those reflected in *Z. h. luteus*.

Colonization or immigration-mediated signatures may reflect three different processes: 1) shared haplotypes among geographic localities resulting in multiple, sequentially structured haplotypes from a repetitive source, 2) a structured event (e.g. ancient vicariance) which is now mixed geographically, 3) or hybridization. Marmots (*Marmota flaviventris*) in the Great Basin appear to have sequential structure (Floyd *et al.*, 2005) whereas tree frogs (*Hyla arenicolor/H. wrightorum*) in the Grand Canyon have experienced recent hybridization (Bryson *et al.*, 2010). Finally, ongoing gene flow should result in haplotypes shared across geographic localities as detected in California voles (*Microtus californicus;* (Conroy & Neuwald, 2008; Adams & Hadly, 2010) and Pacific jumping mice (*Z. trinotatus;* (Vignieri, 2005). We document a low level of haplotype sharing between nearby regions which is due to a lack of lineage sorting, rather than ongoing gene flow.

Management Recommendations

As demonstrated here, isolated populations are not always highly divergent but may still retain distinctive signatures worth preserving as they reflect the complex history of the lineage. *Zapus h. luteus* has experienced recent rapid decline with extirpations of populations as a consequence of anthropogenic land use practices and drought (Frey & Malaney, 2009), however these recent declines were not reflected in the genetic signatures as the coalescent does not always detect very recent processes (Arbogast *et al.*, 2002; Wakeley, 2008). Mesic habitats, including riparian areas, are limited in the xeric Southwest and projected to experience significant declines within the next century (Moritz *et al.*, 2008). Management actions that aim to maintain or bolster populations of *Z. h. luteus* may be required. Repatriation efforts, in particular, will need to be properly planned to insure the genetic integrity of populations. Hence, we recommend additional studies using independent nuclear markers, given the shortcomings of a single-locus mtDNA data set, to more fully assess the relationships and diversification of geographically isolated populations (Brito & Edwards, 2009; Edwards, 2009). For example, some regions that we initially expected to be genetically similar, were not (northern and middle Rio Grande populations) while others show genetic distances that generally parallel landscape distances (Fig. 4). Finally, consequences of repatriation and artificial admixture of populations in attempts of genetic rescue (Hedrick, 2004) could have profound implications for altering the course of diversification for organisms that have begun independent evolutionary trajectories in contemporary isolation, thereby erasing early signatures of incipient speciation and biogeographic history. Consequently, conservation should preferentially focus on restoration of habitats and *in situ* expansion of remaining remnant populations with repatriation considered only as secondary measures.

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APPENDIX

Appendix S1 – GenBank accession numbers for taxa used in the manuscript with associated museum and tissue numbers; CR – mitochondrial control region and cyt *b* – mitochondrial cytochrome *b* gene. Geographic regions: JMZ - Jemez Mountains, MRG - Middle Rio Grande Valley, SAC - Sacramento Mountains, SDC - Sangre de Cristo Mountains, SAJ - San Juan Mountains, URG - Upper Rio Grande Valley, WHT - White Mountains. Haplotypes are listed that correspond with Fig. 4 and associated samples cited in the text with sampling localities represented as geographic coordinates (latitude and longitude).

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
	DMNH 8630	*Z. h. luteus*	AY598192.1		9	SDC	36.99667	-104.36750
	DMNH 8631	*Z. h. luteus*	AY598193.1		10	SDC	37.00111	-104.35833
	DMNH 8632	*Z. h. luteus*	AY598194.1		11	SDC	37.00056	-104.36083
	DMNH 8633	*Z. h. luteus*	AY598195.1		11	SDC	37.00056	-104.36083
	DMNH 8634	*Z. h. luteus*	AY598196.1		11	SDC	37.00056	-104.36083
	DMNH 8635	*Z. h. luteus*	AY598197.1		11	SDC	37.00056	-104.36083
MSB 37154		*Z. h. luteus*	AY598172.1		11	SAC	33.00437	-105.65555
MSB 40949	NK 1584	*Z. h. luteus*	JN546447	JN546501	13	WHT	33.78980	-109.41290
MSB 40950	NK 1585	*Z. h. luteus*	JN546448	JN546502	13	WHT	33.78980	-109.41290
MSB 40951	NK 1592	*Z. h. luteus*	JN546449	JN546503	14	WHT	33.78980	-109.41290
MSB 40952	NK 1593	*Z. h. luteus*	JN546450	JN546504	13	WHT	33.78980	-109.41290

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 40953	NK 1594	*Z. h. luteus*	JN546451	JN546505	14	WHT	33.78980	-109.41290
MSB 40954	NK 1595	*Z. h. luteus*	JN546452	JN546506	13	WHT	33.78980	-109.41290
MSB 40956	NK 1598	*Z. h. luteus*	JN546453	JN546507	14	WHT	33.78980	-109.41290
MSB 40994	NK 1603	*Z. h. luteus*	JN546454	JN546508	13	WHT	33.78980	-109.41290
MSB 40995	NK 1604	*Z. h. luteus*	JN546455	JN546509	14	WHT	33.78980	-109.41290
MSB 40996	NK 1605	*Z. h. luteus*	JN546456	JN546510	13	WHT	33.78980	-109.41290
MSB 40997	NK 1606	*Z. h. luteus*	JN546457	JN546511	13	WHT	33.78980	-109.41290
MSB 40998	NK 1607	*Z. h. luteus*	JN546458	JN546512	15	WHT	33.78980	-109.41290
MSB 41055	NK 856	*Z. h. luteus*	JN546461	JN546515	1	JMZ	35.88434	-106.72327
MSB 41058	NK 878	*Z. h. luteus*	JN546469	JN546523	1	SAC	32.95170	-105.70409
MSB 41059	NK 879	*Z. h. luteus*	JN546470	JN546524	1	SAC	32.95170	-105.70409

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 41060	NK 874	*Z. h. luteus*	JN546465	JN546519	1	SAC	32.95170	-105.70409
MSB 41061	NK 877	*Z. h. luteus*	JN546468	JN546522	1	SAC	32.95170	-105.70409
MSB 41062	NK 876	*Z. h. luteus*	JN546467	JN546521	1	SAC	32.95170	-105.70409
MSB 41063	NK 873	*Z. h. luteus*	JN546464	JN546518	1	SAC	32.95170	-105.70409
MSB 41064	NK 875	*Z. h. luteus*	JN546466	JN546520	1	SAC	32.95170	-105.70409
MSB 41065	NK 871	*Z. h. luteus*	JN546462	JN546516	1	SAC	32.95170	-105.70409
MSB 41066	NK 872	*Z. h. luteus*	JN546463	JN546517	1	SAC	32.95170	-105.70409
MSB 41223	NK 884	*Z. h. luteus*	JN546471	JN546525	19	MRG	33.80214	-106.86759
MSB 41224	NK 885	*Z. h. luteus*	JN546472	JN546526	19	MRG	33.80214	-106.86759
MSB 41225	NK 886	*Z. h. luteus*	JN546473	JN546527	19	MRG	33.80214	-106.86759
MSB 41226	NK 887	*Z. h. luteus*	JN546474	JN546528	19	MRG	33.80214	-106.86759

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 41227	NK 888	*Z. h. luteus*	JN546475	JN546529	19	MRG	33.80214	-106.86759
MSB 41228	NK 889	*Z. h. luteus*	JN546476	JN546530	19	MRG	33.80214	-106.86759
MSB 41229	NK 890	*Z. h. luteus*	JN546477	JN546531	19	MRG	33.80214	-106.86759
MSB 41230	NK 892	*Z. h. luteus*	JN546478	JN546532	19	MRG	33.80214	-106.86759
MSB 41231	NK 893	*Z. h. luteus*	JN546479	JN546533	19	MRG	33.80214	-106.86759
MSB 41232	NK 894	*Z. h. luteus*	JN546480	JN546534	19	MRG	33.80214	-106.86759
MSB 41233	NK 895	*Z. h. luteus*	JN546481	JN546535	19	MRG	33.80214	-106.86759
MSB 41234	NK 896	*Z. h. luteus*	JN546482	JN546536	19	MRG	33.80214	-106.86759
MSB 41235	NK 897	*Z. h. luteus*	JN546483	JN546537	19	MRG	33.80214	-106.86759
MSB 56979	NK 3832	*Z. h. luteus*	DQ664623.1	DQ664979.1	1	JMZ	35.88434	-106.72327
MSB 56980	NK 3835	*Z. h. luteus*	DQ664626.1	DQ664981.1	1	JMZ	35.88434	-106.72327

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 56981	NK 3837	*Z. h. luteus*	DQ664628.1	DQ664983.1	1	JMZ	35.88434	-106.72327
MSB 56982	NK 3826	*Z. h. luteus*	DQ664618.1	DQ664973.1	1	JMZ	35.88434	-106.72327
MSB 56983	NK 3833	*Z. h. luteus*	DQ664624.1		1	JMZ	35.88434	-106.72327
MSB 56984	NK 3830	*Z. h. luteus*		DQ664977.1	1	JMZ	35.88130	-106.71880
MSB 56985	NK 3838	*Z. h. luteus*	DQ664629.1	DQ664984.1	1	JMZ	35.85686	-106.75928
MSB 56986	NK 3842	*Z. h. luteus*	DQ664633.1	DQ664988.1	1	JMZ	35.93195	-106.79207
MSB 56987	NK 3844	*Z. h. luteus*	DQ664635.1	DQ664990.1	1	JMZ	35.99404	-106.71312
MSB 56988	NK 3845	*Z. h. luteus*	DQ664636.1	DQ664991.1	1	JMZ	35.99404	-106.71312
MSB 56989	NK 3843	*Z. h. luteus*	DQ664634.1	DQ664989.1	1	JMZ	35.99404	-106.71312
MSB 56990	NK 3839	*Z. h. luteus*	DQ664630.1	DQ664985.1	1	JMZ	35.99404	-106.71312
MSB 56991	NK 3840	*Z. h. luteus*	DQ664631.1	DQ664986.1	1	JMZ	35.94228	-106.64365

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 56992	NK 3841	*Z. h. luteus*	DQ664632.1	DQ664987.1	1	JMZ	35.94228	-106.64365
MSB 56993	NK 3827	*Z. h. luteus*	DQ664619.1	DQ664974.1	1	JMZ	35.92680	-106.70280
MSB 56994	NK 3828	*Z. h. luteus*	DQ664620.1	DQ664975.1	1	JMZ	35.92680	-106.70280
MSB 56995	NK 3831	*Z. h. luteus*	DQ664622.1	DQ664978.1	1	JMZ	35.88434	-106.72327
MSB 56996	NK 3829	*Z. h. luteus*	DQ664621.1	DQ664976.1	1	JMZ	35.88434	-106.72327
MSB 56997	NK 3834	*Z. h. luteus*	DQ664625.1	DQ664980.1	1	JMZ	35.88434	-106.72327
MSB 58368	NK 9976	*Z. h. luteus*	JN546484	JN546538	19	MRG	34.88138	-106.71688
MSB 58369	NK 9995	*Z. h. luteus*	AY598178.1		1	URG	36.09970	-106.14141
MSB 58370	NK 9993	*Z. h. luteus*	AY598179.1		1	URG	36.05861	-106.08245
MSB 61684		*Z. h. luteus*	AY598174.1		1	SAC	32.95170	-105.70409
MSB 61690		*Z. h. luteus*	AY598175.1		1	SAC	32.81698	-105.77523

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 61693		*Z. h. luteus*	AY598176.1		1	SAC	32.77649	-105.67578
MSB 61696		*Z. h. luteus*	AY598173.1		1	SAC	32.85526	-105.59927
MSB 61712		*Z. h. luteus*	AY598177.1		1	SAC	32.81047	-105.64305
MSB 62096	NK 17857	*Z. h. luteus*	AY598185.1		1	JMZ	35.78882	-106.73233
MSB 62103		*Z. h. luteus*	AY598186.1		19	MRG	34.57234	-106.75696
MSB 86344	NK 31194	*Z. h. luteus*	JN546459	JN546513	16	WHT	33.77000	-109.43726
MSB 89194	NK 10218	*Z. h. luteus*	AY598169.1		17	WHT	33.77051	-109.46096
MSB 91627	NK 10198	*Z. h. luteus*	AY598170.1		17	WHT	33.88827	-109.47548
MSB 91675	NK 31195	*Z. h. luteus*	JN546460	JN546514	16	WHT	33.77000	-109.43726
MSB 154917	NK 156087	*Z. h. luteus*		JN546499	18	SAJ	37.23880	-107.75859
MSB 155117	NK 156132	*Z. h. luteus*		JN546500	18	SAJ	37.23880	-107.75859

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
MSB 212593	NK 3836	*Z. h. luteus*	DQ664627.1	DQ664982.1	1	JMZ	35.88434	-106.72327
MSB 212976	NK 1475	*Z. h. luteus*		JN546498	19	MRG	34.88138	-106.71688
	FT 353	*Z. h. luteus*	JN546435	JN546485	1	JMZ	35.92505	-106.70552
	FT 358	*Z. h. luteus*	JN546436	JN546486	2	SAC	32.70958	-105.67150
	FT 359	*Z. h. luteus*	JN546437	JN546487	1	SAC	32.99900	-105.66298
	FT 360	*Z. h. luteus*	JN546438	JN546488	1	JMZ	35.88402	-106.64775
	FT 506	*Z. h. luteus*	JN546439	JN546489	3	SDC	36.97457	-104.39480
	FT 507	*Z. h. luteus*	JN546440	JN546490	4	SDC	36.97937	-104.37553
	FT 520	*Z. h. luteus*	JN546441	JN546491	5	SDC	36.95765	-104.38635
	FT 521	*Z. h. luteus*	JN546442	JN546492	6	SDC	36.95768	-104.38632
	FT 528	*Z. h. luteus*	JN546443	JN546493	7	SDC	36.97173	-104.39448

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
	FT 541	*Z. h. luteus*	JN546444	JN546494	8	SDC	36.99058	-104.38128
	FT 604	*Z. h. luteus*	JN546445	JN546495	12	SDC	36.16980	-105.23218
	FT 605	*Z. h. luteus*	JN546446	JN546496	12	SDC	36.17153	-105.23340
	FT 613	*Z. h. luteus*		JN546497	1	JMZ	35.85437	-106.76382
	Zhc_032	*Z. h. campestris*	DQ664704.1	DQ665046.1				
	Zhc_087	*Z. h. campestris*	DQ664758.1	DQ665100.1				
	Zhi_011	*Z. h. intermedius*	DQ664780.1	DQ665113.1				
	Zhi_015	*Z. h. intermedius*	DQ664784.1	DQ665116.1				
	Zhp_007	*Z. h. preblei*	DQ664804.1	DQ665133.1				
	Zhp_019	*Z. h. preblei*	DQ664812.1	DQ665142.1				
	Zhpa_002	*Z. h. pallidus*	DQ664845.1	DQ665173.1				

Museum #	Tissue #	Taxon	CR	cyt *b*	Hap	Region	Latitude	Longitude
	Zhpa_006	*Z. h. pallidus*	DQ664849.1	DQ665177.1				

FIGURES

Figure 1. Distribution of all known records (circles) for the New Mexico meadow jumping mouse (*Zapus hudsonius luteus)* in the American Southwest with elevation shading above 2000 m in dark grey and over 3000 m in light grey. Holocene fossil record from the Plains of San Agustín is indicated by a square. *Inset map* shows the distribution of *Z. hudsonius* in North America (modified from Frey & Malaney, 2009).

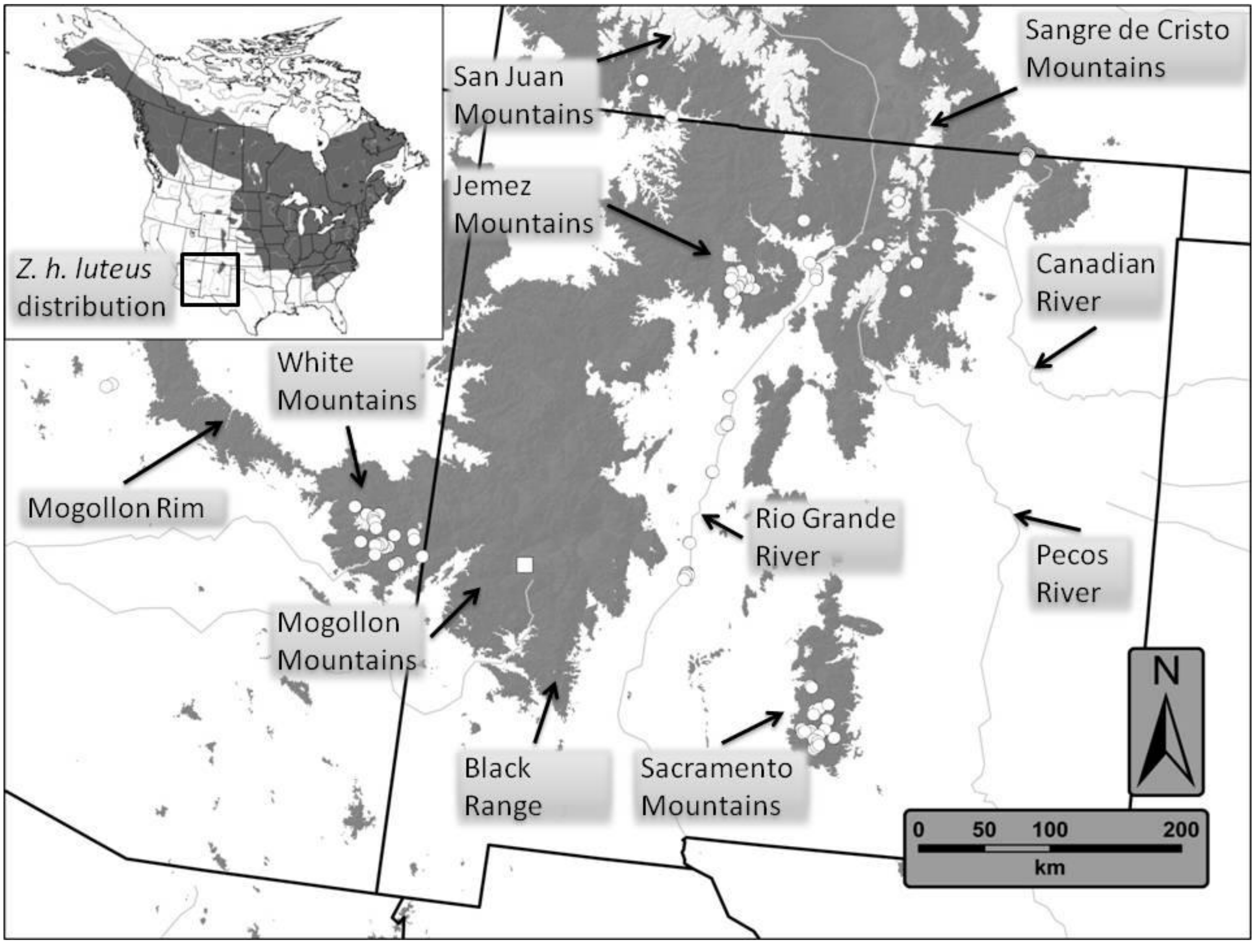


Figure 2. Bayesian inference majority rules consensus tree produced using GTR + Γ model for 93 individuals of *Z. h. luteus* and sister taxa for 1514 bp of concatenated mitochondrial CR and cyt *b* genes. Stars at nodes correspond to posterior probabilities (>0.95, PP) from 50k post burn-in trees and 1k non-parametric bootstraps (>.95 ML, >.70 MP). Grey bars around nodes reflect the 95% CI for lineage divergence time with a relaxed molecular clock calibrated by fossils. *Demographic hypotheses inset* – Alternative hypothesis parametric bootstrap (coalescent modelling) tests for *Z. h. luteus* with 90% confidence intervals and effective population size scaled to each contemporary population. The arrow highlights the empirical tree value for Slatkin and Maddison's *s*.

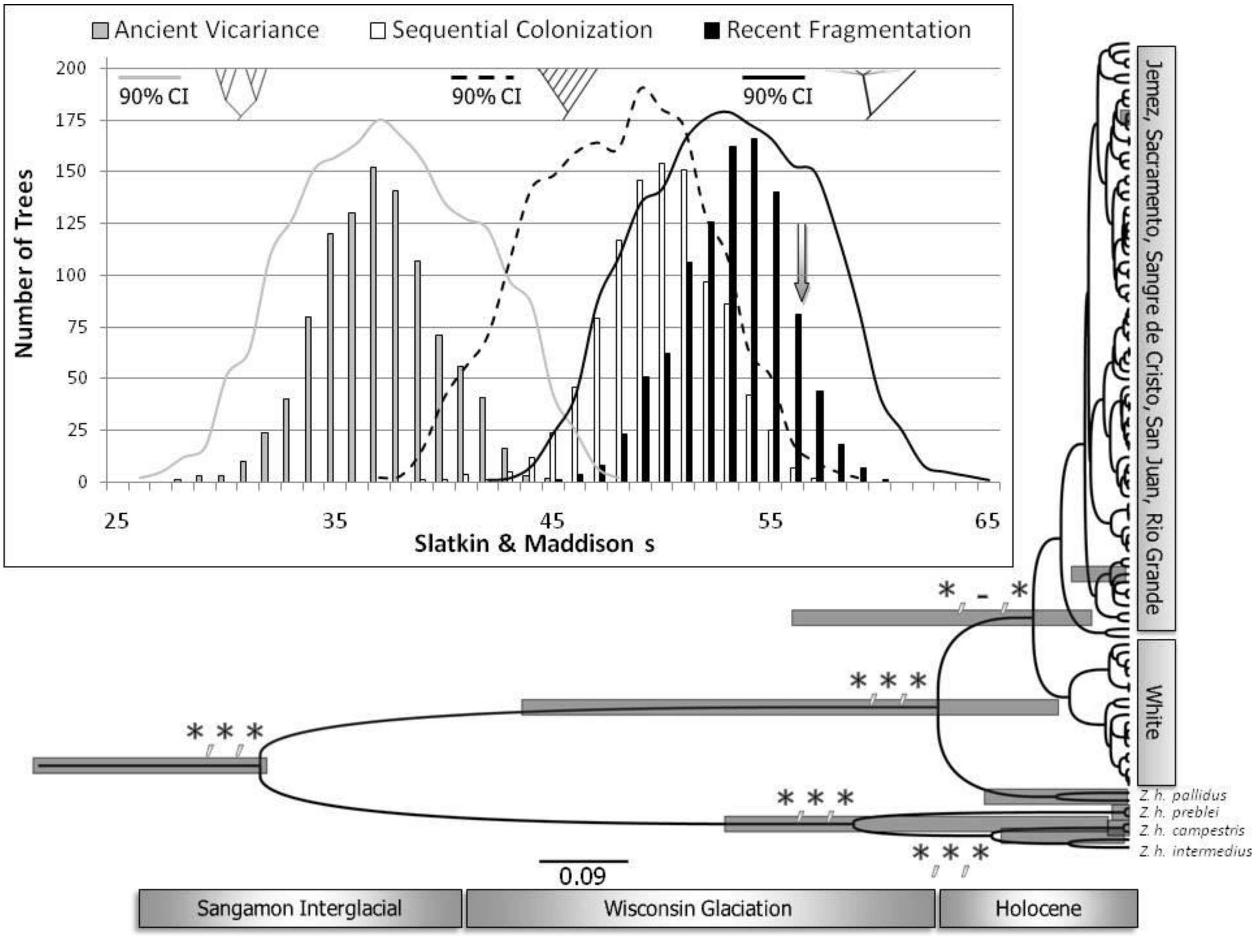


Figure 3. Species Distribution Models – (A) contemporary SDM for 92 records (circles) of *Zapus hudsonius luteus* based on point-wise mean logistic bootstrap prediction with 20 replicates. Thresholds for probability of occurrence are white <0.5, light grey 0.5 – 0.7, dark grey > 0.7. (B) Paleodistribution models of *Z. h. luteus* and 60 records (stars) of sister taxon *Z. h. pallidus*. Thresholds for probability of occurrence are >0.70 for all models. Light grey is *Z. h. pallidus*, dark grey is *Z. h. luteus*, and medium grey is combined *Z. h. luteus + Z. h. pallidus*. Fossil records are indicated by a square (Holocene; Plains of San Agustín) and triangles (Wisconsin glaciation – Late Pleistocene).

Figure 3 (a)

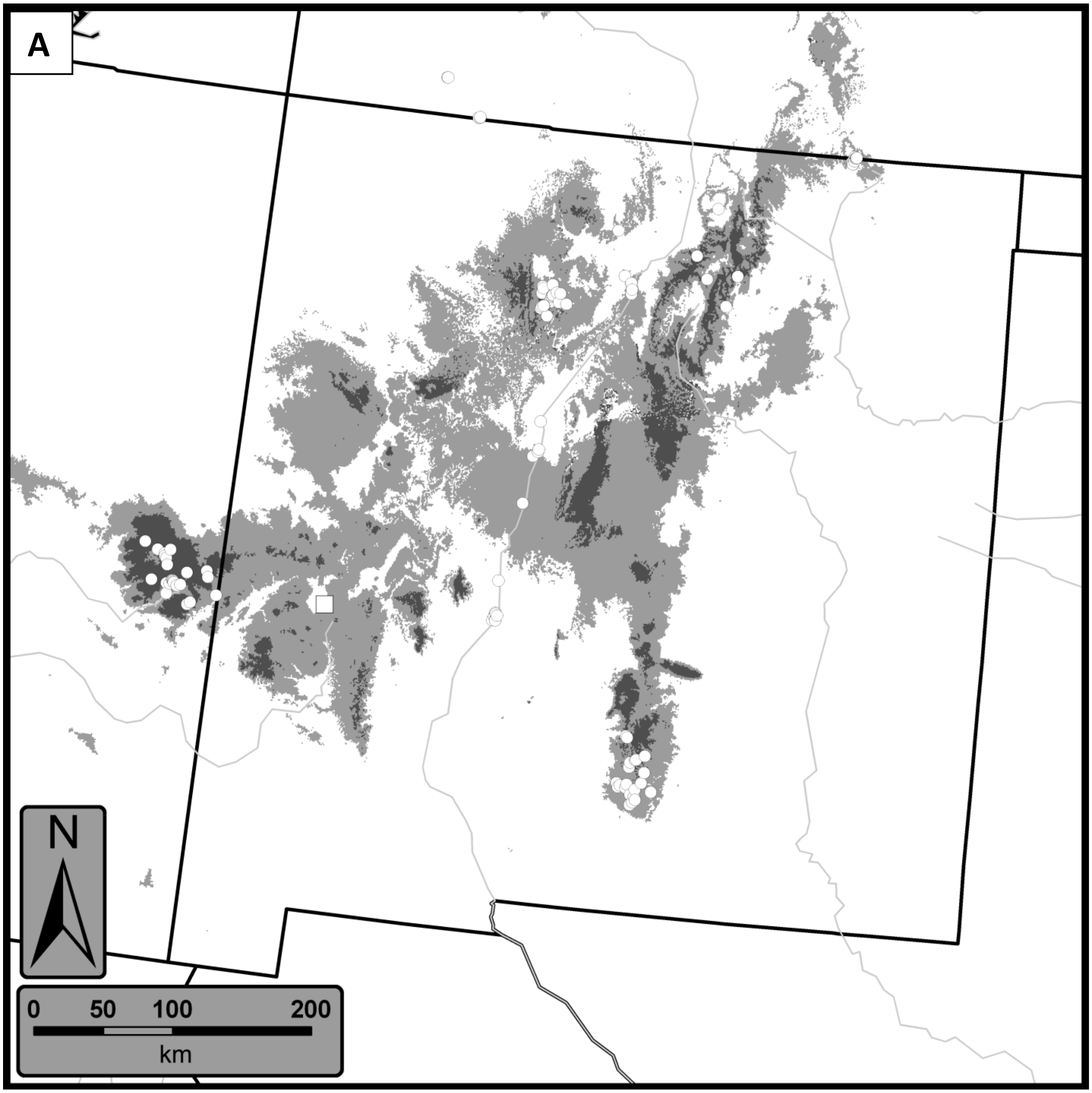


Figure 3(b)

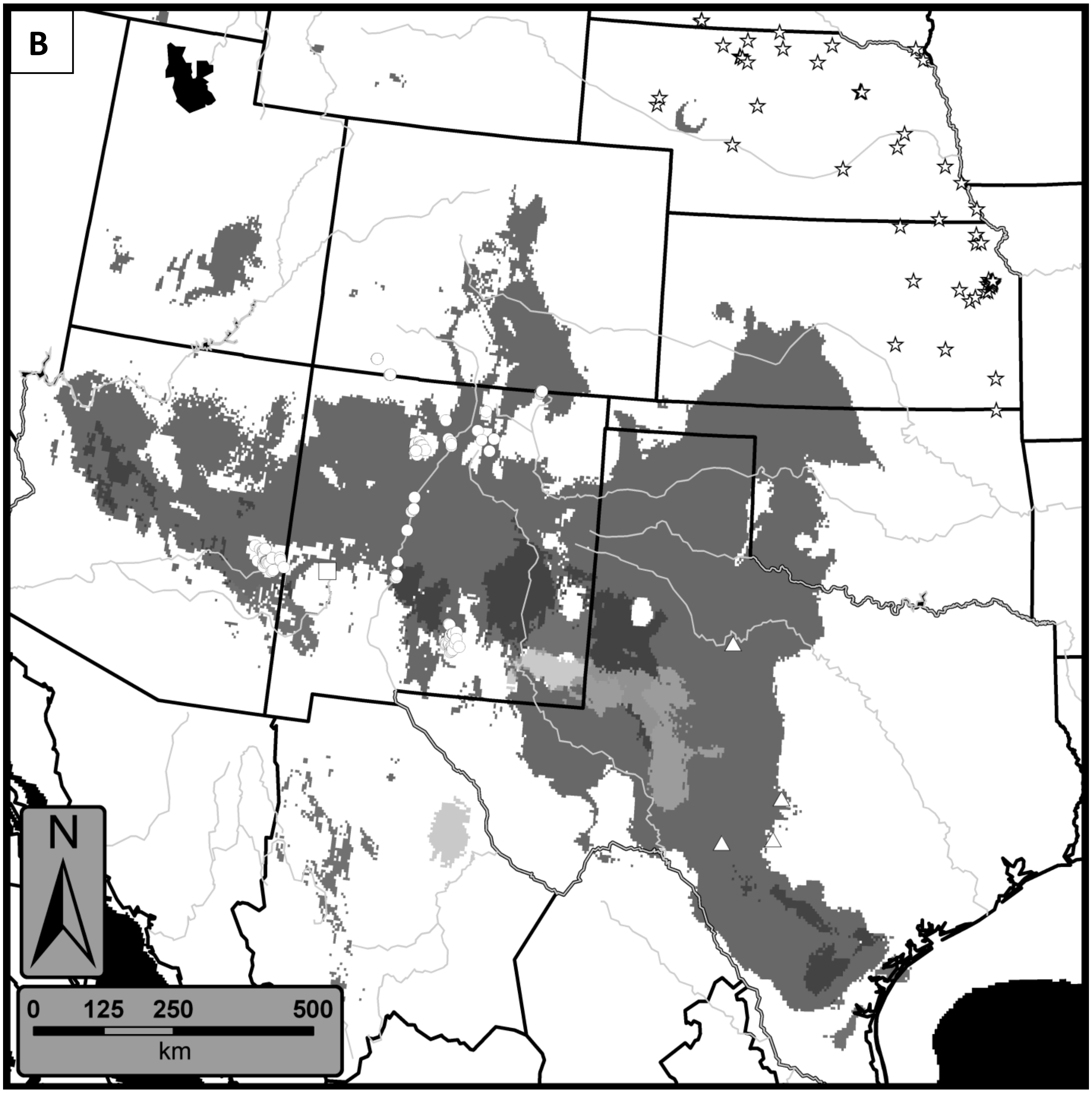
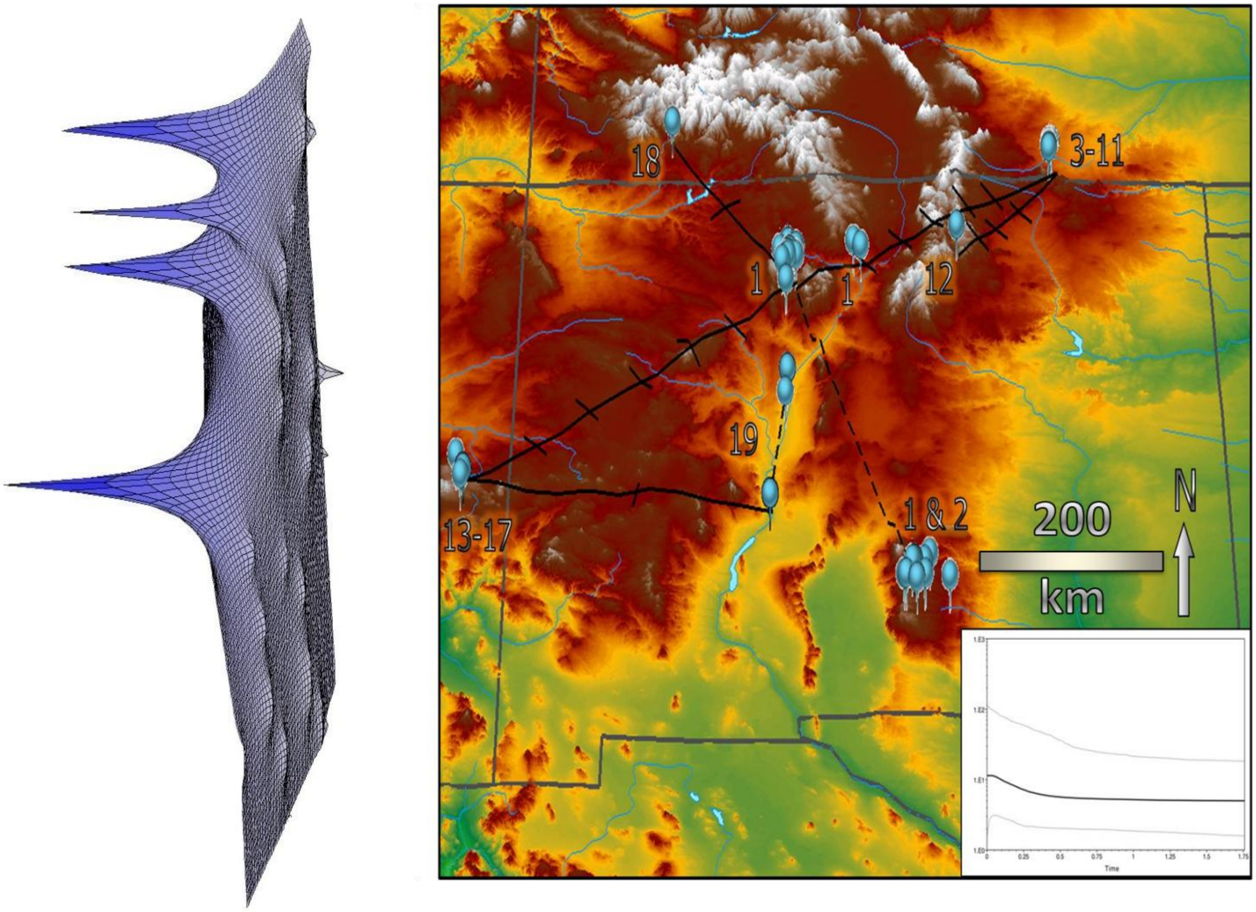


Figure 4 – Left panel: A graphical interpolation-based representation of the genetic structure for *Zapus hudsonius luteus* in the American Southwest. Corners represent geographic coordinates, while surface heights indicate genetic distances between adjacent locations. Peaks (darker) and valleys (lighter) are indicative of areas with high or low (respectively) pair-wise genetic distances between samples over the geographical landscape. Right panel: Median joining network of *Z. h. luteus* for mitochondrial DNA with respect to sampling localities. Haplotypes are listed in Appendix S1. Individual tick marks represent one polymorphic site (mutation). Dashed lines represent shared haplotypes between localities (no mutation). Localities with multiple haplotypes present have no more than two mutations among haplotypes. *Bayesian skyline plot inset* – Effective population size since 175kyr BP for *Z. h. luteus*. Time is in units of thousands of years (i.e. 0.50 = 50kyr BP).



TABLES

Table 1 – Polymorphism data for the full 1514 bp of concatenated control region (CR) and cytochrome *b* (cyt *b*) genes for 49 individual *Zapus hudsonius luteus*. Data are either partitioned or combined (Total) for analyses. S = polymorphic sites, ε = total number of mutations, Hap = number of haplotypes, Hd = haplotype diversity, π = nucleotide diversity (per site), k = average number of nucleotide differences, θn = Theta-W per site from S, θg = Theta-W per sequence.

Gene	**Sites**	**S**	**ε**	**Hap**	**Hd**	**π**	**k**	**θn**	**θg**
CR	372	4	4	4	0.67	0.0026	0.9558	0.0024	0.8971
cyt *b*	1140	32	32	15	0.83	0.0040	4.5629	0.0063	7.1768
Total	1514*	36	36	19	0.88	0.0037	5.5187	0.0053	8.0739

* Plus two insertions in the CR dataset

Table 2 – Coalescent simulations (10,000 replicates) of neutrality tests for 49 individual *Zapus hudsonius luteus* with complete 1514 bp of concatenated control region and cytochrome *b* genes (no missing data). Values correspond to calculations based on Theta (θ) and S for the test statistics Tajima's *D* and Fu's *Fs*.

	D		*Fs*	
	θ	S	θ	S
Observed Statistic	-1.072		-3.520	
Average (*P*-value)	**-0.036** (0.1290)	**0.083**(0.1190)	**-0.228**(0.1310)	**-0.364**(0.1570)
95% CI	-1.637 to 1.926	-1.622 to 1.871	-6.268 to 7.751	-7.296 to 7.576

CHAPTER 2

PHYLOGEOGRAPHY OF THE WESTERN JUMPING MOUSE (*ZAPUS PRINCEPS)* DETECTS DEEP AND PERSISTENT ALLOPATRY WITH EXPANSION

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ABSTRACT

Understanding how diversity is partitioned across the landscape provides perspectives on the environmental processes that have influenced the evolutionary history of organisms. We analyzed spatial demography, historical biogeography, and niche divergence of the western jumping mouse (*Zapus princeps*) using molecular DNA sequences of the mitochondrial cytochrome-*b* gene and nuclear glucocerebrosidase and myosin heavy chain 2 markers recovered from 7 of the 11 subspecies in western North America. Phylogeographic structure within *Z. princeps* was partitioned across 5 clades (Boreal, Northern Sierra, Southern Rockies, Southern Sierra, and Uinta). Two lineages detected in the Sierra Nevada's of California (Northern Sierra and Southern Sierra) were more closely allied to *Z. trinotatus* than to other lineages of *Z. princeps* and species distribution models mirror these phylogenetic signatures by detecting wide overlap in niches for Sierran jumping mice and *Z. trinotatus* as compared to other *Z. princeps*. Four southern lineages are deeply divergent and limited to highly disjunct mesic and montane habitats within the xeric southwestern United States, while the fifth lineage is widespread, extending from Wyoming to Alaska and reflecting expansion northward following deglaciation, a common pattern in boreal mammals.

INTRODUCTION

Western North America has a diverse biota that is the product of complex evolutionary and environmental processes (Lomolino et al. 2006). Significant intraspecific genetic variation in mammals in the region is hypothesized to have been shaped by extreme topographic heterogeneity and repeated glaciations during the Quaternary (Riddle and Hafner 2006). Molecular investigations of western mammals have provided new views of diversification, occasionally revealing unexpected genetic architectures (Alvarez-Castaneda and Patton 2004; Galbreath et al. 2010; Matocq 2002b; Riddle et al. 2000). Documentation of geographic molecular variation in organisms, when combined with assessments of demography, historical biogeography, and niche variation, can provide insight into key questions related to climate change, post-Pleistocene colonization, habitat fragmentation, and possible future response to changing environments (Avise 2000). We assess phylogeographic structure in the western jumping mouse (*Zapus princeps*) to further explore the biogeographic history of western North America.

The western jumping mouse is an inhabitant of mesic and montane habitats ranging from New Mexico and central California northward through most of western North America (Fig. 1) to southeast Alaska and southern Yukon Territory (Hafner et al. 1981; Hall 1981; Jones 1981; Krutzsch 1954). Because much of this widespread range was glaciated during the late Quaternary, the patterns and levels of connectivity of the mesic environments they inhabit have changed, potentially leaving an imprint on molecular variation in the species (Hewitt 1996, 2000; Waltari and Guralnick 2009). The dynamic geologic history, variable topography, and patchy mesic environments of western North America provide a series of evolutionary experiments as multiple mountain ranges may represent replicated isolation events. We explore historical-biogeographic questions related to the effects of Pleistocene fragmentation on mesic-associated biota by testing two primary ideas using molecular variation and niche modeling in jumping mice. First, we explore lineage divergence related to glacial cycling by asking whether jumping mice lineages were in wide contact during glaciations or if they remained geographically isolated, similar to their current distribution. Second, given that their contemporary northern range was blanketed by ice until the end of the Pleistocene, we test the scenario that southern lineages of *Z. princeps* reflect signatures of genetic structure that are deeper (due to persistence) than northern lineage(s) which presumably expanded (ephemeral) from the south following the latest Pleistocene deglaciation.

Two mutually exclusive and competing hypotheses, related to lineage divergence and historical biogeography, are plausible. The admixture (AM) scenario, with populations of jumping mice isolated during interglacials on montane islands (e.g., the contemporary condition) but in wide contact during glacial advances, predicts genetic signatures should reflect high levels of exchange. Previous studies in western montane environments have identified different forms and levels of mixing (admixture, introgression, hybridization) in grasshoppers (Knowles 2001), birds (Mettler and Spellman 2009; Spellman and Klicka 2007), pika (Galbreath et al. 2009, 2010), and rodents (Good and Sullivan 2001; Spaeth et al. 2009). Alternatively, jumping mice lineages may have remained independent and evolved *in situ* due to sustained geographic isolation or persistent allopatry (PA). Evidence for the persistent allopatry scenario would include geographically structured lineages. Signatures of genetic divergence and geographically structured variation in montane organisms have been recorded for alpine stonecrops (DeChaine and Martin 2005b), foxtail pine (Eckert et al. 2008), kittentails (Marlowe and Hufford 2008), alpine butterflies (DeChaine and Martin 2005a), birds (Spellman et al. 2007), and various mammals (Demboski and Cook 2001; Hornsby and Matocq 2011; Sullivan et al. 2000).

North American environments have not been static and organisms have presumably tracked climate change (Hewitt 2000), with many species dispersing northward following glacial retreat (Anderson and Borns 1994; Lessa et al. 2003). In Canada and Alaska, northern populations of *Z. princeps* are likely the result of post-Pleistocene colonization of deglaciated terrains as observed in other mammals (Arbogast 1999; Conroy and Cook 2000b; Runck and Cook 2005). Southwestern peripheral populations of jumping mice, in contrast, are comparatively more fragmented and largely restricted to dense alder (*Alnus* spp.), willow (*Salix* spp.), and aspen (*Populus* spp.) stands typically associated with riparian systems and high elevation mesic habitats (Frey and Malaney 2009; Hart et al. 2004; Krutzsch 1954; Quimby 1951). Because these habitats are limited in extent and isolated within predominantly xeric environments, populations of montane mesic-associated mammals are hypothesized to exhibit a deeper divergence than their northern counterparts. For example, genetic breaks across arid barriers such as the Columbia and Wyoming Basins (Carstens et al. 2005; Carstens and Richards 2007; DeChaine and Martin 2005b; Nielson et al. 2001) suggest that isolation during warm interglacial periods may contribute to allopatric divergence in mammals (Demboski and Cook 2001; Demboski and Sullivan 2003; Galbreath et al. 2010; Good et al. 2008; Hornsby and Matocq 2011). Persistent allopatric divergence is expected to result in deeper genetic distance and lineage cohesion suggesting limited or no mixing through multiple glacial cycles (DeChaine and Martin 2006; Nielson et al. 2001, 2006).

We begin by assessing how past events influenced the phylogenetic signature, demography, and historical biogeography of the western jumping mouse. We test if the phylogenetic signal is the result of admixture (AM) or persistent allopatry (PA) using coalescent simulations. Next, we examine the existing taxonomic framework for *Z. princeps*, originally based on morphological features (Krutzsch 1954), and then assess environmental variation with species distribution models (SDMs) and test for niche and range overlap among paraphyletic clades. Finally, we propose a set of alternative biogeographic hypotheses based on allopatric modes of speciation that may account for the observed phylogenetic signal.

METHODS

DNA Extraction and Sequencing.– We included specimens from the Museum of Southwestern Biology (MSB – University of New Mexico – Albuquerque), the Museum of Vertebrate Zoology (MVZ – University of California – Berkley), and the University of Alaska Museum of the North (UAM – University of Alaska – Fairbanks; Appendix I). Specimens represent 7 of the 11 subspecies *(Z. p. idahoensis, Z. p. minor, Z. p. oregonus, Z. p. pacificus, Z. p. princeps, Z. p. saltator, Z. p. utahensis)* recognized by Krutzsch (1954) and Hall (1981) and range from southeast Alaska and Yukon Territory southward throughout most western states to the species' southern limits in California and New Mexico (Fig. 1). Detailed information related to voucher specimens is available through the ARCTOS database (http://arctos.database.museum/SpecimenSearch.cfm). The mitochondrial (mtDNA) cytochrome-*b* (cyt*b* – 1140bp) gene was obtained for 91 specimens (see Appendix) representing 46 locations across the range of Z. *princeps*. In addition, samples of *Z. trinotatus* (4), *Z. hudsonius* (6), and *Napaeozapus insignis* (1) were included. Independent perspectives were gained by sequencing two nuclear (nuDNA) markers to test major lineage breaks identified by mtDNA; glucocerebrosidase (GBA – 347bp) and myosin heavy chain 2 (MYH2 – 267bp).

Total genomic DNA was extracted from frozen or ethanol preserved tissues (heart or liver). Amplification of the cyt*b* gene was conducted with primers L14724 and H15915 (Irwin et al. 1991) or with a combination of MVZ05-MVZ16 and MVZ127-MVZ108 (Leite and Patton 2002; Smith and Patton 1993) using protocols previously established (Halanych et al. 1999; Lessa and Cook 1998; Patton et al. 2008). PCR products were sequenced using BigDye Terminator Cycle Sequencing Ready Reaction mix. v. 3.1 (Applied Biosystems) with combinations of amplification primers. Heavy and light strands were sequenced in both directions using an Applied Biosystems 3100 automated DNA sequencer in the Molecular Biology Facility, Biology Department, University of New Mexico, Albuquerque, or at the Museum of Vertebrate Zoology, University of California, Berkeley. Sequences were analyzed using SEQUENCHER 4.9 (Gene Codes) with a reference sequence from GenBank (*Z. trinotatus*, AF119262).

We sequenced two fragments of nuclear introns (GBA and MYH2) for several specimens using published primers and protocols (Lyons et al. 1997). We sequenced a minimum of 2 randomly selected individuals from mitochondrial clades of *Z. princeps* (30 GBA and 14 MYH2), *Z. trinotatus* (2), and *Z. hudsonius* (2) with 1 *Napaeozapus insignis* used to root phylogenies. All individuals were sequenced in both directions. Heterozygous positions were identified and polymorphic alleles were assessed using PHASE 2.1 (Stephens and Scheet 2005; Stephens et al. 2001) in DNASP (Librado and Rozas 2009; Rozas et al. 2003) with haplotypes inferred from multi-allelic loci using a Bayesian framework with 0.90 cutoff and 10,000 iterations. Unresolved haplotypes were coded as missing data.

Alignments were completed using default parameters and algorithms of CLUSTAL X (Larkin et al. 2007) in the program MEGA 5.05 (Tamura et al. 2011). Contigs for all genes (un-phased) are available on GenBank (Appendix).

Diversity Measures.– Molecular diversity and demographic estimates from each marker were determined for putative *Z. princeps* (Table 1). Neutrality and population equilibrium were assessed via Tajima's D and Fu's F_S tests and 10,000 coalescent simulations to assess significance. The mtDNA dataset was partitioned into clades to assess demographic change. Net sequence divergence (d_A) was calculated between the observed mtDNA clades (Nei 1987). We calculated segregating sites (S), haplotypes (h), haplotype diversity (η), and nucleotide diversity (π) for each marker with DNASP (Librado and Rozas 2009; Rozas et al. 2003).

Phylogenetic and Phylogeographic Analyses.– Our aligned mitochondrial and nuclear data were processed via MRMODELTEST (Nylander 2004) performing hierarchical likelihood ratio tests (hLRT) and calculating Akaike Information Criterion (AIC); both measures agreed for all genes. General Time Reversal (Tavaré 1986) plus gamma (1.6506) plus proportion (0.4875) of invariant sites model (GTR+Γ+I, log likelihood = -5760.9790, K = 10, AIC = 11541.9580) was selected as the most appropriate evolutionary model for the mitochondrial marker and subsequently used in Bayesian inference and maximum likelihood analyses. The Kimura (1980) model (K80, log likelihood = -661.0489, K = 1, AIC = 1324.0778) was selected for the GBA gene. The Hasegawa, Kishino, and Yano (1985) plus proportion (0.9085) invariant sites model (HKY+I, log likelihood = 436.1803, K = 5, AIC = 882.3607) was identified for the MYH2 gene.

Bayesian reconstruction was performed using MRBAYES 3.1.2 (Huelsenbeck and Ronquist 2001; Lakner et al. 2008) beginning with random trees and Markov chain sampled every 1000th tree for 2 million generations and 4 chains run simultaneously with temperature set to 0.20 for 3 chains and 1 cold chain. Three replicate runs were completed to confirm consistency and each marker was run with distinct priors set from MRMODELTEST output. Chain stationarity was assessed by inspecting the standard deviation of split frequencies consistently below 0.05 and confirmed complete via the graphical output from the initial 50,000 generations with 0.20 of each replicate discarded as burn in (Huelsenbeck and Imennov 2002). Nodal strength (posterior probability – PP) was identified in the consensus of the residual trees and the midpoint rooted majority rule consensus tree was visualized in FIGTREE ver.1.3.1 (Fig. 2).

Maximum likelihood (ML) optimality criteria were used for phylogenetic reconstruction using GARLI v2.0 Parallel (Zwickl 2006). We considered all characters as unordered with 4 possible states (A, C, G, T) with heuristic searches. Distinct models of evolution were applied to each marker with discrete base frequencies and rate categories for each from MRMODELTEST. Tree bisection-reconnection (TBR) branch swapping was employed with 100 random stepwise additions. Three runs were conducted to ensure consistency and non-parametric bootstrap support (Felsenstein 1985) was evaluated with 1000 pseudo-replicates (Fig. 2).

The median joining statistical parsimony algorithm (Bandelt et al. 1999) in the program NETWORK ver. 4.2 (Fluxus engineering, Suffolk, U.K.) was employed to produce a haplotype network (Fig. 3) for each marker given that intraspecific phylogenetic methods may fail (Posada and Crandall 2002). This algorithm calculates the similarity between haplotypes into a network where the combined probability is >95% (Templeton et al. 1992).

Taxonomic Evaluation.– We compared the morphological taxonomic classification of *Z. princeps* (Krutzsch 1954) against the mitochondrial framework using the Shimodaira-Hasegawa (1999) test. A maximum-likelihood tree constrained to reflect monophyly of *Z. princeps, Z. trinotatus*, and *Z. hudsonius* was compared to the unconstrained best maximum-likelihood tree using PAUP* v.4.0b10 (Swofford 2003), GTR+Γ+I model of nucleotide substitution, and 10,000 resampling of estimated log-likelihoods (RELL) bootstrap replicates (Hasegawa and Kishino 1994).

*Coalescent Simulations.–*We conducted coalescent simulations using the parametric bootstrap method (Goldman et al. 2000). Our aim was to test alternative hypotheses of admixture (AM) versus persistent allopatry (PA) using a likelihood based or frequentist approach (Hickerson et al. 2010; Knowles and Maddison 2002) with coalescent simulations in the program MESQUITE (Maddison and Maddison 2009). Alternative hypothesized phylogenies (AM vs. PA) were simulated for 1000 replicates to produce gene matrices using ancestral $N_{E(f)}$ (183,779) from our estimate of the parameter θw (calculated in DNASP), branches scaled to branching pattern, one-year generation time (Brown 1970; Cranford 1983), and ancestral divergence estimates from zapodid fossil records (Hafner 1993; Kurtén and Anderson 1980; Ruez and Bell 2004). To assess the validity of each model and determine overlap between models, we used upper and lower confidence intervals (90%) of θw (Knowles and Carstens 2007) on independent runs.

From the 1000 gene matrices, we constructed genealogies in PAUP* using heuristic parsimony searches with 10 random addition replicates, TBR branch swapping with max-trees set to 100, and produced a majority-rule consensus tree. Next we calculated the discord between the reconstructed gene tree and the assignment of individuals into separate lineages using Slatkin and Maddison's *s* (1989) as implimented in MESQUITE. Finally, assessment of our two-tailed test was considered significant if the empirical data occur outside of the 90% CI of the simulation data.

Our θ estimates (effective population size scaled to the neutral mutation rate) were calibrated to recent fossil dates using the equation $\theta = 4N_{E(f)}\mu$, assuming $\mu = 3.14$ substitutions per million years as calculated by Malaney et al. (2011) and scaled branch widths of θ were used for the competitive hypotheses.

Species Distribution Modeling.– Climate variables such as temperature and precipitation are known to effect the metabolic rates of jumping mice (Cranford 1975) and can provide insight into the spatial distribution of environmental characteristics for monophyletic lineages. We obtained bioclimatic variables from 2.5 minute (4km) resolution coverages from the WorldClim database (http//www.worldclim.org; Hijmans et al. 2005). Torpor in jumping mice is impacted by elevation (Cranford 1978; Muchlinski and Rybak 1978), so we included this coverage.

We followed species distribution modeling (SDM) procedures from previous studies (Waltari and Guralnick 2009; Waltari et al. 2007) by clipping the coverages to the study area (North America) and reducing the dataset (Rissler and Apodaca 2007) to the 12 most biologically meaningful and uncorrelated coverages (Bio1 - Annual Mean Temperature, Bio2 - Mean Diurnal Range, Bio3 - Isothermality, Bio7 - Temperature Annual Range, Bio8 - Mean Temperature of Wettest Quarter, Bio9 - Mean Temperature of Driest Quarter, Bio15 - Precipitation Seasonality, Bio16 - Precipitation of Wettest Quarter, Bio17 - Precipitation of Driest Quarter, Bio18 - Precipitation of Warmest Quarter, Bio19 - Precipitation of Coldest Quarter, and elevation). Localities for *Z. princeps* and *Z. trinotatus* were downloaded from MANIS (8 Jan 2010). Localities with >0.5km^2 uncertainty were discarded and several records were georeferenced (JLM) using BioGeomancer (http://bg.berkeley.edu/, Guralnick et al. 2006). To account for sampling biases (Reddy and Davalos 2003) which may result in model over-fitting and subjective outcome, we spaced localities at least 10km by removing intervening records. To test if the Sierra Nevada lineages reflect phylogenetic signal in niche occupancy, we further partitioned localities of *Z. princeps* (see below). We constructed SDMs using the default settings in the program MAXENT version 3.3.3a (Elith et al. 2006; Phillips et al. 2006) and ran 20 replicates with randomized 20th percentile training presence and depicted results using the point-wise bootstrap mean.

To identify overlap between taxonomic divisions and establish whether Sierra Nevada clades occupy analogous environments to *Z. trinotatus* or other *Z. princeps,* we completed a series of niche tests. Localities were partitioned into three groups reflecting DNA phylogenetic signal: *Z. trinotatus*, Sierran (Southern and Northern Sierra) clades, and remaining *Z. princeps* (Boreal, Southern Rockies, Uinta) clades. First, we calculated the proportion of pixels (km^2) where overlap between suitable niches occur using ARCGIS v.10.0. Threshold values were determined from the conservative “last sample included” criterion and were 0.21 for *Z. princeps*, 0.24 for *Z. trinotatus*, and 0.28 for Sierran. Quantifying niche overlap was accomplished with three metrics using ENMTOOLS (Warren et al. 2010); Schoener's *D* (Schoener 1968), Warren's *I* (Warren et al. 2008), and relative ranks (*RR*; Warren and Seifert 2011). Each measure identifies pair-wise niche overlap values between 0 (none) and 1 (full). We calculated 100 pseudo-replicates of niche models (Warren et al. 2008, 2010) and corresponding measures of niche overlap among lineages following methods of Pyron and Burbrink (2009). This conforms to a one-tailed test to identify if niche models are significantly different from a null distribution by randomly assigning lineage membership to the occurrence points for any two lineages. All SDMs have basic assumptions including niche conservatism (Wiens and Graham 2005), whether coverages (environmental data) are adequate to generate predictions of a species' distribution (Kozak et al. 2008; McCormack et al. 2010), and adequate occurrence points to encapsulate the range of environmental conditions in the species niche (Pearson et al. 2007).

RESULTS

Molecular Diversity.– The cyt*b* gene was obtained for 91 *Z. princeps* specimens, 4 *Z. trinotatus*, 6 *Z. hudsonius*, and 1 *Napaeozapus insignis* (Appendix). Excluding *N. insignis*, there were 157 segregating sites (Table 1). Nucleotide composition (28.4% adenine, 32.0% thymine, 26.9% cytosine, and 12.7% guanine), transition:transversion ratio (R = 4.73), and codon position changes (6-1st position, 0-2nd position, 39-3rd position) among *Zapus* lineages were consistent with other measures of genuine cyt*b* gene for mammals (Irwin et al. 1991).

Twenty-seven (GBA) and 20 (MYH2) randomly selected individuals of *Z. princeps* from the 5 mitochondrial clades were sequenced for the nuclear introns (Lyons et al. 1997) plus 2 *Z. hudsonius*, 2 *Z. trinotatus*, and 1 *N. insignis*. For the GBA marker nucleotide composition was 21.6% adenine, 24.1% thymine, 28.3% cytosine, and 26.0% guanine. There were 22 segregating sites, 1 site with more than 2 variants, transition:transversion ratio of 2.26, plus an 2 bp insertion-deletion between *Zapus* - *Napaeozapus*. The MYH2 marker had 20.3% adenine, 25.2% thymine, 28.1% cytosine, and 26.4% guanine, 16 segregating and 2 multi-variant sites. Transition:transversion ratio was 2.11 with 9 positions represented by insertion-deletions.

Phylogenetic and Phylogeographic Divergence.– Phylogenetic reconstructions using maximum likelihood (ML) and Bayesian (PP) techniques and the parsimony network indicated congruent topologies (Fig. 2 & 3) for all genes. Seven clades were recovered including discrete *Z. trinotatus* and *Z. hudsonius*, plus 5 putative *Z. princeps* clades (Boreal, Northern Sierra, Southern Rockies, Southern Sierra, Uinta; Fig. 2 & 3). Each of the 7 clades identified in the phylogram (Fig. 2) reflect high bootstrap support (ML) and posterior probabilities (PP) for major nodes. Both of the nuclear perspectives reflect deep nodes but provided less resolution near the tips. Current taxonomy of *Z. princeps* (Holden and Musser 2005) showed a polyphyletic relationship with respect to *Z. trinotatus* based on both the mitochondrial and nuclear data, with

Northern and Southern Sierra clades more closely related to *Z. trinotatus* than to other *Z. princeps* (Boreal, Southern Rockies, Uinta; Fig. 2 & 3).

There were 42 unique cyt*b* haplotypes in our dataset (Hd = 0.993; Fig. 3) with 14 haplotypes representing the Boreal clade, 5 in the Northern Sierra, 7 in the Southern Rockies, 5 in the Southern Sierra, 3 in the Uinta, and 3 in *Z. trinotatus.* Five other haplotypes including 4 in *Z. hudsonius* and 1 in *N. insignis* were identified (haplotypes 38-42 not displayed in Fig. 3). No widespread haplotype sharing was documented (Fig. 2 & 3) but a few haplotypes were shared between adjacent sampling localities within clades. Further, no haplotypes were co-located at a single locality from distinct clades. Several polymorphic sites define each lineage of jumping mice, with highest geographic structure across the 4 southern lineages (Northern Sierra, Southern Rockies, Southern Sierra, Uinta; Fig. 3). For example, >100 steps separated the Uinta from the Southern Rockies and Boreal clades, while at least 47 steps segregated haplotypes of the Boreal and Southern Sierra clades. The Northern Sierra clade and *Z. trinotatus* are segregated by <60 mutational steps. Between *Z. princeps* (Uinta) and *Z. trinotatus* there are 136 steps, while there are at least 147 mutational steps between *Z. trinotatus* and *Z. hudsonius.* Almost 300 mutational steps separated *Z. hudsonius* (haplotype 2; *Z. h. luteus*) and the Uinta *Z. princeps* (haplotype 51). Haplotype structure for the independent nuclear genes was less pronounced (fewer segregating sites) but consistent with the mtDNA signature.

Neutrality tests for mitochondrial lineages (Tajima's *D* and Fu's *Fs*; Table 1) for the Boreal and Southern Sierra clades were significantly negative, suggesting deviation from mutation-drift equilibrium and may suggest population expansion (Excoffier et al. 2009). Neutrality tests for the Southern Rockies clade was not significant and small sample sizes from the Northern Sierra and Uinta clades precluded population-level analyses.

Intra-clade Diversity.– Patterns of intra-clade genetic diversity differed across clades (Table 1). Within the Boreal and Southern Sierra clades, haplotypes showed a “star–like” phylogeny (Fig. 2 & 3) with relatively few mutational steps between haplotypes than other clades. In contrast, the Southern Rockies clade showed higher structure and a greater number of mutational steps between haplotypes. For example, within the Southern Rockies there were 16 steps separating haplotype 16 (Jackson Co., Colorado) and haplotype 21 (Santa Fe Co., New Mexico) over a geographic distance of 500 km. In the Boreal clade there were only 8 steps between haplotypes 11 (Yellowstone National Park) and 4 (Unuk River, Alaska) over a geographic distance of >2000 km (Fig. 3). The Uinta clade was represented by 4 specimens from the same locality (Strawberry Reservoir) and 3 unique haplotypes with 5 mutations. The 5 haplotypes from the Northern Sierra clade were distributed among 3 localities segregated by 4 mutational steps over 250 km. The Southern Sierra clade was represented by 11 unique sampling localities and 5 haplotypes within 200 km.

Taxonomic Evaluation and Coalescent Simulations.– A tree constrained for monophyly of *Z. princeps* was significantly worse ($P < 0.001$) than the unconstrained maximum likelihood topology that showed paraphyly of these lineages ($ML_{best} = -4635.7099$; $ML_{constraints} = -8266.8500$; Shimodaira and Hasegawa 1999). Results of the parametric bootstrap test of alternative hypotheses confirmed the persistent allopatry (PA) hypothesis as the best match to the empirical data (Fig. 4). The empirical data had an *s* value of 13 that was significantly different (2-tailed) from the admixture (AD) hypothesis.

Species Distribution Models.–Modeling procedures had high AUC scores (>0.95 for each model). Models were based from 170 *Z. trinotatus* and 499 putative *Z. princeps* localities; of these, 66 Sierra Nevada localities (*Z. p. pacificus*) were partitioned from other *Z. princeps* lineages. Niche overlap and range overlap (threshold value >0.20) was higher for the Sierran jumping mice and *Z. trinotatus* than the Sierran jumping mice and other *Z. princeps* (Fig. 5). All pair-wise comparisons using pseudo-replicates reflected values significantly different than predicated from random among lineages.

DISCUSSION

We documented a history of demographic and range expansion for the Boreal clade that contrasts with long-term persistent southern clades (Northern Sierra, Southern Rockies, Southern Sierra, Uinta). This spatial and temporal contrast reflects distinctive demographic processes across the distribution of jumping mice of the west. The phylogeny and wide niche overlap between Sierran jumping mice and *Z. trinotatus* are inconsistent with current taxonomy that identifies the former as *Z. princeps* (Hall 1981; Holden and Musser 2005; Krutzsch 1954). Finally, the coalescent-based tests provide clarity on the historical biogeography of jumping mice over multiple glacial cycles.

Spatial Demography. –For species with broad latitudinal distributions in North America, a common pattern of deep southern (persistent) and shallow northern (ephemeral) structure has been documented. This signature is common to other rodents with similar latitudinal range such as *Z. hudsonius* (King et al. 2006), red-backed voles, *Myodes gapperi* (Runck and Cook 2005), long-tailed voles, *Microtus longicaudus* (Conroy and Cook 2000a), deer mice, *Peromyscus maniculatus* (Dragoo et al. 2006), woodrats, *Neotoma cinerea* (Hornsby and Matocq 2011), chipmunks, *Tamias amoenus* and *T. ruficaudus* (Demboski and Sullivan 2003; Good et al. 2003, 2008; Good and Sullivan 2001), red squirrels, *Tamiasciurus hudsonicus,* (Arbogast et al. 2001; Wilson et al. 2005), and flying squirrels, *Glaucomys sabrinus* and *G. volans* (Arbogast 1999). Similarly soricomorphs, such as *Sorex cinereus, S. monticolus, and S. palustris* (Demboski and Cook 2001, 2003; Himes and Kenagy 2010) and lagomorphs (e.g., *Ochotona princeps;* Galbreath et al. 2009, 2010) also show this latitudinal signature suggesting a common set of processes has influenced diversification across these montane organisms.

Characteristic signatures of population expansion following glacial retreat (Excoffier et al. 2009; Hewitt 2004, Lessa et al. 2003, 2010) include minimal haplotype sorting, low nucleotide diversity, lack of equilibrium between mutation-drift and migration-drift, and star-like phylogeny which were detected for the Boreal clade of jumping mice. Specific results of tests of neutrality (Table 1) are suggestive of demographic instability since the Last Glacial Maximum (LGM). Ancestors of the Boreal clade likely expanded northward in the Holocene due to glacial retreat (Graham et al. 1996; McGill et al. 2005) and in this case, a few closely related haplotypes typify populations ranging from Wyoming (Yellowstone National Park) northward to south-coastal Alaska (Fig. 3), probably the most recently colonized region. At that northern limit, populations separated by 100 km share haplotypes. Post-Pleistocene glacial retreat and the signature of genetic expansion (Table 1) suggest smaller ancestral population size. Ancestral populations were likely restricted to refugia as documented for other mammals (Sommer and Zachos 2009; Waltari et al. 2007). The newly formed populations at higher latitudes in Canada and southeast Alaska potentially originated from a source refugium in the south, as reflected by minimal differentiation of haplotypes among populations that span this large area. With the warming climate and retreating glaciers, jumping mice populations likely closely tracked newly available habitats (Hewitt 2004). There is no signal of an isolated refugium in southeast Alaska as proposed by Jones (1981) for jumping mice and hypothesized for other mammals (Cook et al. 2006).

We documented prolonged isolation (Arenas et al. 2012) for the southern clades which reflect expected patterns of complete haplotype sorting, deep genetic divergence across the landscape (Fig. 3), high nucleotide and haplotype diversity, and, in general, mutation-drift and migration-drift equilibrium (except Southern Sierra, Table 1). The Southern Sierra clade, however, reflects a significant departure from neutrality suggestive of a smaller ancestral population (e.g. bottle-neck) and a more complex history than our simple hypotheses (ephemeral vs. persistent). Genetic footprints of population expansion documented for the Boreal and Southern Sierra clades are likely due to different mechanisms (e.g., latitudinal expansion versus elevational expansion), but this comparison will require more detailed analyses of paleoenvironments and expanded sampling. Elevation fluctuations and concordant genetic signatures have been documented for alpine plants, pika, and woodrats (Beever et al. 2010; DeChaine and Martin 2005b; Galbreath et al. 2009, 2010; Matocq 2002b) accross western North America. However, the magnitude of range shifts may differ for species living in montane (elevational shifts) versus more homogeneous environments (latitudinal shifts; Guralnick 2007) and these alternative signatures should be explored further (Rubidge et al. 2012, Parmesan 2006). Shifts in elevation and latitude are projected to correspond to changing temperatures (Parmesan 2006; Petit et al. 2008; Walther et al. 2002) and several species in the Sierras have declined over the last century including jumping mice (Moritz et al. 2008). Other species have shown recent extirpations such as alpine pika (Beever et al. 2010, Galbreath et al. 2009, 2010) with declines also common elsewhere (Albach et al. 2006; DeChaine and Martin 2005a; Haubrich and Schmitt 2007; Knowles and Richards 2005) including jumping mice (Frey and Malaney, 2009).

Niche Overlap. – The Sierran jumping mice and *Z. trinotatus* overlap in niche space more than either does with other lineages of *Z. princeps* (Fig. 5). This overlap may mirror their close evolutionary relationship (Fig. 2); however, overlap may simply reflect the spatial proximity and ecological similarity of the two regions. Still, there is significantly more niche divergence between lineages than expected by chance based on pseudo-replicates of background niche space. Because organisms can shift niche preferences through time (Hadly et al. 2009; Peterson 2011), the roles of niche conservatism (Warren et al. 2008; Wiens 2004; Wiens and Graham 2005) or niche divergence (Raxworthy et al. 2007; Rissler and Apodaca 2007) in speciation warrants further exploration. Both have been shown to operate at various temporal and spatial scales in Mexican Jays (genus *Aphelocoma*; McCormack et al. 2010), common kingsnakes (*Lampropeltis getula*; Pryon and Burbrink 2009), and deer mice (*Peromyscus maniculatus*; Kalkvik et al. 2011). Jumping mice are presumed to have diverged in allopatry based on coalescent simulations (see below, Fig. 4) with both niche conservatism and divergent selection playing roles in the evolution of western jumping mice.

Taxonomic Implications. –Western jumping mice represent a more complex taxonomic assemblage than previously documented. Deep molecular divergence discovered among southern populations of the western jumping mouse, including paraphyly with respect to *Z. trinotatus,* significantly alters our understanding of species limits in this group (Hall 1981; Holden and Musser 2005; Krutzsch 1954). Hall (1981) recognized 11 subspecies of *Z. princeps* and 4 subspecies of *Z. trinotatus* following Krutzsch's (1954) extensive review of morphological characters. Our molecular and niche assessment suggests that the initial alignment of the Sierra Nevada populations (Elliot 1898; Howell 1920; Preble 1899) close to *Z. trinotatus* is appropriate. Gene trees based on mtDNA may not always reflect species limits due to historical mitochondrial introgression (Good et al. 2008; Runck et al. 2009), but in this case, the independent nuclear perspectives corroborate mtDNA and demonstrate the need for revision of species limits in western jumping mice. A comprehensive re-evaluation of morphological variation across nominal *Z. princeps* and *Z. trinotatus* coupled with development of additional nuclear markers and exploration of finer scale niche variation might provide clarity on the spatiotemporal aspects of diversification.

Historical-biogeographic Patterns. – Phylogeographic structure in the Sierran jumping mice appears to reflect long-term sustained faunal isolation, north-south division of lineages, and elevational shifts with warming climates (Moritz et al. 2008). Other vertebrates in the Sierra Nevada's also show a pronounced north-south split such as wood rats (Matocq 2002a, 2002b; Matocq and Murphy 2007; Matocq et al. 2007), salamanders, and newts (Tan and Wake 1995; Wake 1997). A concordant signature among several species may reflect the influence of glaciers and pluvial lakes formed during the Pleistocene that impeded gene-flow (Gillespie and Zehfuss 2004; James et al. 2002). Further evaluation of shifts in elevation through glacial cycles, in combination with comparative assessments of temporal and spatial congruence in lineage diversification across co-distributed taxa, is needed for the region.

In general, Southern clades of *Z. princeps* demonstrate strong phylogeographic structure that reflects long periods of isolation without mixing of lineages. There were no haplotypes shared among geographic regions (Fig. 3) with molecular signatures (Table 1) indicative of long-term segregation during the LGM in a series of isolated refugial areas across western North America. Coalescent simulations reject an admixture hypothesis but not the persistent allopatric hypothesis (Fig. 4). Jumping mice lineages exhibit higher levels of mtDNA divergence than documented for many other sister-species comparisons in mammals (Baker and Bradley 2006). Further, segregation may have persisted over multiple glacial cycles. Multi-locus data, coupled with fossil calibration and relaxed molecular clocks (Drummond et al. 2006; Heled and Drummond 2010), have been used to establish initial isolation events in birds and mammals in western North America (McCormack et al. 2011; Reid et al. 2011). Independent lines of evidence suggest there is a common process of allopatric divergence, with historical vicariance via intervening xeric environments, responsible for phylogeographic signatures in DNA and niches among co-distributed taxa (Arbogast and Kenagy 2001; Carstens et al. 2005; Sullivan et al. 2000; Zink 2002). Implications of a common signature suggest shared biogeographic processes (Gutierrez-Garcia and Vazquez-Dominguez 2011; Ronquist and Sanmartin 2011) at the community level. Thus, projected climate change and potential shifts in distribution may have more profound (community level) effects that previously considered (Ackerly et al. 2010; Moritz et al. 2008; Thomas et al. 2004).

In conclusion, deep molecular divergence within *Z. princeps* is accentuated over the southern portion of its current distribution. The wide latitudinal range of *Z. princeps* provides future opportunities to test hypotheses of incipient speciation using multi-locus models and coalescent techniques (Carstens et al. 2005; Lessa et al. 2003). Refinement of the persistent allopatric hypothesis includes testing among vicariant speciation models but serves as a working hypothesis to explore concerted signatures among co-distributed species. These preliminary data suggest geographic separation between southern lineages has been a dominant and persistent force shaping divergence within *Z. princeps* and presumably sympatric mammals. Whether these vicariant signatures are suggestive of a common process that is spatially and temporally shared across co-distributed mammals, versus simply idiosyncratic responses to fluctuating climate, should be explored.

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APPENDIX

Specimens examined are listed by scientific name, collection localities, source museums (museum catalog number), and corresponding GenBank accession numbers (mitochondrial DNA cytochrome *b* [cyt*b*], nuclear DNA glucocerebrosidase gene [GBA] and myosin heavy chain 2 [MYH2], or - for not applicable) for jumping mice samples used in this study. Acronyms for museum accessions are MSB - Museum of Southwestern Biology - University of New Mexico, Albuquerque; MVZ - Museum of Vertebrate Zoology - University of California, Berkley; UAM - University of Alaska Museum of the North, Fairbanks. Locality abbreviations: Apache Sitgreaves National Forest (ASNF), Inyo National Forest (INF), Kings Canyon National Park (KCNP), Lassen National Forest (LNF), Lassen Volcanic National Park (LVNP), Peppers Lake Recreation Area (PLRA), Point Reyes National Seashore (PRNS), Powdermill Nature Reserve (PNR), Routt National Forest (RNF), Santa Fe National Forest (SFNF), Yellowstone National Park (YSNP), Voyageurs National Park (VNP), Yosemite National Park (YNP).

Species	**Subspecies**	**State/Province**	**Locality**	**GenBank accession (cyt*b*,GBA,MYH2) no.(s)**	**Museum accession no.(s)**
Z. princeps	*saltator*	Alaska	Chickamin River	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	UAM-22750; UAM-22760; UAM-22771; UAM-22773
Z. princeps	*saltator*	Alaska	Gwent Cove	xxx.xxx,-,-; xxx.xxx,-,-	UAM-33121; UAM-33122
Z. princeps	*saltator*	Alaska	mouth of Unuk River	xxx.xxx,xxx.xxx,-; xxx.xxx,-,-; xxx.xxx,-,-	UAM-22765; UAM-22748; UAM-22749
Z. princeps	*saltator*	Alaska	Reflection Lake	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	UAM-71051; UAM-71052; UAM-71139

Z. princeps	*saltator*	Alaska	Stikine River	xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	UAM-20805; UAM-20789
Z. princeps	*saltator*	Alaska	Tyee	xxx.xxx,-,-	UAM-52172
Z. princeps	*minor*	Alberta	4 km N, 38 km W Sundre	xxx.xxx,xxx.xxx,xxx.xxx	MSB-55774
Z. princeps	*minor*	Alberta	PLRA	xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,xxx.xxx,-	MSB-55775; MSB-55776
Z. princeps	*saltator*	British Columbia	Nass River Valley	xxx.xxx,-,-	UAM-52267
Z. princeps	*pacificus*	California	Fresno Co., Bullfrog Lake, KCNP	xxx.xxx,-,-	MVZ-224516
Z. princeps	*pacificus*	California	Mariposa Co., 3.2 mi E Chinquapin, YNP	xxx.xxx,-,-	MVZ-201664
Z. princeps	*pacificus*	California	Mariposa Co., Bridalveil Creek, YNP	xxx.xxx,-,-	MVZ-201648
Z. princeps	*pacificus*	California	Mariposa Co., Crane Flat, YNP	xxx.xxx,xxx.xxx,xxx.xxx	MVZ-201646
Z. princeps	*pacificus*	California	Mariposa Co., Merced Grove, YNP	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-	MVZ-201639; MVZ-201640; MVZ-216663; MVZ-216664
Z. princeps	*pacificus*	California	Mariposa Co., Monroe Meadows, YNP	xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	MVZ-201649; MVZ-201650; MVZ-201658; MVZ-201659
Z. princeps	*pacificus*	California	Mariposa Co., Yosemite Creek, YNP	xxx.xxx,-,-	MVZ-201647
Z. princeps	*pacificus*	California	Mono Co., Bohler Creek	xxx.xxx,-,-	MVZ-208346
Z. princeps	*pacificus*	California	Mono Co., Sweetwater Canyon	xxx.xxx,xxx.xxx,xxx.xxx	MSB-53415
Z. princeps	*pacificus*	California	Mono Co., Walker Lake	xxx.xxx,-,-	MVZ-216676
Z. princeps	*pacificus*	California	Mono Co., Warren Fork of Lee Vining Creek	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-	MVZ-208347; MVZ-208348; MVZ-208350
Z. princeps	*pacificus*	California	Nevada Co., Sagehen Research Station	xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,xxx.xxx,xxx.xxx	MVZ-193108; MVZ-193109

Z. princeps	*pacificus*	California	Plumas Co., Willow Lake Campground, LNF	xxx.xxx,-,-	MVZ-200067
Z. princeps	*pacificus*	California	Tehama Co., LVNP	xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,-,-	MVZ-199204; MVZ-199205
Z. princeps	*pacificus*	California	Tulare Co., Little Brush Meadow, INF	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-	MVZ-224512; MVZ-224513; MVZ-224514; MVZ-224515
Z. princeps	*pacificus*	California	Tuolumne Co., North Crane Creek, YNP	xxx.xxx,-,-	MVZ-201636
Z. princeps	*pacificus*	California	Tuolumne Co., upper Lyell Canyon, YNP	xxx.xxx,xxx.xxx,-; xxx.xxx,-,-	MVZ-201665; MVZ-201666
Z. princeps	*pacificus*	California	Tuolumne Co., Glen Aulin, YNP	xxx.xxx,xxx.xxx,-; xxx.xxx,-,-	MVZ-201672; MVZ-201673
Z. princeps	*pacificus*	California	Tuolumne Co., McGee Lake, YNP	xxx.xxx,-,-	MVZ-201674
Z. princeps	*pacificus*	California	Tuolumne Co., Dorothy Lake, YNP	xxx.xxx,-,-; xxx.xxx,-,-	MVZ-216654; MVZ-216655
Z. princeps	*pacificus*	California	Tuolumne Co., Grace Meadow, YNP	xxx.xxx,-,-	MVZ-216657
Z. princeps	*pacificus*	California	Tuolumne Co., Virginia Canyon, YNP	xxx.xxx,-,-; xxx.xxx,-,-	MVZ-216665; MVZ-216666
Z. princeps	*princeps*	Colorado	Jackson Co., Connor Creek	xxx.xxx,xxx.xxx,-; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	MSB-76672; MSB-76673; MSB-76674
Z. princeps	*princeps*	Colorado	Routt Co., RNF, Reed Creek	xxx.xxx,-,-; xxx.xxx,-,-	MSB-76593; MSB-76595
Z. princeps	*idahoensis*	Montana	Gallatin Co., Hyalite Creek	xxx.xxx,-,-; xxx.xxx,-,-	MSB-56732; MSB-56733
Z. princeps	*princeps*	New Mexico	Mora Co., 8 mi N, 6 mi E Tres Ritos	xxx.xxx,xxx.xxx,-	MSB-43520
Z. princeps	*princeps*	New Mexico	Santa Fe Co., 5 mi N, 8 mi E of Santa Fe	xxx.xxx,-,-	MSB-41124
Z. princeps	*princeps*	New Mexico	Santa Fe Co., SFNF, Ski Basin Rd.	xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,xxx.xxx,-; xxx.xxx,xxx.xxx,-	MSB-72781; MSB-72783; MSB-72785
Z. princeps	*princeps*	New Mexico	Taos Co., 4 mi NE of Tres Ritos	xxx.xxx,xxx.xxx,xxx.xxx	MSB-41242
Z. princeps	*princeps*	New Mexico	Taos Co., 4 mi N, 11 mi E Arroyo Hondo	xxx.xxx,-,-	MSB-41333

Z. princeps	*utahensis*	Utah	Wasatch Co., Strawberry Reservoir	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,xxx.xxx,xxx.xxx	MSB-77223; MSB-77224; MSB-77225; MSB-77226
Z. princeps	*princeps*	Wyoming	Carbon Co., Battle Creek,	xxx.xxx,xxx.xxx,-	UAM-51347
Z. princeps	*princeps*	Wyoming	Carbon Co., Snowy Range	DQ665221,-,-	
Z. princeps	*idahoensis*	Wyoming	Park Co., YSNP, Blacktail Cabin	xxx.xxx,-,-; xxx.xxx,xxx.xxx,xxx.xxx; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-	MSB-72296; MSB-72297; MSB-72298; MSB-72299
Z. princeps	*idahoensis*	Wyoming	Park Co., YSNP, Lamar Creek	xxx.xxx,-,-	MSB-72294
Z. princeps	*idahoensis*	Wyoming	Park Co., YSNP, Slough Creek	xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,-,-; xxx.xxx,xxx.xxx,-; xxx.xxx,-,-	MSB-72300; MSB-72301; MSB-72302; MSB-72303; MSB-72304
Z. hudsonius	*alascensis*	Alaska	Murray Lake	xxx.xxx,xxx.xxx,xxx.xxx	MSB-247097
Z. hudsonius	*hudsonius*	Minnesota	St Louis Co., VNP	xxx.xxx,xxx.xxx,xxx.xxx	MSB-73498
Z. hudsonius	*luteus*	Colorado	La Plata Co., Florida River	JN546499,xxx.xxx,xxx.xxx	MSB-154917
Z. trinotatus	*orarius*	California	Marin Co., Abbott's Lagoon, PRNS	xxx.xxx,xxx.xxx,xxx.xxx	MVZ-191736
Z. trinotatus	*trinotatus*	Oregon	Benton Co., Prairie Mountain	xxx.xxx, xxx.xxx,xxx.xxx; AF119262,-,-	UAM-67563; UAM-67564
N. insignis	*insignis*	New Brunswick	Kings Co.	xxx.xxx,xxx.xxx,xxx.xxx	MSB-229713

FIGURES

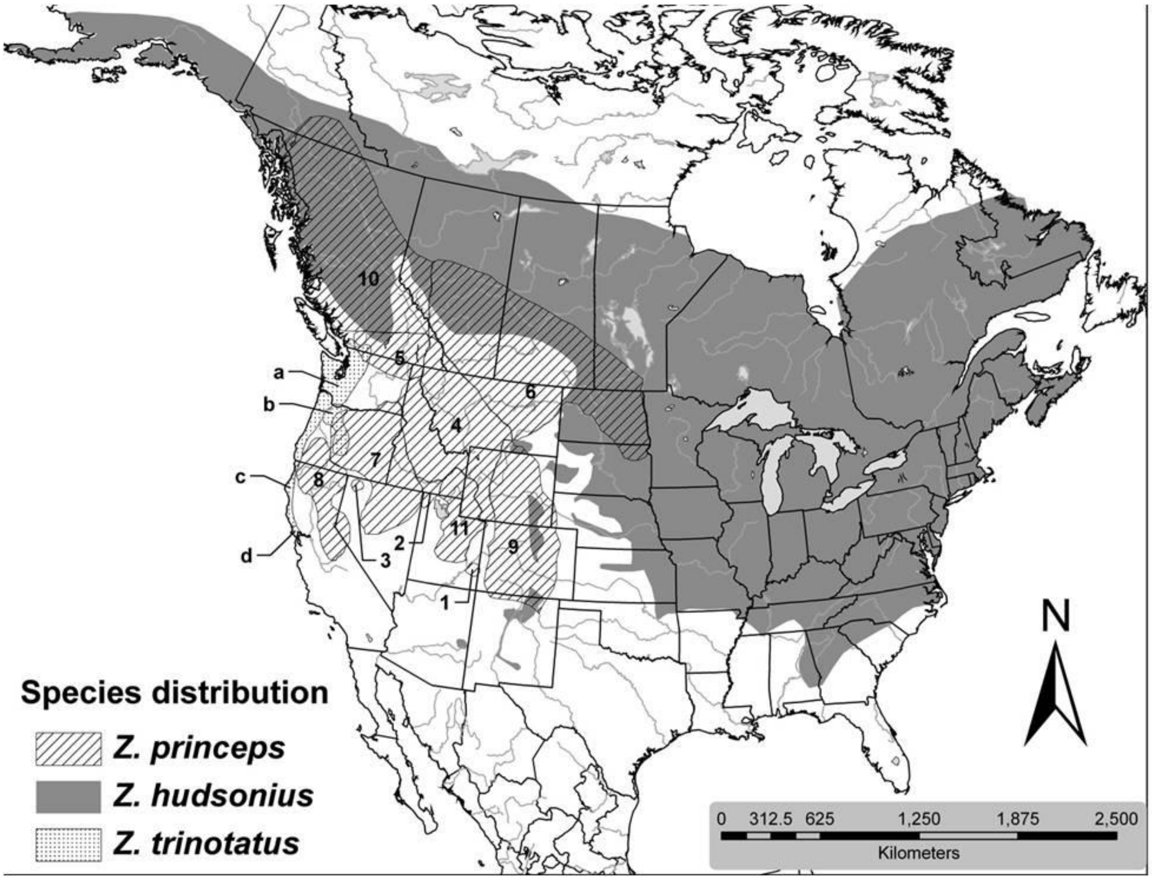

FIG. 1.– Distribution and range limits of North American zapodids - *Zapus hudsonius* (grey), *Z. princeps* (hashes), and *Z. trinotatus* (stipples) modified from Hall (1981). Currently recognized sub-species 1) *Z. p. chrysogenys,* 2) *Z. p. cinereus,* 3) *Z. p. curtatus,* 4) *Z. p. idahoensis*, 5) *Z. p. kootenayensis,* 6) *Z. p. minor,* 7) *Z. p. oregonus,* 8) *Z. p. pacificus,* 9) *Z. p. princeps,* 10) *Z. p. saltator,* 11) *Z. p. utahensis*, a) *Z. t. trinotatus*, b) *Z. t. montanus*, c) *Z. t. eureka*, d) *Z. t. orarius*. Sub-species of *Z. hudsonius* not shown.

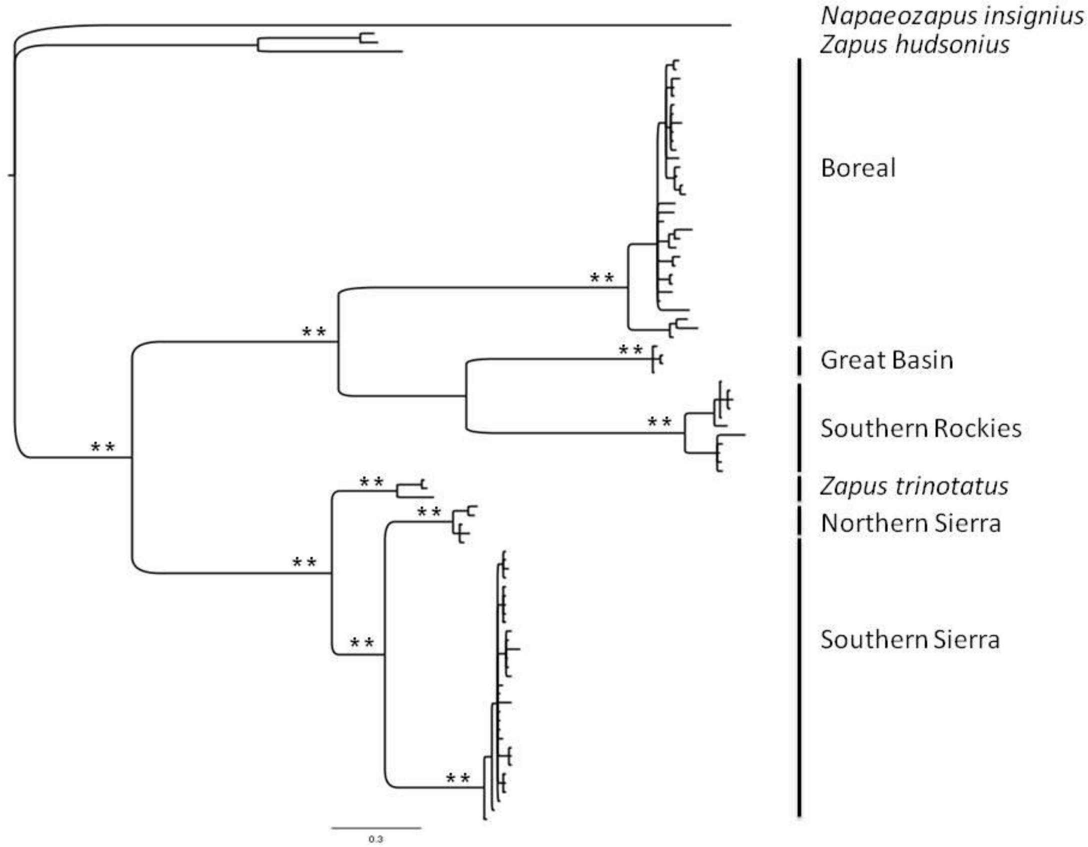

FIG. 2.– Phylogram of Bayesian inference majority rules consensus tree produced using GTR+I+Γ model and samples of *Z. princeps* and other taxa for the mitochondrial cyt*b* gene. Stars at nodes correspond to posterior probabilities (>0.95, PP) from 50k post burn-in trees and 1k non-parametric bootstraps (>.90 ML).

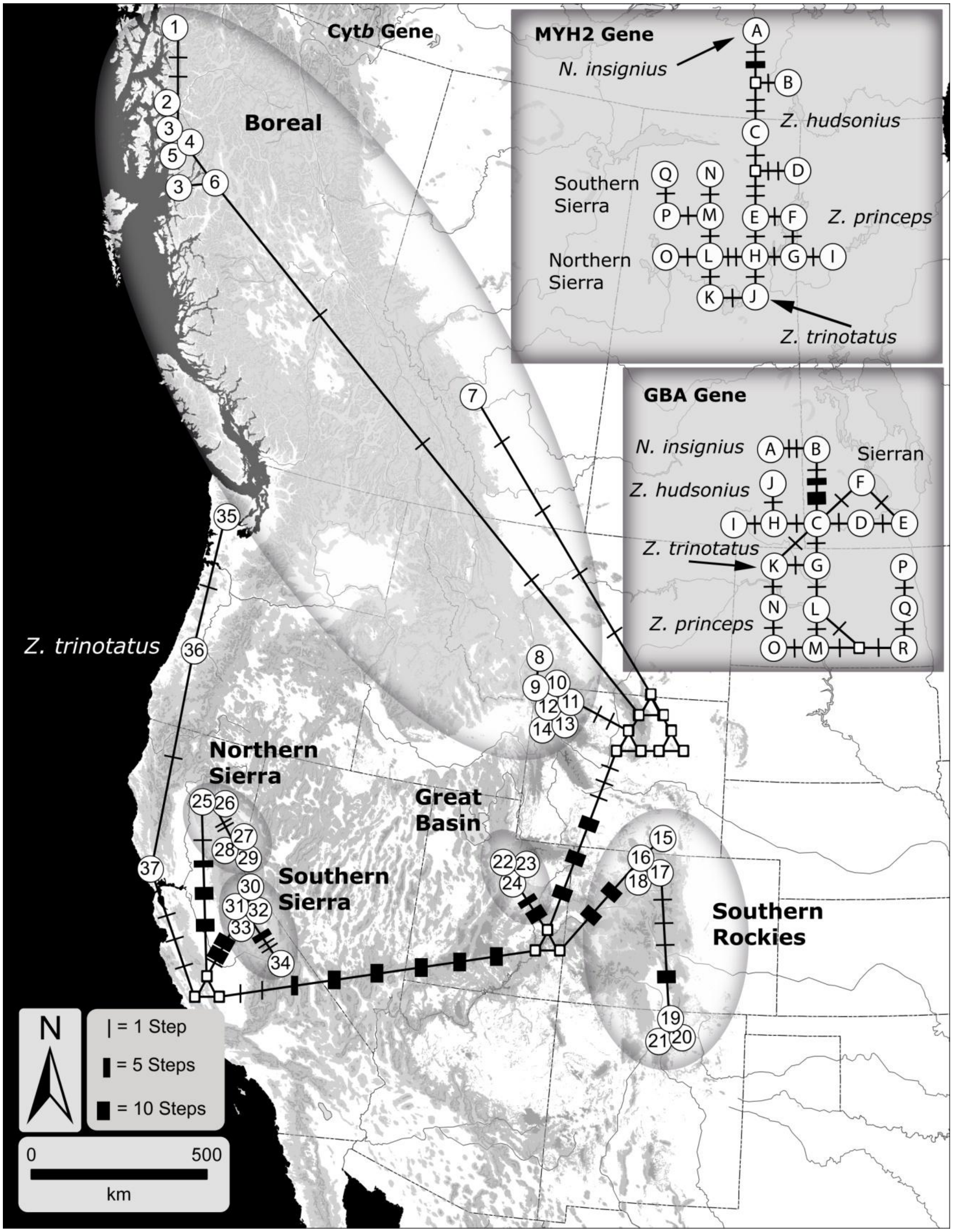

FIG. 3.– Median joining statistical parsimony networks for jumping mice mtDNA (cyt*b*) with respect to geography and nDNA (GBA and MYH2 - inset). Individual tick marks

represent one polymorphic site or mutation (step) and squares represent missing or ancestral haplotypes. Note multiple haplotypes per locality in southern lineages reflecting deep phylogenetic history but haplotypes shared among geographic locations in the most northern populations of the Boreal clade reflecting recent demographic history.

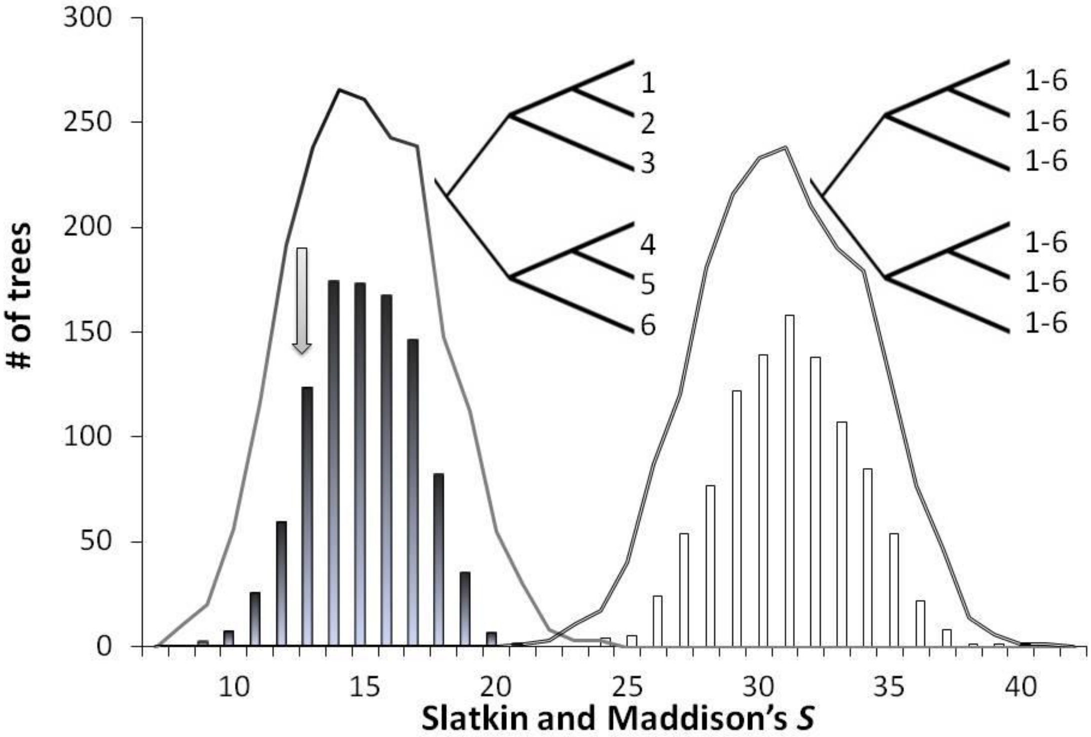

FIG. 4.– Alternative demographic hypotheses for *Zapus princeps* using the parametric bootstrap test (coalescent simulations) of divergence patterns in jumping mice with 90% confidence intervals. Hypotheses of persistent allopatry (PA, grey) versus admixture (AM, white) with the arrow highlighting the empirical tree value for Slatkin and Maddison's *s* (1989; *s* = 13). Numbers correspond with geographic ranges and clades in PA (1 = *Z. trinotatus*, 2 = N. Sierra, 3 = S. Sierra, 4 = Boreal, 5 = Uinta, 6 = S. Rockies) but clades are represented geographically (mixed) in AM.

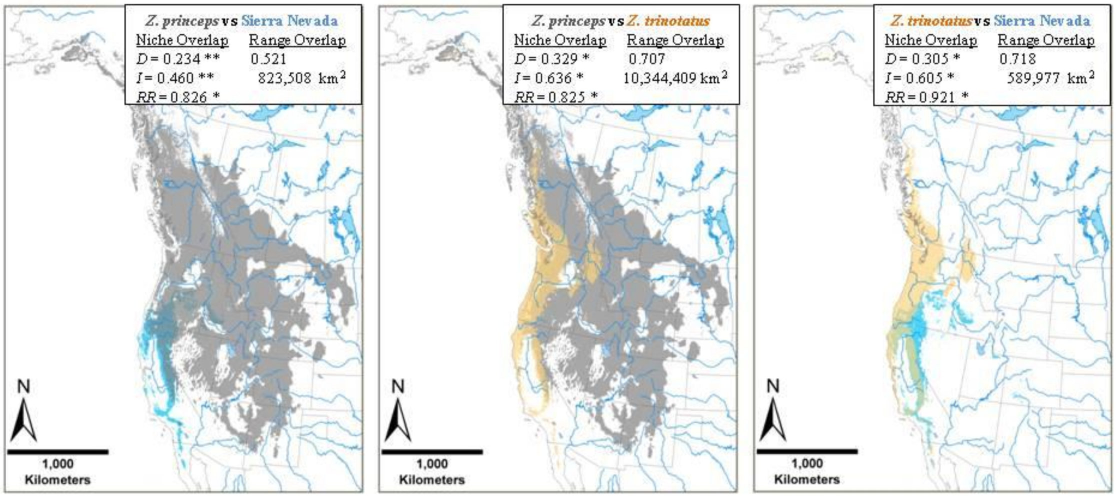

FIG. 5.– Phylogenetically-informed species distributions models using MAXENT based on point-wise mean logistic bootstrap prediction from 20 replicates and minimum training presence threshold rule (>0.20) from 12 environmental variables for *Z. princeps*, *Z. trinotatus,* and Sierran jumping mice. Geographic overlap was calculated in km^2 for each pair and indices (*D*, *I*, *RR*; Warren et al. 2008, 2010) with significance (* < 0.05, **< 0.001) via 100 pseudo-replicates using ENMtools.

TABLES

Table 1. – Molecular diversity indices of mtDNA (cyt*b*) and nDNA (GBA and MYH2) for North American jumping mice calculated in DnaSP; N = Number of individuals sampled, S = polymorphic sites, h = number of haplotypes, η = haplotype diversity and standard deviation (sd), π = nucleotide diversity (per site), and neutrality estimates. Tajima's *D* and Fu's *Fs* were calculated with coalescent simulations (10,000 replicates) with values that correspond to calculations based on the Waterson estimator theta (□$_{W}$). Stars represent significance *<0.05, **<0.01. *Napaeozapus* excluded from cyt*b* analyses.

	N	**S**	**h**	**η** **(sd)**	**π**	***D***	***F$_s$***
cyt*b* gene	101	157	41	.933 (0.018)	0.093	1.303	6.981
Boreal	32	75	14	0.986 (0.013)	0.010	-1.710*	-11.732**

Northern Sierra	5	11	5	1.000 (0.126)	0.005		
Southern Rockies	14	30	7	0.846 (0.061)	0.011	0.992	4.720
Southern Sierra	36	15	5	0.546 (0.094)	0.005	-1.626*	-5.789**
Uinta	4	3	3	0.833 (0.222)	0.002		
Z. trinotatus	4	20	3				
Z. hudsonius	6	82	4				
GBA gene	32 (64)	22	18	0.895	0.010	-1.030	-5.893*

MYH2 gene	25 (50)	16	17	0.938	0.014	-0.305	-9.214*

CHAPTER 3

USING HISTORICAL BIOGEOGRAPHY TO INFORM CONSERVATION: THE CASE OF PREBLE'S MEADOW JUMPING MOUSE

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ABSTRACT

The last Pleistocene deglaciation shaped temperate and boreal biotic communities in North America. Rapid northward expansion into high latitudes created distinctive spatial genetic patterns including distant populations of widespread species that are closely related while adjacent populations, especially those near the southern periphery, often are distinctive due to long-term disjunction. Across a spatial expanse that includes both recently colonized and long-occupied regions, we analyzed molecular variation in zapodid rodents to explore how historical climate shifts influenced diversification in this group. By combining molecular analyses with species distribution modeling and tests of ecological exchangeability, we show that the lineage including the Preble's meadow jumping mouse (*Zapus hudsonius preblei*), a federally listed taxon of conservation concern, is not restricted to the southern Rocky Mountains. Rather, populations along the Front Range are part of a single lineage of ecologically indistinct populations that extends to the far north. Of the 21 lineages identified, this Northern lineage has the largest geographic range and relatively low measures of genetic diversity, consistent with recent northward expansion. Comprehensive sampling combined with coalescent-based analyses and niche modeling lead to a radically different view of geographic structure within jumping mice and indicates the need to re-evaluate their management. Our study highlights a fundamental principle in conservation biology, that biogeographic history should be central to establishing conservation priorities for sound management initiatives.

keywords. conservation prioritization | evolution | niche modeling | phylogeography | speciation

INTRODUCTION

Historical biogeography provides the spatiotemporal context to document geographic variability and to explore processes responsible for generating diversity (1, 2). A growing body of knowledge from fossils (3) and DNA analyses (4) demonstrates massive pole-ward shifts (5, 6) of biota since the last glacial maximum (LGM 26.5-19.0 ka; (7)), reflecting the role of Pleistocene climate fluctuations in shaping present-day distributions and patterns of diversity. Analogous shifts to higher elevations with warming conditions are also documented (8, 9). In North America, molecular signatures reveal that across multiple species, many high-latitude populations share recent ancestry with distant low-latitude populations due to rapid northward colonization following glacial retreat (4). Conversely, adjacent low-latitude populations are often genetically divergent, reflecting enduring spatial disjunction. Identifying distinct evolutionary lineages and their spatial distribution is central to understanding the processes that lead to biological diversification, but these entities are also the units that are the target of conservation action. Deciphering molecular signatures across the entire range of a species should be an essential first step toward executing effective conservation and management strategies, but this step requires broad sampling across multiple components (taxonomic, genetic, geographic, ecological) to ensure variation and historical signatures are rigorously assessed (10-12).

The federal Endangered Species Act (ESA) is a cornerstone of management practices in the United States and often guides conservation spending, however, implementation of the ESA can be problematic (13-15). Debate persists on how best to assess imperilment, but a foundational principle is to conserve diversity, often by identifying evolutionarily divergence (16-19). Limited ranges also are widely considered to increase conservation concern (20, 21). Conservation decisions often need to be made quickly and, thus, using available information, which can often be datasets based on a single character type (usually morphology) analyzed decades ago, before the sophisticated quantitative methods available to modern studies. Consequently, conservation efforts frequently rely on antiquated intraspecific taxonomy (i.e., subspecies) as the primary roadmap identifying diversity (22), yet federal managers are bound by statute to follow the ‘best-available science’. Allocation of finite conservation resources should hinge on the ability to define geographic variation (e.g., Evolutionarily Significant Units – ESU) within species (23, 24) and assess ecological exchangeability within and among ESUs (25-27). These goals depend on adequate sampling across genes to identify units of significant evolutionary distinction and across the spatial and ecological breadth of lineages (28-30) to ensure evolutionary history is well established. We implement conservation phylogenetic methods (31-34) by integrating genetic and ecological approaches to assess whether genetic subdivisions are consistent with jumping mice taxonomic hypotheses. Then we develop conservation priorities that reflect a historical-biogeographic perspective (35-38) predicated on extinction threats. Conservation phylogenetic techniques have been developed (39, 40) in an effort to more objectively prioritize protection efforts. We explore the historical signatures (genetics and niches) of jumping mice and simultaneously test alternative hypotheses of evolutionary independence across this group to better inform conservation action.

Broadly, our aim is to highlight that unraveling biogeographic signatures of the past is an essential step in conservation efforts. Our specific goal is to examine whether geographic structure of evolutionary diversity is reflected in taxonomy which is the current foundation of the politically-charged management of zapodid rodents in North America (41, 42). Specifically we integrate phylogeographic structure, including historical demographic signals and spatial shifts, into conservation prioritization. Through a coalescent-based approach (43, 44), populations of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*, Fig. 1B) along the Front Range of Colorado and Wyoming (45, 46) are minimally diverged from populations extending far northward to western Canada and Alaska (Fig. 1A, 2). Since 1998, controversy regarding the federal listing of this subspecies has led to rancorous debates in popular press (47, 48), science (49-55), policy (56, 57), and law (58). Conservation efforts for *Z. h. preblei* in the past were estimated at nearly $172 million (59) and may cost an additional $268 million in the next 2 decades (60, 61). Our work extends previous efforts to test the distinctiveness of this subspecies (49, 55) by placing *Z. h. preblei* populations within an expanded context of evolutionary diversification and ecological variation across all zapodid taxa, not just adjacent subspecies.

METHODS

Our generalized workflow began with sequencing genes from all jumping mice taxa using samples from natural-history museums and targeted fieldwork (2007 and 2010) to obtain topotypes, but also considering a broader phylogenetic context. Single gene and multilocus phylogeny reconstructions (e.g. species-tree) were used to identify lineages (e.g. ESUs). Coalescent-based population summary statistics (mtDNA) and multilocus Extended Bayesian Skyline analyses were conducted to document historical demographic change for each lineage. Phylogenetically-informed species distribution models (SDM) were constructed from contemporary locality records and projected to the past (66, 80, 112, 121) to identify potential paleodistributions (i.e. at LGM). Fossils were integrated for the species-tree phylogeny and to independently confirm paleodistributions. Finally, evolutionary distinctiveness (i.e. monophyly), population size change (contemporary and past), contemporary range size, historical range size, and existing risks were integrated to define extinction threats (SI Appendix, Table S1) and each lineage was assigned an updated regional IUCN score (117). IUCN scores were then converted using ranks-to-extinction probability transformations and applied to the taxonomy-based species-tree phylogeny (33, 39) to more objectively measure and assess conservation priorities.

Genetic Data. We obtained DNA sequences for 762 jumping mice across North America from existing natural-history collections and targeted fieldwork at type localities (i.e. topotypes) of subspecies. We extracted and sampled DNA from 430 individuals and sequenced the complete mitochondrial cytochrome *b* gene (cyt*b* – 1140 bp). To more fully explore genomic diversity, we also sequenced a subset of these specimens for 2 nuclear introns and 2 nuclear exons. Partial introns included Apolipoprotein B (APOB) and Glucocerebrosidase (GBA), and partial exons Breast Cancer Susceptibility (BCRA1), and the beta-myosin heavy chain (MYH7). Partial (1006 bp) cyt*b* data were obtained from GenBank for 332 samples (predominantly *Z. hudsonius*) from previous molecular studies (49, 55). Samples were partitioned by species; 31 *N. insignis* (5 subspecies), 455 *Z. hudsonius* (12 subspecies), 223 *Z. princeps* (10 subspecies), and 53 *Z. trinotatus* (4 subspecies) to address conservation-phylogenetic and historical-biogeographic questions and assess if phylogeographic structure is reflected in the existing taxonomy (41, 42, 85); Fig. 2, *SI Appendix*, Fig. S1). Polymerase chain reactions (PCR) and cycle sequencing followed protocols previously established (84, 122, 123) and heterozygous positions were scored using the IUPAC nucleic acid code.

Specific nDNA alleles were identified using statistical methods with haplotypes inferred from multi-allelic loci using a Bayesian framework via PHASE (124, 125) in DNASP v. 5.10.01 (126). We conducted three independent runs for each locus for 1k iterations with alterations in block size for the partition-ligation procedure. Individual haplotypes that could not be statistically resolved (<90% posterior probability) were coded as missing data. Homologous sequences were aligned using MUSCLE v. 3.7 (127) and validated visually. Individual contigs were deposited in GenBank (xxxx.xxxx-xxxx.xxxx).

Phylogenetic Analyses. We conducted phylogenetic analyses using a Bayesian inference (BI) framework for each locus with MRBAYES v. 3.1.2 (128, 129). Aligned datasets were subjected to alternative models of sequence evolution in jModelTest (130) where Bayesian information criterion (BIC) (131) was used to determine the best-fit nucleotide substitution model (*SI Appendix,* Table S4). Phylogenetic reconstructions were initiated with random trees, run with 4 chains (default heating values) for 5 million generations, with sampling every 5k generations. Convergence diagnostics were completed with the program AWTY (132) and optimal parameter estimates were examined in TRACER (133). Nodal support (posterior probability – PP) was identified in the consensus of the residual trees with the first 5k trees discarded (134) and three independent runs were performed to ensure replicated convergence and trees were depicted with FIGTREE.

Given that tree-based methods may fail to reveal reticulate evolution (135) often inherent to recent divergences, we also conducted a phylogenetic statistical-parsimony network analysis (120) for each species and each gene using TCS v. 1.21 (119). For Cyt*b*, we detected 102 haplotypes in our *Z. hudsonius* dataset, and 33 within the Northern lineage as a distinct network with a significant (95%) limit at 5 steps (other networks not presented). We failed to detect haplotype H from King et al. (49) and the reported sample is identical to A. We document 4 other errors in reporting data. In Douglas Co. Colorado, both haplotypes C and I were reported, but all available datasets reflect only haplotype J at this locality. GenBank does not return haplotypes E or S, but reported F and V have 2 distinct haplotypes each that we inferred respectively (highlighted with an asterisk in *SI Appendix*, Fig. S4). We detected the widespread I haplotype from two new locations plus one additional haplotype in Colorado. Twelve closely related haplotypes were detected in the far North.

Species-Tree Estimation and Divergence. Single-gene analyses often indicate a lack of monophyly at the species level and may vary in comparisons among loci (136), so we estimated the phylogeny with *BEAST (65) using a subset of the molecular data from each subspecies (topotypes). We used species-tree methods (136) to assess if phylogeographic structure is reflected by the morphologically-based subspecies taxonomy of North American jumping mice (42). We sampled at least one representative individual topotype for each subspecies but generally >3 representatives for all genes conforming to a multilocus, multispecies, coalescent-based framework. Analyses were setup in BEAUti v. 1.7.0 and run with BEAST v.1.7.0. Fossil calibration points for divergences were used at several nodes (137), Fig. 2) of the species-tree from well-dated fossils of North American zapodids (92, 116, 138-141) and correspond to paleodistribution reconstructions (see below) and established estimates of spatiotemporal divergence. A strict molecular clock (0.05) was used for the mtDNA dataset and estimated clocks for nDNA. Models of sequence evolution were used for each locus with remaining parameters set to default. Runs were conducted for 50M generations, sampled every 5k, and we examined ESS values (>200) in TRACER and split frequencies across the Markov-chain in AWTY (132) indicating stabilization.

Demographic Tests. Molecular diversity indices (142) were calculated in DNASP and determined for each gene, by species, and by lineage (Table 2; only mtDNA presented) including segregating sites (S), number of haplotypes (N_h), haplotype (h) and nucleotide (π) diversity, and mean nucleotide differences (K). Population equilibrium tests for the mtDNA dataset were conducted by each lineage and included Tajima's D (143) Fu's F_S (144), and R_2-test (88), and significance was assessed using a null distribution of 10,000 coalescent-based simulations. Population equilibrium tests (D, F_S, R_2) have high power for revealing demographic change under a model of sudden expansion (88) where significant negative values of D and F_S and small positive values of R_2 are indicative of population growth. Tajima's D (large sample size) and the R_2-test (small sample size) estimates demographic change using information from segregating sites whereas Fu's F_s uses information from haplotype frequencies based on Ewens' (145) sampling distribution.

Given that single gene summary statistics (e.g. D, F_S, R_2) may not accurately capture or assess all historical demographic information, we also analyzed the changes in population size through time using the Bayesian-skyline (single locus(90)) and extended Bayesian-skyline (multilocus (89)) analyses. These coalescent-based approaches calculate the posterior distribution of effective population size at intervals along the phylogeny. We performed analyses for each zapodid lineage using the model of nucleotide substitution, fixed the mtDNA substitution rate to 1 (substitution per site) and maintained a strict molecular clock, but estimated clocks for the nDNA datasets. Default setting for the skyline model (constant) and number of groups (10, except n-1 for Coastal, Northern Sierra, Okanogan, and Southern Cascade) were retained.

Species Distribution Modeling. We used SDM to assess niche envelopes of each lineage with 2.5 minute (4km) resolution, bioclimatic variables (146) from the WorldClim database (http//www.worldclim.org) for contemporary and LGM. Modeling procedures followed previous studies (68, 147) by clipping the coverages to the study area (North America). Niche variables may be highly correlated and influence projections, so we used the 11 most biologically meaningful and uncorrelated coverages (Bio1-3, 7-9, 15-19; (82). Localities for each taxon were downloaded from MANIS (Jan 2011) and updated using biogeomancer workbench (148). To account for sampling biases (149) that may result in model over-fitting, we discarded localities with >0.5km^2 uncertainty and down-sampled (aka culled) records so that only a single record was represented within 10 km^2. We partitioned localities by species-tree lineages rather than nominal subspecies to reconstruct SDMs for contemporary and ancestral conditions. However, one exception includes a finer analysis of the Northern lineage to test if *Z. h. preblei* is ecologically exchangeable (see below) with conspecifics (i.e. *Z. h. alascensis, Z. h. tenellus; SI Appendix*, Table S2). Partitioned SDMs were used to inform regional IUCN rankings for each lineage (see below, *SI Appendix,* Table S1).

SDMs were constructed using default settings in the program MAXENT version 3.3.3a (114, 121) with 20 replicate runs. When possible, localities with genetic data were used as an alternative training dataset. When insufficient genetic samples were available, we randomly reserved 20% of available localities as training datasets. Models used the point-wise bootstrap median of replicated runs with the '90% of the samples included' as the projection criterion. Given that changes in population size and range size are correlated (87, 91), we relate LGM and contemporary predicted SDM to historical and contemporary N_e that were then incorporated into IUCN rankings (see below).

Niche conservation is a continuum (69, 150) where closely related taxa (i.e. lineages) generally share niche space more frequently than randomly expected, but rarely are environmental envelopes identical. Ecological exchangeability is expected when niches are sufficiently similar (26). To detect the degree of ecological exchangeability among jumping mice we assessed niche overlap between pairs of lineages using two metrics: the *I* statistic (69) and relative rank (*RR*; (151). With both metrics, pairwise overlap values range from 0.0 (completely discordant) to 1.0 (identical environmental envelopes). We also conducted 'niche identity tests' to assess if environmental envelope overlap is significantly different (one-tailed test) from a null expectation for populations within the Northern lineage. Niche identity tests randomize sample points and reconstruct an expected degree of niche overlap from an underlying distribution. ENMTOOLS v.1.3 (152) was used to assess niche overlap (*I*, RR) and conduct randomized tests (niche identity) using 100 pseudoreplicates for each analysis (*SI Appendix*, Table S2).

Conservation Prioritization. Regional IUCN rankings were updated using established criteria (21, 117) and applied to each lineage to address both risk of extinction and conservation priority. Rankings are characterized by threats to extinction (*SI Appendix,* Table S1), which simultaneously incorporates independent datasets. These include current conservation concerns, phylogenetic distinctiveness, SDMs reflecting current range size and range size change since LGM relative (to conspecifics), plus contemporary and historical change in population size (84, 86, 104). IUCN rankings included: Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC). The rankings Extinct, Extinct in the Wild, and Regionally Extinct (EX/EW/RE) and Data Deficient, Not Applicable, and Not Evaluated (DD/NA/NE) were not implemented in this study.

Next, regional IUCN ranks were converted using the IUCN_{100} (39, 98) ranks-to-extinction probability transformations with the TUATARA module (153) in MESQUITE v.2.75 (154). There are several ranks-to-extinction transformations, but the IUCN_{100} (Fig. 3) is thought to most accurately reflect threats to extinction within the next 100 years considering ongoing and future anthropogenic pressure (98).

RESULTS

Sampling. Using museum collections and targeted fieldwork, we obtained range-wide samples that represented all extant zapodid taxa (i.e. complete taxon sampling, 32 subspecies of 4 extant species), and then sequenced multiple genetic loci and inferred niche space to assess if genetic structure accurately reflects the nominal taxonomy (41, 42). We simultaneously tested the genetic structure against the existing taxonomy and set the historic framework with a species-tree phylogeny (62-65). Then, by sampling niches using phylogenetically-informed SDMs (66, 67), we explored potential contemporary and paleodistributions (68) to assess ecological exchangeability (25, 26, 69).

Phylogenetic Analyses. Bayesian gene-tree analyses of individual loci produced different estimates of divergence (*SI Appendix*, Fig. S1) and varying degrees of lineage sorting among phylogeographic groups (i.e. lineages). The mtDNA dataset had the strongest phylogenetic signal and support values (posterior probabilities ≥ 0.95) identifying 12 clades as deeply divergent. Phylogenetic analyses for the nuclear loci reflect some degree of allele sharing across the range of jumping mice, but in general, alleles are well partitioned among species and lineages (*SI Appendix*, Fig. S1).

Species-Tree Estimation and Divergence. Our taxonomy-based species-tree reflected strong support for 21 phylogeographic lineages, but failed to document significant support for all morphologically-based subspecies (Fig. 2). Further, the species-tree revealed novel intraspecific relationships. For example, past assessments of the validity of *Z. h. preblei* focused on geographically proximate taxa that were assumed to be close phylogenetic relatives (*SI Appendix*, Fig. S2). Instead, far northern (geographically distant) subspecies (i.e. *Z. h. alascensis, Z. h. tennellus,* and western populations of *Z. h. hudsonius*) form a closely related clade with Front Range *Z. h. preblei* (Fig. 2). This widespread lineage separated from the Southern Plains lineage (*Z. h. campestris, Z. h. hudsonius, Z. h. intermedius*) at the end of the last glacial period. This distilled understanding of shared biogeographic history and wide range of closely related haplotypes may alter conservation priorities for Front Range jumping mice.

Demographic Tests. Assessments of changes in effective population size N_e were evaluated using both single-locus (mtDNA) and multi-locus techniques, with signatures for both generally concordant (Table 2, *SI Appendix*, Fig. S3). Ten lineages experienced significant shifts in $N_{e.}$ The Northern lineage experienced the most pronounced historical demographic expansion signatures (Table 2, Fig. 1D, *SI Appendix*, Fig S3B), while the Uinta lineage reflected historical demographic declines (*SI Appendix*, Fig. S3C).

Species Distribution Modeling. Climate-based SDMs predicted for each lineage reflect geographically restricted populations with varying degrees of niche overlap, but generally over-prediction was minimal (*SI Appendix*, Fig. S2). An exception is the Northern Cascade and Southern Cascade lineages that show niche overlap (I = 0.875, RR = 0.929), but deep divergence (middle Illinoisan; Fig. 2). Reconstructed SDMs fail to predict separation at the Columbia River. Relative influences of environmental parameters are typically lineage specific (*SI Appendix*, Table S3) but not for the Northern Cascade and Southern Cascade lineages. For example, Mean Temperature of Driest Quarter (Bio9), Precipitation of Coldest Quarter (Bio19), and Precipitation Seasonality (Bio15) had similar combined contributions (82.7% and 83.2%) for these lineages, a pattern that typifies niche models for recently diverged lineages (e.g. Acadian and Allegheny). Tests of niche evolution (69) for subspecies within the Northern lineage suggest there is minimal differences among populations across this wide range (*SI Appendix*, Table S2).

Conservation Prioritization. Key metrics (*SI Appendix*, Table S1; (20)) that elevate conservation ranking include genetic distinctiveness (Fig. 2), comparatively low N_e (Table 2, *SI Appendix*, Fig. S3), population declines (historical or contemporary), spatial declines (Table 1), non-overlapping niches (i.e., not ecologically exchangeable; *SI Appendix*, Table S2), and existing management efforts (e.g., *Z. h. preblei*). We defined the risk of extinction for all lineages by first establishing genetic distinctiveness (Fig. 2), then calculating effective population sizes (N_e; Table 2, *SI Appendix*, Fig. S3), population declines (historical and contemporary), spatial shifts in distribution (Table 1), and overlap in niche space (i.e., ecologically exchangeability) among lineages. Risks of extinction ranged from Least Concern (0.0001) to Critically Endangered (0.999) and were applied in a phylogenetic context to determine conservation priority. The lineage that includes the federally threatened subspecies *Z. h. preblei* has low priority (Fig. 3) while other lineages without protection are identified as high priority (i.e., high extinction threat of a divergent lineage).

DISCUSSION

This study highlights how historical biogeography can be used to lay a foundation for conservation action. Specifically, the federally listed *Z. h. preblei* is part of the wide-ranging Northern lineage, composed of closely related populations that expanded north- and westward following the last deglaciation of North America. Under a variety of well-established conservation criteria, this widespread set of populations would hold lower conservation priority than other lineages that are genetically divergent, ecologically distinct, and geographically restricted units (i.e., endemic lineages) with molecular signatures indicative of declines (34, 70-72). We suggest that management plans for species-of-concern should, at a minimum, require comprehensive sampling of a species range coupled with phylogeographic analyses to establish a broad spatial and temporal perspective on diversity as a strong foundation for prioritizing conservation efforts. Second, inadequate sampling can lead to a failure to identify and test relevant taxonomic hypotheses, and thus fail to rigorously assess signatures of diversification and demography. Third, conservation phylogenetics (32), set within a broader lineage-based context that explicitly integrates historical signatures (e.g. demographic and spatial shifts), provides a more objective means of prioritizing management efforts (33). Finally, museums harbor an irreplaceable wealth of spatiotemporal data for deciphering changing conditions and informing conservation (9, 73).

Comprehensive sampling reveals diversification that informs conservation. A requisite, but often overlooked, first step in any conservation study is establishing the systematic relationships and geographic limits of the taxon of concern (20). A key assumption in systematics is complete taxon sampling (29, 74, 75) to distinguish among alternative phylogeographic hypotheses (11, 76, 77). By using comprehensive taxon sampling, assessing variation across multiple genetic loci (78, 79), and implementing an integrative approach that includes niche characterization (66, 80), we uncovered 21 divergent lineages across North American jumping mice (Fig. 2). Generally, lineages differed in niche space (*SI Appendix,* Table S3) and these are interpreted as ecologically inexchangeable. For example, the Uinta lineage (*Z. p. utahensis*), is sufficiently distinctive based on genetic and niche variation to warrant specific status via classic measures (81-84) and within a generalized lineage context (43, 44). Similarly, using this approach, and accounting for limited morphological variation (42), *Z. h. preblei* would be considered synonymous with *Z. h. alascensis* and *Z. h. tenellus.* We suggest that jumping mice taxonomy (41, 85) currently under-represents species-level variation with both phylogenetic and niche datasets implying management should focus on lineages (84, 86), rather than subspecies, as the requisite backdrop to conservation action. More specifically, several divergent lineages other than the one including *Z. h. preblei* should be carefully assessed and monitored.

Signatures of diversification and demography contradict taxonomic assumptions. We used extended Bayesian sky-line analyses to assess historic demographic signals (Fig. 1D). The integrated molecular and niche approach reveals spatial shifts since the LGM (latitudinal, longitudinal, or elevational) that can be placed into four general models. [i] *Demographic* (4, 87) *& Spatial (*latitudinal*) Expansion*. The genetic signatures of Acadian, Appalachian, Boreal, Canadian, Great Plains, Northern (including *Z. h. preblei*), and the Northern Plains lineage (Table 2, Fig. 1D) significantly deviate from neutrality (88) with comparatively lower nucleotide diversity, increased haplotype diversity (87), and recent population increases (*SI Appendix*, Fig. S3, (89, 90). Further, each lineage reflects spatial expansion from disjunct late-Pleistocene ancestral ranges (Fig. 1C, Table 1, *SI Appendix*, Fig. S2). [ii] *Demographic & Spatial Contraction* (91). Conversely, the low-latitude and montane-associated Great Basin, Northern Sierra, Okanogan, Southern Cascades, Southern Rockies, and the Uinta lineages reflect signatures of demographic stasis or contraction with concordant spatial contraction during Holocene warming. [iii] *Demographic Expansion with Elevational Shift*. The Southern Sierra lineage recently experienced demographic expansion to higher elevations (not latitudes) since the LGM (86). [iv] *Demographic Stability but Spatial Shift* (84). Finally, the Coastal, Southern Plains, and the Southwestern lineage shifted from ancestral ranges, but experienced no significant demographic change.

The Northern lineage extends from Colorado northwest to the Alaskan Peninsula (Fig. 1A), a distance of >4700 km and the broadest distributional range of all jumping mice (Table 1). Among 16 lineages with >5 haplotypes, the Northern lineage has the lowest haplotype diversity (*h*), lowest nucleotide diversity (□), and fewest nucleotide differences (*K*). Together (Table 2) these metrics indicate recent demographic growth (4, 87). Further, populations across this wide range appear ecologically exchangeable (i.e., occupy equivalent niche space, *SI Appendix*, Table S2). Fossils dated to the Late Pleistocene from the Great Plains coincide with the paleodistribution models (Fig. 1C) (92) with the hind-cast narrow-range agreeing with low-density ancestral effective population sizes (Table 2, Fig. 1D). During the early Holocene as glaciers retreated, ancestors of the Northern lineage may have tracked suitable conditions westward from the Great Plains to regions along the Front Range of the Southern Rockies (49, 51, 55) and northward to Alaska. Northward expansion signatures were detected in 6 other jumping mice lineages (Table 2), mirroring a common process (1, 4, 6, 87). However, no other zapodid reflects demographic expansion metrics near the magnitude of the Northern lineage (Table 2; Fig. S3).

Morphologically-based taxonomy (41, 42) and previous molecular studies of Preble's jumping mice (49, 55) assumed that spatially adjacent subspecies were most closely related, leading to limited sampling of taxa (1/2 subspecies) and geographic breadth (<1/4 *Z. hudsonius* range) as the basis for the federal listing (52). In this case, spatially proximal subspecies are not necessarily closely related. *Zapus h. preblei* was described in 1954 based on 4 adult specimens (42). Although diagnostic morphological characters (42) broadly overlap with northern subspecies (i.e., *Z. h. alascensis* and *Z. h. tenellus*), those subspecies were never directly compared, likely due to their tremendous geographic distance from the southern Rocky Mountain populations. Instead taxonomic evaluation of the jumping mice (49, 51, 53, 55) compared Southern Rocky Mountains with adjacent Plains and Southern subspecies (i.e., *Z. h. preblei* against *Z. h. campestris, Z. h. intermedius*, *Z. h. luteus*, *Z. h. pallidus*). This study reinforces the need to assess evolutionary variation within a comprehensive historical-biogeographic context, as a first step in evaluating conservation status (23, 39, 93, 94) or exploring other processes (25, 26). Further, observations of morphological similarity across jumping mice were part of the basis for a proposal to remove recognition of all *Z. hudsonius* subspecies (95), but that conclusion was not incorporated in a formal taxonomic revision. Our tests of adaptive niche variation are across multiple populations of the Northern lineage that showed no statistically significant ecological differences (*SI Appendix*, Table S2). To fully address conservation of North American jumping mice, a comprehensive taxonomic re-evaluation of all lineages and subspecies is needed and should include a set of tests that encompasses the emerging historical-biogeographic perspective, and more finely assesses hypotheses of both evolutionary independence and adaptive variation.

Conservation prioritization informed by historical factors. Over seventy-five percent (16/21) of jumping mice lineages rank higher in conservation priority than the Northern lineage that includes the state and federally listed subspecies *Z. h. preblei* (Fig. 3). Furthermore, the 7 lineages (Acadian, Appalachian, Boreal, Canadian, Great Plains, Northern, Northern Plains) that experienced Model [i](i.e. Demographic and Spatial Expansion) are among the lowest conservation priorities (Fig. 3). Each of these lineages are recently diverged (Fig. 2, since Late-Pleistocene), have wide ranges that spatially expanded since LGM, reflect comparatively large N_e, and experienced recent demographic growth (Table 2; *SI Appendix*, Fig. S3). Moreover, *Z. h. preblei* is ecologically exchangeable with far northern subspecies (e.g. *Z. h. alascensis* and *Z. h. tenellus*). Combined, these metrics and regionally updated IUCN scores, suggest the Northern lineage is Least Concern (LC = 0 threats; Weights = 0.001 (40). However, given the ongoing management concerns in the Front Range of Colorado and Wyoming, we used the Near Threatened (NT = 0+ threats; Weights = 0.05, Fig. 3) for this lineage.

In contrast, lineages that are endemic to southern mountains and mesic coasts have remained relatively stable over glacial cycles (Model iv) or contracted to higher elevations (Model iii). Both are histories that largely preserved accrued genetic variation and ecological differentiation. These signatures demonstrate that climate-mediated demographic histories (96, 97) are mirrored in genes and niches with the 5 jumping mice lineages with highest extinction threat over the next century (Fig. 3) are endemic to low-latitude montane regions (Allegheny, La Sal, Southwestern, and Uinta) and the Redwood Coast of California (Coastal). Among these, the neoendemic Southwestern lineage (USFWS candidate *Z. h. luteus*) has an order of magnitude higher conservation priority (Fig. 3) than the Northern lineage (using IUCN_{100} (40, 98). The Allegheny (*N. i. roanensis*) lineage should have comparable priority over the Northern lineage, but has no protected status. Other jumping mice exhibiting higher conservation metrics, yet no protected status, include two populations of the La Sal lineage (*Z. p. chrysogenys*), the contracting Uinta lineage (*Z. p. utahensis*), and relict populations of the Coastal lineage in California (*Z. t. eureka + Z. t. orarius*). Thus, existing management plans targeting only *Z. h. preblei* may be missing key elements of evolutionary history. An integrative approach to conservation of zapodids should target distinct lineages at higher risk of extinction, particularly those that are endemic to regions with critical land use issues. Shrinking mesic habitats at lower latitudes are due to the synergy (99) between climate change (100-102) and anthropogenic fragmentation (103) that may precipitate jumping mice declines (84, 104). Conversely, high-latitude lineages of zapodids are the result of expanded ranges during the warming phase of the Holocene epoch (*4*) and generally have lower extinction risk because of more limited human use of these landscapes.

Taken together, these data may counter the proposed listing of *Z. h. preblei* under the ESA (105, 106) based on traditional measures of rarity, such as limited range for an ecologically and genetically discrete taxon (107, 108). Conservation efforts targeting jumping mice within the Front Range of Colorado and Wyoming (109) should be carefully re-evaluated in light of the projected wide distribution of the Northern lineage.

Localized population declines, as reported for *Z. h. preblei* (45, 110, 111), are problematic for mesic-associated organisms throughout the xeric environments of the West (104). These analyses identified lineages elsewhere with higher conservation priority, reinforcing the premise that management efforts should first identify and preserve the most ecologically and genetically divergent units (112). Furthermore, these results suggest management action should not rely principally on taxonomy that may be in need of revision (22) to more accurately reflect ecological distinction and evolutionary history.

Specimen-based conservation remains undervalued. Finally, we underscore the point that museum collections directly facilitate and inform conservation efforts by providing temporal, spatial, and taxonomic breadth of samples. Integrative conservation analyses directly depend on widespread specimen representation in two phases: georeferenced occurrence records to project SDMs (113, 114) and high-quality specimens that preserve tissues and morphological features. Specimens link genes to the phenotype and the organism to the environment providing the necessary framework to refine our understanding of how phenotypes are interacting with changing conditions. Analyses that are spatiotemporally anchored by fossil specimens further highlight the value of integration across independent datasets to build robust taxonomies (43) and falsifiable measures of diversity, critical for any conservation effort (115).

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FIGURES

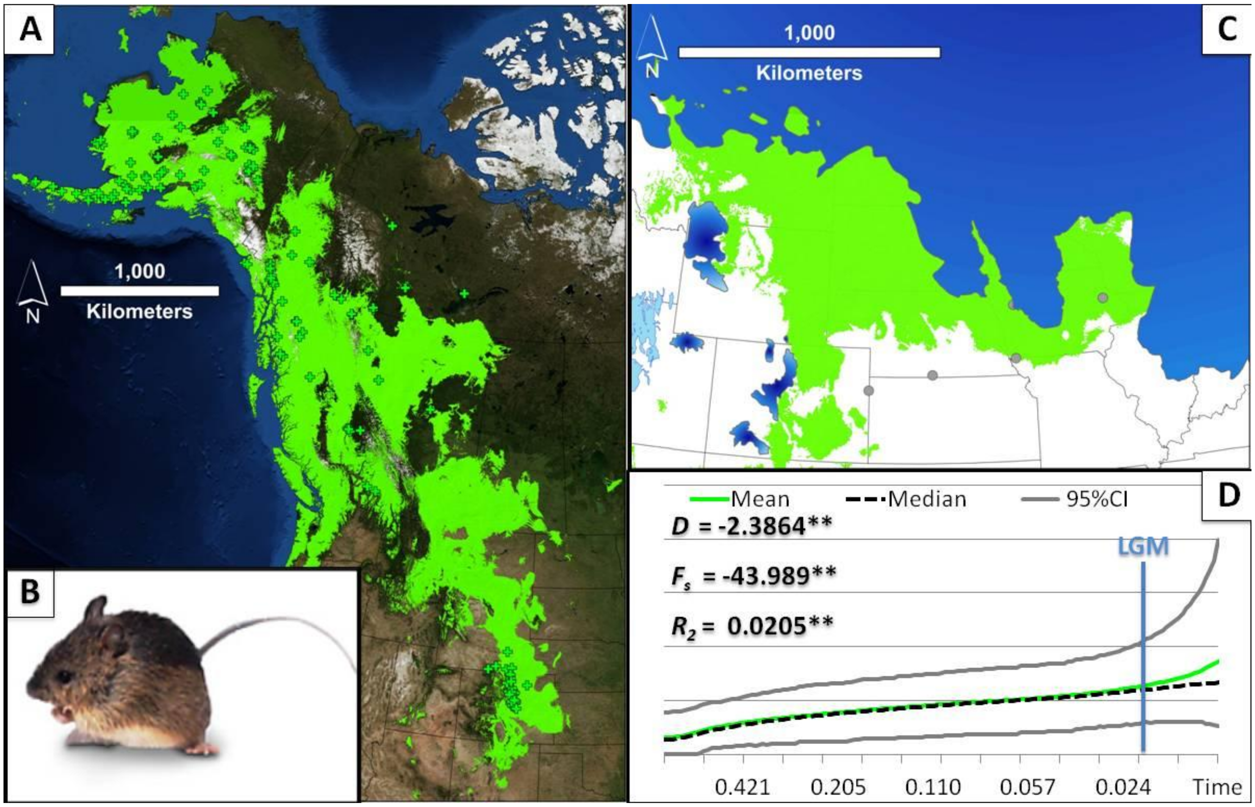

Fig. 1. (*A*) Potential contemporary distribution of the Northern lineage (includes USFWS threatened *Z. h. preblei*.) (*B*) Photograph of Preble's jumping mouse. (*C*) SDM for Northern lineage at the LGM. Note a significant expansion from ancestral range(s) to both high latitudes (e.g., Alaskan Peninsula) and Front Range of Colorado and Wyoming during the Holocene. Fossils (● dated to LGM on the Great Plains are consistent with the paleodistribution reconstruction with a narrow-range hind-cast projection. (*D*) Shallow divergence, wide range, and recent population changes (coalescent-based demographic tests: multilocus Extended Bayesian Skyline Plot and mtDNA summary statistics) all reflect significant demographic and spatial expansion following Pleistocene deglaciation.

This common historical-biogeographic process led to widespread and genetically similar populations that represent a low extinction threat of the lineage.

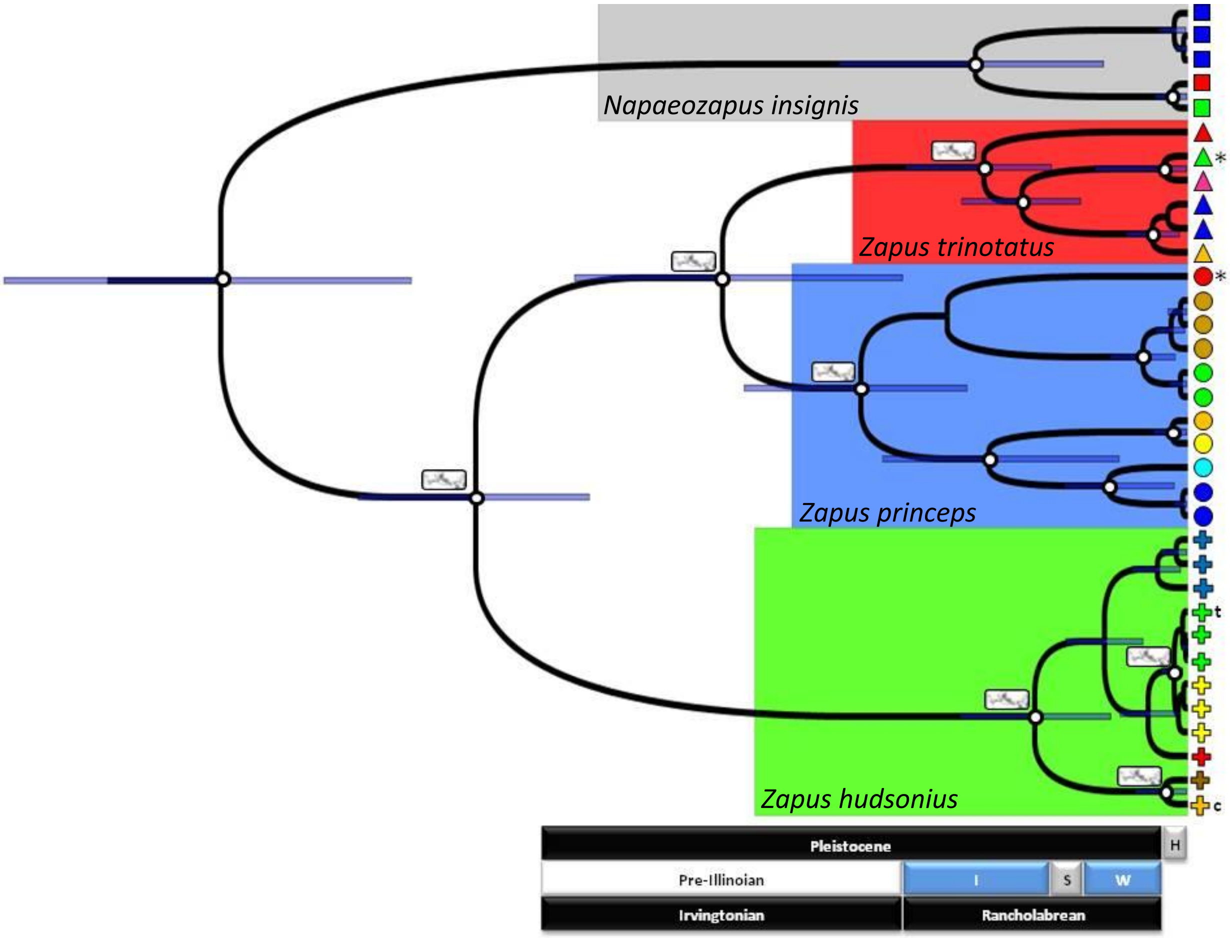

Fig. 2. Coalescent-based Bayesian fossil-calibrated multilocus species-tree phylogeny (79) for North American jumping mice. Open circles (○ at nodes represent >.95 posterior probability (PP), with skulls denoting fossil calibrations (92, 116) and bars highlighting 95% highest posterior density interval (HPD) of divergence time. Background shading corresponds to species with tips reflecting the 32 subspecies + 2 cryptic, significantly divergent lineages (*). Tip shapes represent 21 significantly divergent historical-biogeographic lineages and correspond with other Tables and Figures. Taxa of conservation concern include (*t*) the federally threatened subspecies (*Z. h. preblei*) and (*c*) the federal candidate subspecies (*Z. h. luteus*). Grey boxes below reflect interglacial (*H*–Holocene; *S*–Sangamonian) and glacial periods (blue; *I*–Illinoian; *W*–Wisconsinan)

through the Pleistocene and corresponding Irvingtonian and Rancholabrean North American land mammal stages.

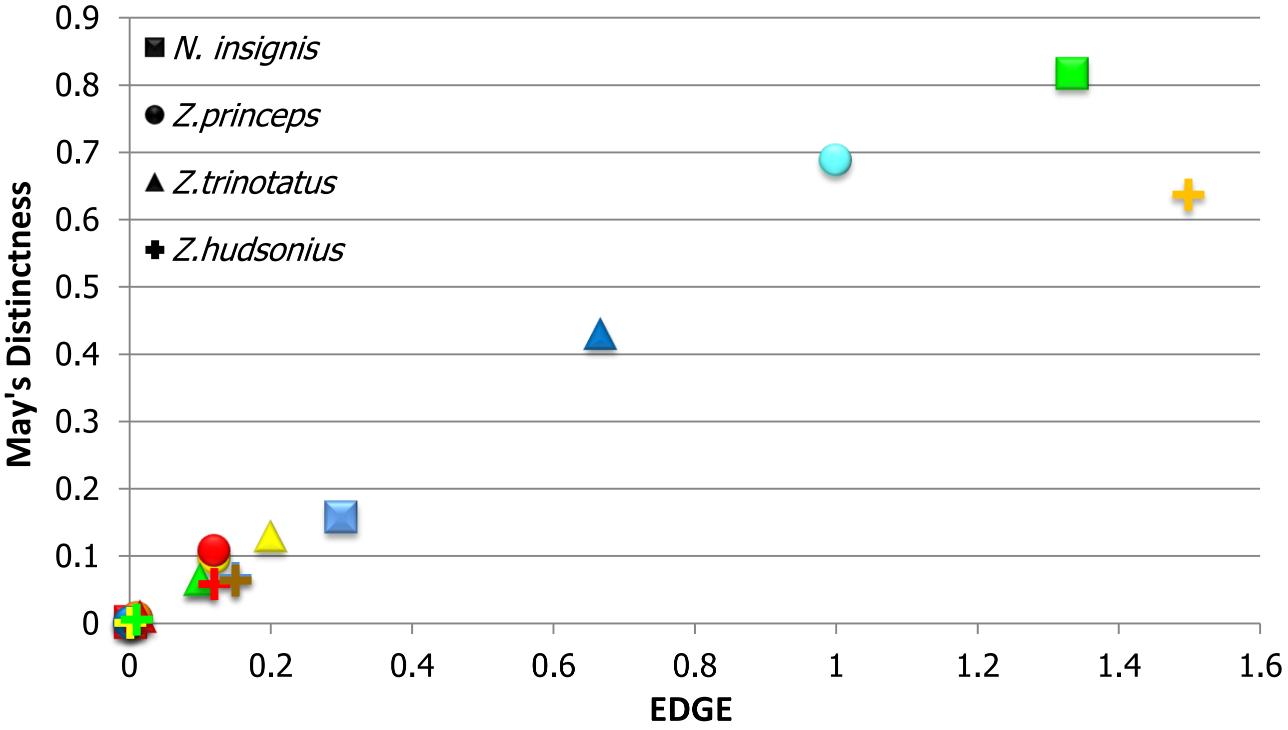

Fig. 3. Conservation prioritization (Evolutionarily Distinct + Globally Endangered – EDGE vs. May's Distinctness) scores contrasted for 21 divergent North American jumping mice lineages. The lineage that includes the federally threatened taxon (*Z. h. preblei* – green cross) is among the lowest conservation priorities using the IUCN_{100} ranks-to-extinction probability transformation (40, 98).

TABLES

Table. 1. Lineages with associated subspecies, range areas (km^2) and furthest distributed range (km) using 90% minimum presence threshold for contemporary and LGM median SDMs (see Fig. 1 and *SI Appendix*, Fig. S2), and updated regional IUCN$_{100}$ scores (40, 98, 117) following the ranks-to-extinction probability transformation. *Cryptic and un-described taxa (86). #Current range area based on georeference and associated uncertainty (118).

Species & Lineage	subspecies	Current km^2 area	LGM km^2 area	km range	IUCN$_{100}$
N. insignis					
Acadian 🟥	*insignis*	499,470	687,711	1,486	0.01
Allegheny 🟩	*roanensis*	450,840	645,627	926	0.667
Canadian 🟦	*abietorum* *frutectanus* *saguenayensis*	990,523	204,610	2,329	0.001

Z. hudsonius					
Appalachian ✚	*acadicus* *americanus* *ladas*	907,822	53,898	2,744	0.1
Can. Shield ✚	*canadensis*	1,505,480	989,855	2,080	0.1
Northern ✚	*alascensis* *preblei tenellus*	2,421,006	914,388	4,701	0.01
N. Plains ✚	*campestris* *hudsonius* *intermedius*	2,166,740	1,020,983	2,559	0.001
S. Plains ✚	*pallidus*	430,561	789,993	958	0.1
Southwestern ✚	*luteus*	208,817	429,565	787	0.999
Z. princeps					

Boreal ●	*idahoensis* *saltator*	710,746	131,824	2,624	0.001
Great Basin ●	*cinereus* *curtatus* *oregonus*	206,593	536,630	877	0.1
Great Plains ●	*minor* *kootenayensis*	624,282	525,904	1,703	0.001
La Sal ●	*chrysogenys*	36[#]	N/A	13	0.1
Okanogan ●	Un-described*	38,523	60,880	220	0.1
S. Rockies ●	*princeps*	204,470	473,724	1,031	0.01
Uinta ●	*utahensis*	89,441	190,592	596	0.667
Z. trinotatus					
Coastal ▲	*eureka* *orarius*	7,861	38,909	481	0.667

N. Cascade ▲	*trinotatus*	115,012	356,987	577	0.01
S. Cascade ▲	*montanus*	83,659	322,589	473	0.1
N. Sierra ▲	*Z. p. pacificus*	29,675	66,584	449	0.1
S. Sierra ▲	*Z. p. pacificus**	14,781	68,989	361	0.1

Table. 2. Species and intraspecies, lineage-based molecular diversity indices for 762 mtDNA samples (cyt*b* gene). Indices include segregating sites (S), number of haplotypes (N_h), haplotype (*h*) and nucleotide (π) diversity, mean nucleotide differences (*K*), plus population equilibrium tests Tajima's *D*, Fu's F_S, and Ramos-Onsins and Rozas R^2. *=P<0.05, **=P<0.01.

Species[a] & Lineage	N	S	N_h	*h*	π	*K*	*D*	F_S	R_2
N. insignis	**31**	**162**	**28**	**0.991**	**0.0617**	**70.389**			
Acadian 🟥	14	31	13	0.992	0.0045	5.1416	-1.8635*	-9.980**	0.0676*
Allegheny 🟩	2[b]		2						
Canadian 🟦	15	29	13	0.971	0.0064	7.2571	-1.0068	-4.661**	0.1007
Z. hudsonius	**455**	**178**	**102**[c]	**0.952**	**0.0312**	**31.374**			
Appalachian ✚	21	36	13	0.924	0.0056	6.4095	-1.4093	-2.32	0.1003
Canadian Shield ✚	2[b]		2						
Northern ✚	182	33	33	0.830	0.0018	1.5670	-2.0939**	-32.556**	0.0244*
N. Plains ✚	130	50	40	0.866	0.0030	3.0552	-2.0651**	-32.310**	0.0287*

S. Plains ✚	49	18	9	0.842	0.0030	3.1000	-0.7325	0.442	0.0880
Southwestern ✚	71	12	8	0.649	0.0023	2.2913	-0.2155	0.587	0.0935
Z. princeps	**223**	**313**	**130**[c]	**0.992**	**0.0863**	**86.778**			
Boreal ●	62	101	47	0.983	0.0069	7.9038	-2.2426**	-37.499**	0.0334**
Great Basin ●	48	83	27	0.959	0.0235	26.8221	1.2550	-3.906*	0.1058
Great Plains ●	21	27	16	0.971	0.0036	4.0619	-1.8452*	-9.315**	0.0601*
La Sal ●	4[b]		3						
Okanogan ●	6	2	3	0.733	0.0008	0.8667	-0.0500	-0.427	0.2291
S. Rockies ●	42	63	29	0.967	0.0120	12.0260	-0.7304	-7.935*	0.0877
Uinta ●	40	61	24	0.971	0.0051	5.8320	-2.1341**	-10.271**	0.0535*
Z. trinotatus	**53**	**167**	**31**	**0.970**	**0.0351**	**39.964**			
Coastal ▲	7	19	5	0.905	0.0054	6.0950	-1.1987	0.678	0.2366

N. Cascade ▲	1[b]		1						
N. Sierra ▲	5	11	5	1.000	0.0049	5.6000	0.4362	-1.167	0.1916
S. Cascade ▲	8	14	5	0.857	0.0052	5.9050	0.1835	0.617	0.1699
S. Sierra ▲	32	22	15	0.929	0.0025	2.8508	-1.6620*	-6.685**	0.0648*

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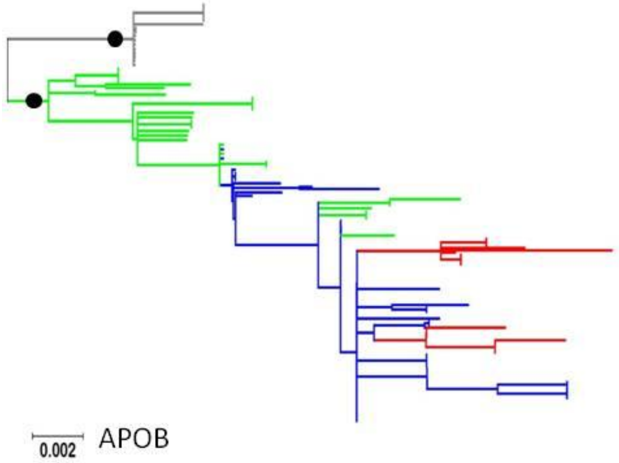
[a] Species level demographic tests not conducted (violation of population assumption).

[b] Sample size <5 and thus not tested for population indices.

[c] Smaller values are due to the reduced (1006 bp) dataset of King et al. (49) – missing data excluded.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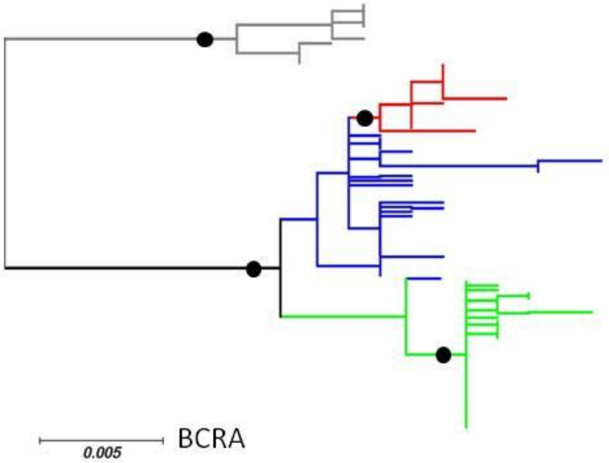
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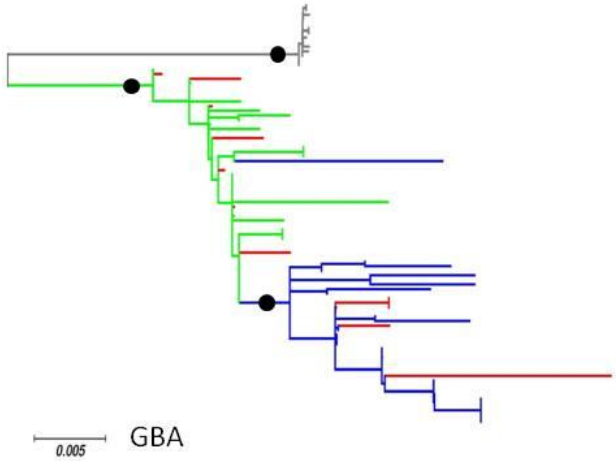
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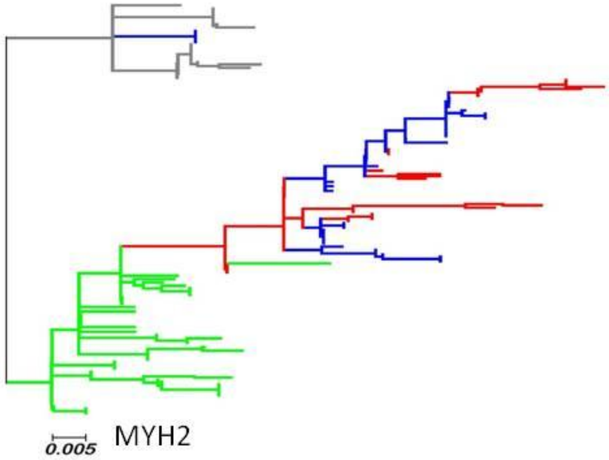
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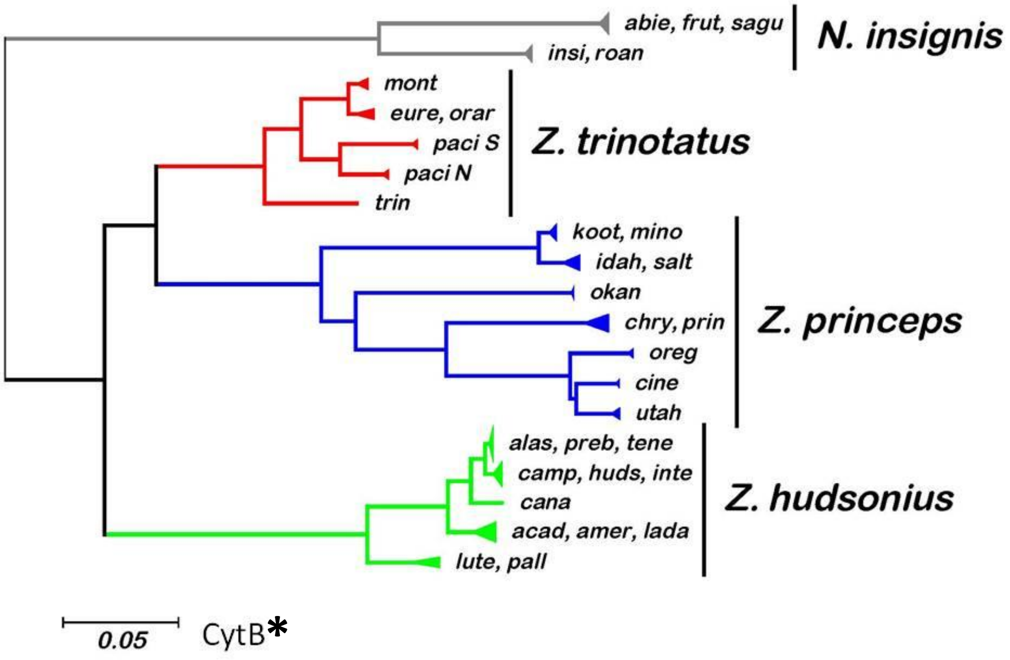
abie, frut, sagu
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okan
chry, prin
oreg
cine
utah
Z. princeps
alas, preb, tene
camp, huds, inte
cana
acad, amer, lada
lute, pall
Z. hudsonius
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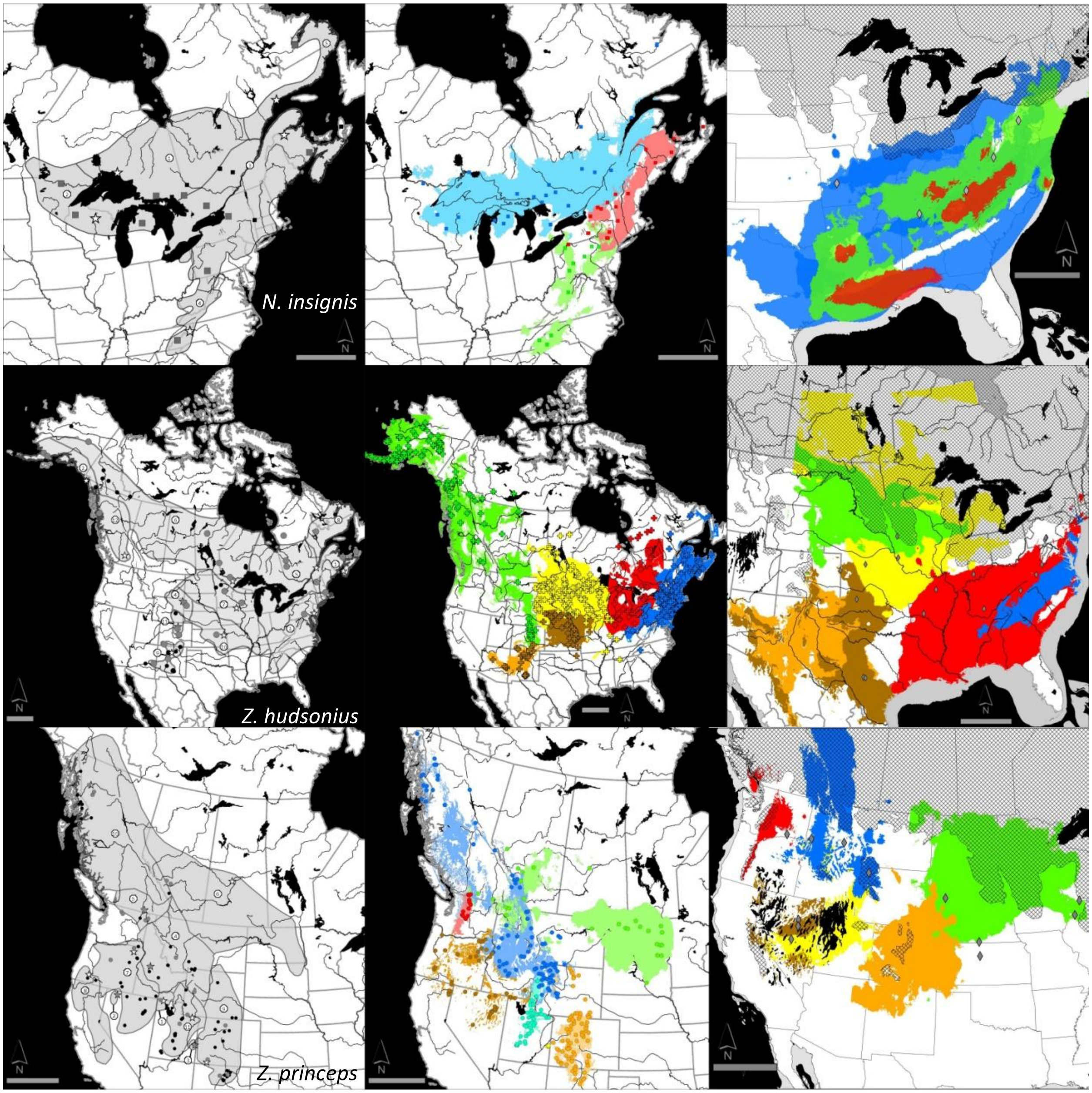
CytB*

Fig. S1. Bayesian gene trees with posterior probabilities indicated on branches next to supported nodes (●). Branches are colored for each species: grey – *N. insignis*, green – *Z. hudsonius*, blue – *Z. princeps*, red – *Z. trinotatus*. Genes include the mitochondrial cytochrome *b* gene (Cyt*b* – 1006-1140 bp) and 4 nuclear introns and exons, including 346 bp of Apolipoprotein B (APOB), 824 bp of Breast Cancer Susceptibility (BCRA), 347 bp of Glucocerebrosidase (GBA), and 267 bp of the beta-myosin heavy chain (MYH2). Subspecies are indicated on the Cyt*b* gene-tree for all monophyletic lineages (i.e. all nodes significant) but statistics removed for clarity (*).



Subspecies Taxonomy Current SDM Paleodistribution

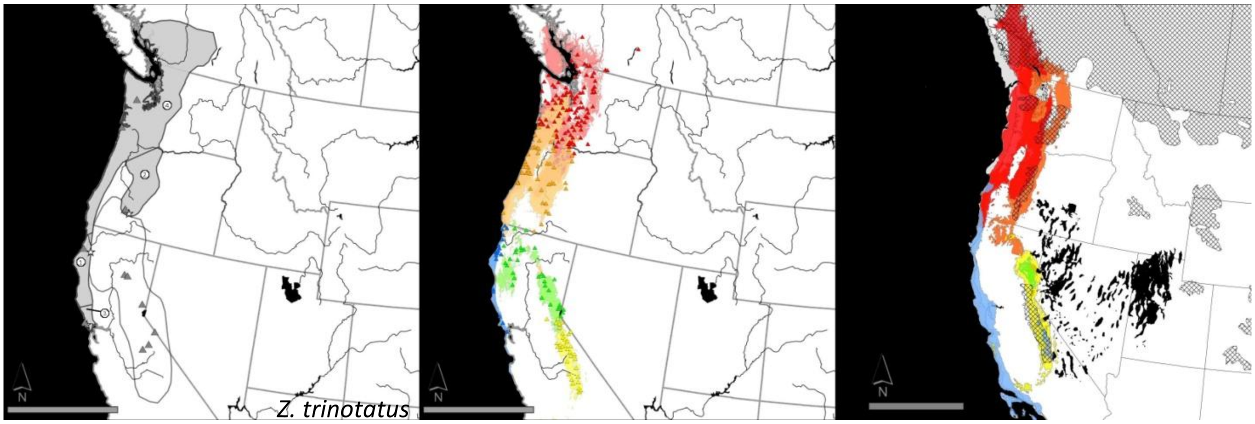


Fig. S2. Subspecies (32 taxa) taxonomy and species distribution models (current & LGM) for 21 lineages of North American jumping mice (see Table 1). Left: The subspecies of each taxon is identified with an alphabetically ordered numerical hexagon, stars depict the type locality for each subspecies, grey symbols are sampling localities for constructing the species tree (e.g. topotypes), and small black symbols reflect mtDNA (cytb) geographic samples used in demographic tests. ***Napaeozapus insignis*****:** 1) *N. i. abietorum*, 2) *N. i. frutectanus*, 3) *N. i. insignis*, 4) *N. i. roanensis*, 5) *N. i. saquenayensis*. ***Zapus hudsonius*****:** 1) *Z. h. acadicus*, 2) *Z. h. alascensis*, 3) *Z. h. americanus*, 4) *Z. h. campestris*, 5) *Z. h. canadensis*, 6) *Z. h. hudsonius*, 7) *Z. h. intermedius*, 8) *Z. h. ladas*, 9) *Z. h. luteus*, 10) *Z. h. pallidus*, 11) *Z. h. preblei*, 12) *Z. h. tenellus*. ***Zapus princeps*****:** 1) *Z. p. cinereus*, 2) *Z. p. chrysogenys*, 3) *Z. p. curtatus*, 4) *Z. p. idahoensis*, 5) *Z. p. kootenayensis*, 6) *Z. p. minor*, 7) *Z. p. oregonus*, 8) *Z. p. pacificus*, 9) *Z. p. princeps*, 10) *Z. p. saltator*, 11) *Z. p. utahensis*. ***Zapus trinotatus*****:** 1) *Z. t. eureka*, 2) *Z. t. montanus*, 3) *Z. t. orarius*, 4) *Z. t. trinotatus*. Note *Z. p. pacificus* range depicted given cryptic diversity recently documented in the Sierra Nevada's (86) and the Okanagan lineage has no described subspecies but overlaps with the far northeastern range of *Z. h. trinotatus*. Center: Current SDMs for lineages of each species. Symbols are localities used in constructing the model and correspond with other Tables and Figures. Right: Projected Paleodistributions of lineages for each species. Diamonds depict fossils that correspond to the Late Pleistocene and Early Holocene transition period (92) for each species.

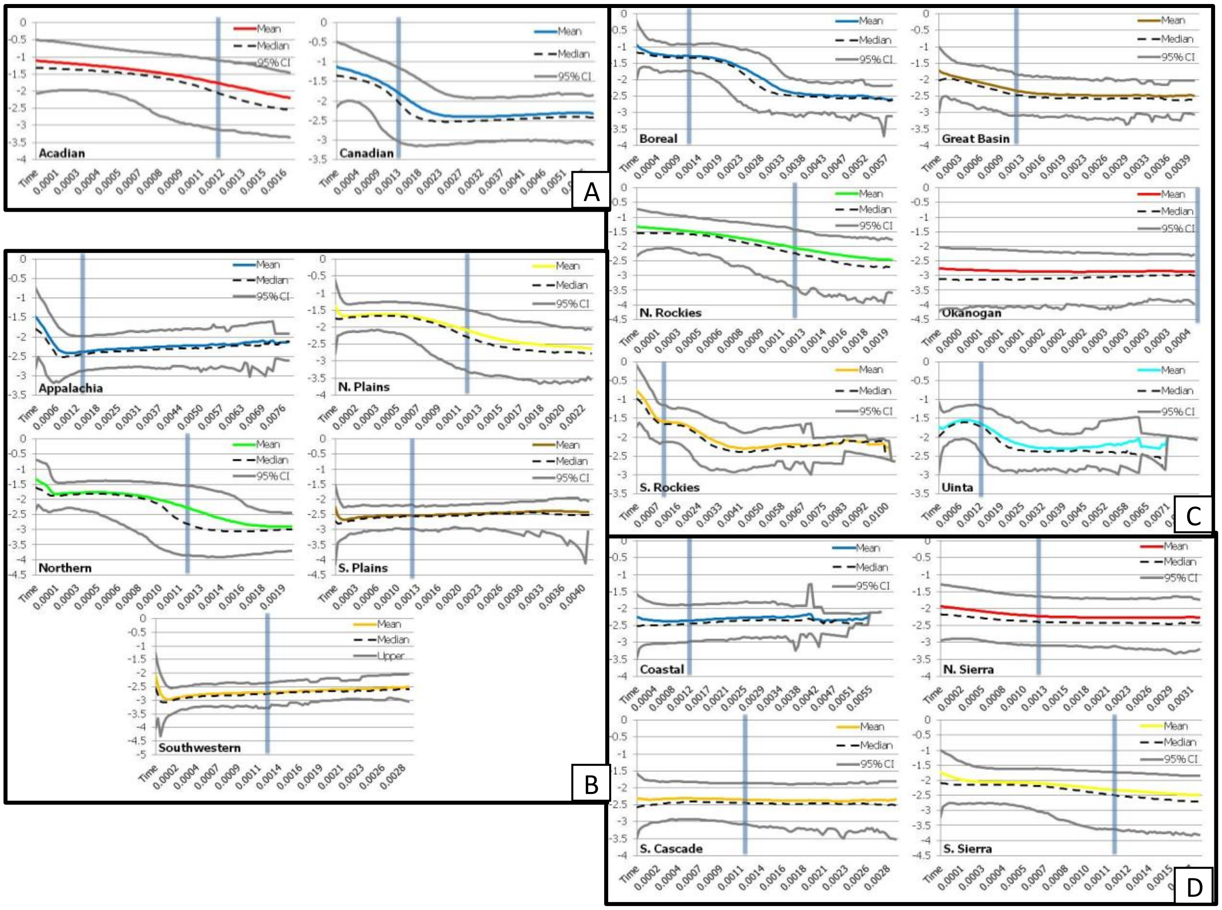


Fig. S3. Bayesian skyline plots (mtDNA) for North American jumping mice lineages showing effective population size (scaled by mutation rate) plotted as a function of time. Time 0 (present) begins on the left and progresses to the right in substitutions per million years. Colored (mean) and dashed (median) lines reflect estimates effective population size with gray lines denoting the 95% credibility interval (CI). The position of the Last Glacial Maximum (~21 ka) is indicated with a blue vertical line. [A] *Napaeozapus insignis* lineages, [B] *Zapus hudsonius* lineages, [C] *Zapus princeps* lineages, [D] *Zapus trinotatus* lineages.

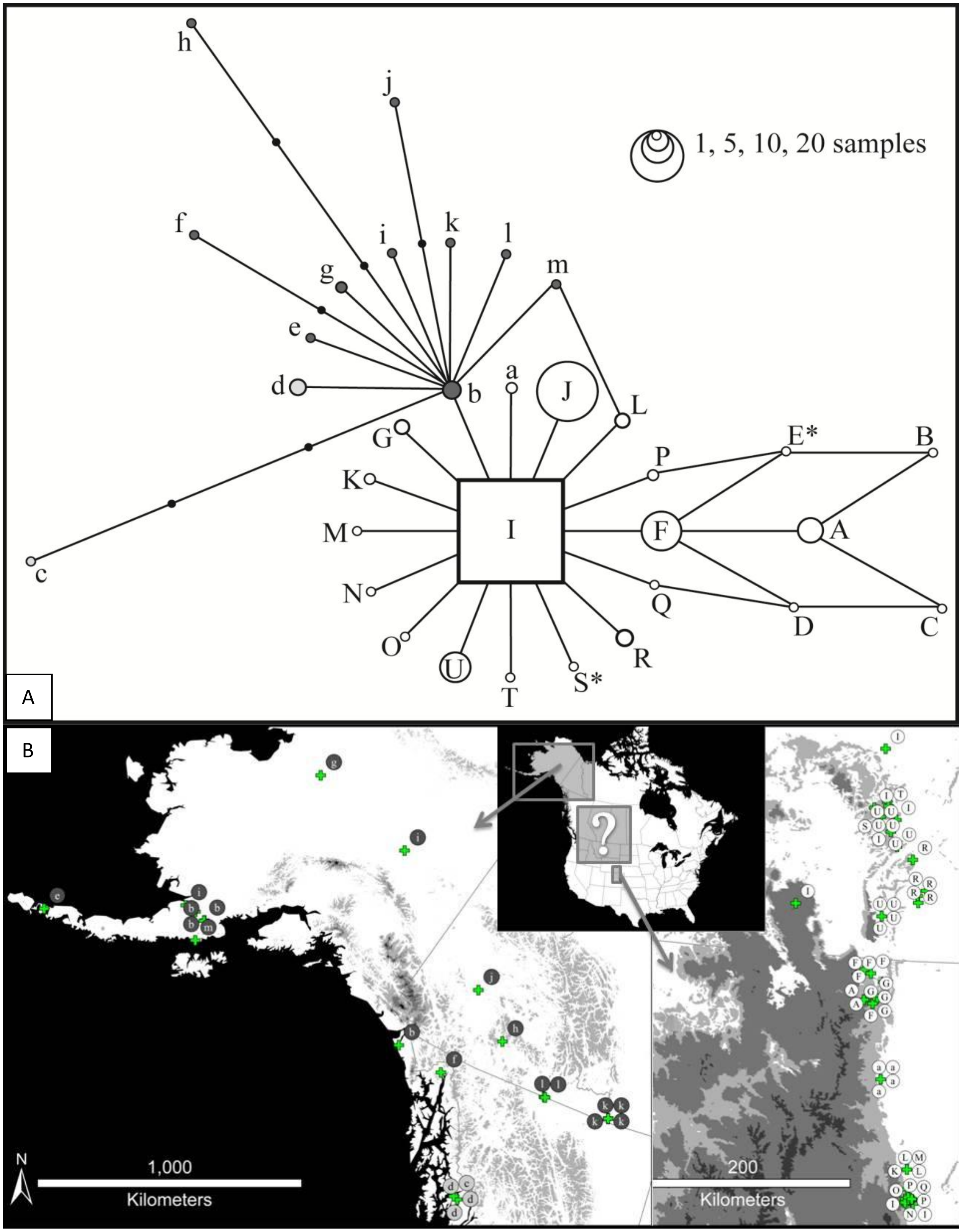

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Fig. S4. [A] Northern lineage, mtDNA cytochrome *b* gene haplotype network via statistical parsimony (119, 120). This dataset was spatially and taxonomically sampled [B] and reveals recent demographic expansion to the Front Range of the southern Rockies and the far North for the Northern lineage. Capital letters reflect data (20 haplotypes) from King et al. (49) and lower case letters (13 haplotypes) were detected in this study. Asterisks (*) are inferred haplotypes due to data discrepancies (see methods and materials). Size is proportional to frequency with those >10 placed inside the symbol. Colors mirror morphological-based nominal (42) subspecies (dark grey = *Z. h. alascensis*, white = *Z. h. preblei*, light grey = *Z. h. tenellus*) and each branch is proportional to one mutation.

Table. S1. Conservation phylogenetics, within a broader coalescent framework, was used to define priority scores by updating regional IUCN scores and then ranking divergent jumping mice lineages. Population size changes include, I – increasing, S – stable, D – declining, and ? – unknown. High threats to extinction (red) include declining population(s) or small range(s), low threats (orange) are stable populations and medium ranges (or unknown - ?), and non-threats (white) include increasing populations and large range. Plus symbols (+) associated with threats highlight the condition where taxa meet the lower criteria but localized population(s) experience a threat. For example, the Northern lineage meets the Least Concern (LC) criteria but given localized declines and defined conservation concerns in the Front Range (i.e. *Z. h. preblei*) permits using Near Threatened (NT; i.e. 0.001 to 0.01). Other criteria include Threatened (TH), Endangered (EN), and Critically Endangered (CE). Weighting (*W*) scheme follows the IUCN$_{100}$ ranks-to-extinction probability transformation (98).

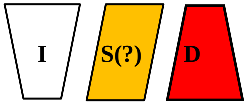
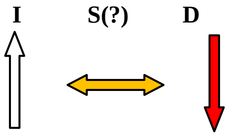
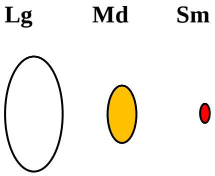
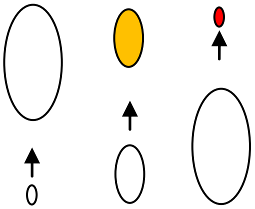
W	Threats	**Historical Δ in population size**	**Contemporary Δ in population size**	**Relative Range**	**Historical Range Δ**
0.999	3+ = CE				
0.667	2+ = EN				
0.1	1+ = TH				
0.01	0+ = NT				
0.001	0 = LC				

Table. S2. Measures of niche overlap (ecological exchangeability), Warren's *I* and Relative Ranks (RR) between subspecies comprising the Northern lineage. Values near 1.0 are considered highly exchangeable versus near 0.0 are considered inexchangeable. Significance (niche identity) tests were conducted with 100 pseudo-replicates of randomized localities for paired taxa but no comparison was significantly different suggesting niche space is analogous across all taxa pairs (figure). Jumping mice populations along the Front Range appear to be ecologically exchangeable with populations in the far north.

Northern lineage taxa pairs	***I***	**RR**	
Z. h. alascensis vs. *Z. h. preblei*	0.7493	0.9665	■
Z. h. alascensis vs. *Z. h. tenellus*	0.8657	0.9604	□
Z. h. preblei vs. *Z. h. tenellus*	0.8444	0.9669	▩

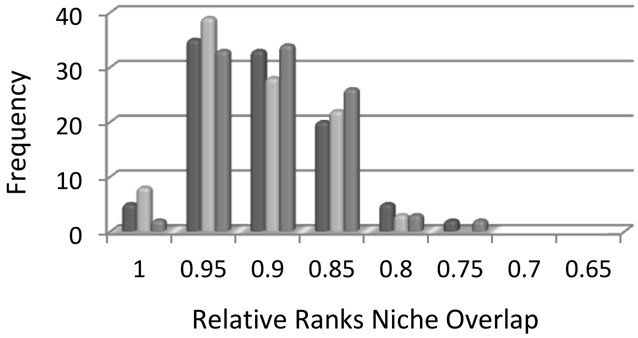


Table. S3a-d. Bioclimatic variables ranked according to their overall model contribution, highest, lowest, and decreased gain based on a jackknife test of variable importance, plus mean area under receiver operating curve (AUC) and standard deviation from 20 replicate Maxent runs for the North American jumping mice lineages, separated by nominal species. Asterisks (*) highlight the variable with the highest permutation importance.

Table S3a. *Napaeozapus insignis* lineages

Rank	Acadian 🟥	Allegheny 🟩	Canadian 🟦
1	52.0 – Bio1*	48.3 – Bio1*	26.6 – Bio1
2	29.3 – Bio15	34.9 – Bio15	20.2 – Bio17
3	10.2 – Bio17	5.8 – Bio18	15.2 – Bio9
4	6.6 – Bio9	4.4 – Bio17	8.3 – Bio15
5	1.1 – Bio8	4.3 – Bio8	6.0 – Bio7
6	0.3 – Bio18	2.1 – Bio9	5.5 – Bio16
7	0.2 – Bio7	0.1 – Bio7	5.2 – Bio2

8	0.2 – Bio3	0.0 – Bio2	4.1 – Bio19
9	0.1 – Bio16	0.0 – Bio19	3.8 – Bio8
10	0.1 – Bio2	0.0 – Bio16	3.1 – Bio3*
11	0.0 – Bio19	0.0 – Bio3	1.9 – Bio18
Highest Gain	Bio15	Bio15	Bio17
Lowest Gain	Bio9	Bio9	Bio8
Decreased Gain	Bio15	Bio15	Bio1
AUC	0.988 (0.007)	0.989 (0.009)	0.955 (0.066)

Table S3b. *Zapus hudsonius* lineages

Rank	Appalachia ✚	Canadian Shield ✚	Northern ✚	N. Plains ✚	S. Plains ✚	Southwestern ✚
1	58.4 – Bio15	39.2 – Bio9	21.4 – Bio3	40.3 – Bio1	40.9 – Bio1	39.3 – Bio1*
2	10.5 – Bio1	20.9 – Bio17	21.1 – Bio9	15.5 – Bio9	25.9 – Bio9	24.0 – Bio3
3	7.3 – Bio17*	10.5 – Bio15	12.1 – Bio18	12.4 – Bio8	13.4 – Bio15	10.3 – Bio17
4	7.2 – Bio3	10.2 – Bio19*	9.3 – Bio15	9.6 – Bio16	6.0 – Bio3*	9.5 – Bio2
5	5.0 – Bio16	6.7 – Bio1	6.9 – Bio1	6.4 – Bio7	5.8 – Bio18	6.7 – Bio9
6	4.6 – Bio19	5.6 – Bio8	6.5 – Bio8	5.9 – Bio18	3.0 – Bio7	4.9 – Bio9
7	2.3 – Bio2	2.4 – Bio3	6.1 – Bio7*	4.3 – Bio19*	2.8 – Bio16	3.2 – Bio15
8	1.6 – Bio18	1.6 – Bio16	5.6 – Bio2	3.0 – Bio15	1.1 – Bio17	0.8 – Bio19
9	1.5 – Bio7	1.2 – Bio18	4.2 – Bio17	1.2 – Bio17	0.6 – Bio8	0.6 – Bio7
10	1.0 – Bio9	1.1 – Bio2	4.0 – Bio19	1.2 – Bio2	0.4 – Bio19	0.6 – Bio16

11	0.6 – Bio8	0.4 – Bio7	2.6 – Bio16	0.3 – Bio3	0.2 – Bio2	0.2 – bio18
Highest Gain	Bio15	Bio19	Bio9	Bio8	Bio1	Bio3
Lowest Gain	Bio8	Bio7	Bio2	Bio15	Bio15	Bio18
Decreased Gain	Bio1	Bio9	Bio9	Bio1	Bio1	Bio3
AUC (SD)	0.980 (0.015)	0.974 (0.006)	0.952 (0.020)	0.980 (0.009)	0.995 (0.001)	0.997 (0.002)

Table S3c. *Zapus princeps* lineages

Rank	Boreal ●	Great Basin ●	Great Plains ●	Okanogan ●	S. Rockies ●	Uinta ●
1	32.1 – Bio1	43.6 – Bio9	56.2 – Bio1	40.9 – Bio9	40.1 – Bio3	33.4 – Bio1
2	31.0 – Bio3	19.9 – Bio18*	9.4 – Bio16*	36.4 – Bio8	31.9 – Bio1	16.9 – Bio15
3	10.0 – Bio8	11.5 – Bio1	6.9 – Bio2	8.1 – Bio1	7.1 – Bio15	10.6 – Bio18
4	9.4 – Bio15	5.6 – Bio8	6.3 – Bio19	4.4 – Bio15	4.6 – Bio2	8.7 – Bio8
5	6.1 – Bio7	4.9 – Bio17	6.1 – Bio18	4.3 – Bio18	3.8 – Bio7	7.1 – Bio3
6	3.6 – Bio19	3.9 – Bio15	5.7 – Bio15	3.7 – Bio3*	3.2 – Bio16	6.7 – Bio9
7	2.8 – Bio17	3.3 – Bio2	3.4 – Bio9	1.6 – Bio2	3.1 – Bio18	6.1 – Bio2
8	2.4 – Bio18*	2.7 – Bio3	1.7 – Bio3	0.6 – Bio16	2.7 – Bio17	4.7 – Bio16
9	1.6 – Bio16	2.5 – Bio19	1.5 – Bio7	0.0 – Bio17	1.3 – Bio19	4.0 – Bio17
10	0.9 – Bio2	1.2 – Bio16	1.5 – Bio17	0.0 – Bio19	1.3 – Bio9	1.1 – Bio7

11	0.1 – Bio9	0.9 – Bio7	1.4 – Bio8	0.0 – Bio7	0.9 – Bio8	0.8 – bio19
Highest Gain	Bio3	Bio9	Bio1	Bio8	Bio3	Bio3
Lowest Gain	Bio16	Bio16	Bio8	Bio2	Bio8	Bio16
Decreased Gain	Bio3	Bio9	Bio1	Bio8	Bio3	Bio1
AUC	0.987 (0.003)	0.960 (0.041)	0.967 (0.043)	0.999 (0.001)	0.995 (0.002)	0.995 (0.002)

Table S3d. *Zapus trinotatus* lineages

Rank	Coastal ▲	N. Cascade ▲	N. Sierra ▲	S. Cascade ▲	S. Sierra ▲
1	25.7 – Bio18	38.4 – Bio9	29.8 – Bio9*	30.9 – Bio9	31.7 – Bio8
2	24.8 – Bio24.8	32.9 – Bio19	26.4 – bio18	29.9 – Bio19	17.0 – Bio15
3	20.9 – Bio7	11.4 – Bio15	23.2 – Bio19	22.4 – Bio15	16.9 – Bio9
4	19.5 – Bio9	6.8 – Bio18	7.3 – Bio15	4.0 – Bio1	9.6 – Bio19
5	3.8 – Bio15	6.1 – Bio17	3.5 – Bio2	3.9 – Bio18*	9.5 – Bio18
6	2.1 – Bio8	2.5 – Bio2	3.1 – Bio16	3.0 – Bio17	7.7 – Bio1*
7	1.7 – Bio1	1.2 – Bio7	2.8 – Bio17	2.4 – Bio7	4.4 – Bio2
8	0.9 – Bio2	0.3 – Bio1*	1.6 – Bio8	1.7 – Bio16	2.0 – Bio17
9	0.3 – Bio3	0.2 – Bio16	1.4 – Bio1	1.4 – Bio3	1.1 – Bio7
10	0.2 – Bio17*	0.1 – Bio8	0.8 – Bio3	0.4 – bio8	0.1 – Bio3

11	0.1 – Bio16	0.1 – Bio3	0.0 – Bio7	0.0 – Bio2	0.0 – Bio16
Highest Gain	Bio19	Bio19	Bio19	Bio19	Bio8
Lowest Gain	Bio2	Bio18	Bio17	Bio2	Bio2
Decreased Gain	Bio18	Bio18	Bio18	Bio18	Bio1
AUC	0.997 (0.001)	0.994 (0.001)	0.986 (0.036)	0.997 (0.001)	0.998 (0.001)

Table. S4. Molecular data, character variation, and nucleotide substitution model selected using Bayesian Information Criterion (BIC) for 92 samples of North American jumping mice.

Molecular marker	Characters	Variable characters	Parsimony informative characters	Substitution model
APOB	367	22	19	T92 + Γ
BCRA1	789	204	204	HKY + Γ
Cyt*b*	1140	442	421	GTR + I + Γ
GBA	346	26	26	JC + Γ
MYH2	267	28	25	T92 + I + Γ

CONCLUSIONS

Summary

In chapter 1 (Malaney et al. 2012), I tested alternative historical biogeographic scenarios proposed for a southwestern montane endemic using coalescent simulations (e.g. Parametric Bootstrap). Then, using SDMs and projecting models into the past I reconstruct the LGM paleodistribution and link fossils as spatiotemporal anchors to establish the origination of the New Mexico Meadow Jumping Mouse (*Zapus hudsonius luteus*). Results suggest *Z. h. luteus* diverged from *Z. h. pallidus* (not *Z. h. preblei*) at the LGM on the Edwards Plateau followed by colonization of the montane regions of the American Southwest.

In chapter 2 (Malaney et al. in press), I tested alternate models of divergence, again using coalescent simulations, to establish that populations of the Western Jumping Mouse (*Z. princeps*) in the western United States have been long divergent in an allopatric model. However, not all populations have been stagnant as northern populations have a shallower history with demographic signatures consistent with Holocene expansion. I also detected cryptic variation in the Sierra Nevada's of California where these populations reflect a signal of diversification closer to the coastal Pacific Jumping Mouse (*Z. trinotatus*) than other populations of *Z. princeps*.

In chapter 3 (Malaney and Cook in review), I used complete taxon sampling across all North American jumping mice subspecies and across geography, but coupled with contemporary and paleodistributions (SDMs) to identify the signatures of various lineages that may be important in conservation prioritization. Signatures detected and implemented in conservation assessment include recent and historic declines in both population size and geographic range. When signatures are coupled with the phylogeny we are better able to objectively assess extinction threats for both recently and anciently diverged lineages. Results from this work have important implications given that conservation planning is often predicated on a taxonomy that generally lacks an understanding of the dynamic biogeographic past and often fails to account for evolutionary history. Whereas, linking comprehensive sampling, coalescent-based analyses, species distribution modeling, and fossil evidence points to a drastic shift in understanding conservation priorities and highlights a fundamental concept: systematics coupled with biogeographic history should inform conservation.

Taxonomic implications

EXPLORING THE SPECIES DELIMITATION (AND DEFINITION) CONTINUUM USING AN INTEGRATIVE APPROACH

The three chapters of my dissertation are linked by a broader set of ideas related to incipient speciation and species delimitation. Species definitions and operational criteria reflect variations on how evolutionary diversification is described and species delimitation can be controversial as evidenced by rancorous debates related to the species definition (de Queiroz 1998, 2007). Jumping mice serve as an example of this debate due to the controversial listing of Preble's Jumping Mouse (*Z. h. preblei*). In 1998, this subspecies was listed as federally threatened (USFWS 2002, 2010, 1998). Subsequent to listing efforts and in response to concerns about whether Front Range populations were a discrete subspecies, two studies found contradicting evidence of subspecies validity using analogous datasets (King et al. 2006; Ramey et al. 2005). Both studies implemented a limited sampling strategy predicated on the assumption that geographically adjacent subspecies were most closely related. Following these contradictory studies, further debates around this controversial listing boiled over into the incipient-species taxonomic debate (Crifasi 2007; Ramey et al. 2006; Vignieri et al. 2006). Still, others debated the use of statistics (Brosi and Biber 2009; Skalski et al. 2008) and issues related to policy advocacy (Carolan 2008; Scott et al. 2007) and economic impacts (Foulke et al. 2010; Industrial Economics 2010, 2002) that now are projected to top $440 million by the end of 2030.

Here, I aim to update the taxonomy of North American jumping mice using sound theoretical and statistical contexts that account for evolutionary history and echoes the perspective of Adaptive Evolutionary Conservation (AEC; (Fraser and Bernatchez 2001). My efforts also reflect the need for an integrative taxonomy (Fujita et al. 2012; Padial et al. 2010). However this study differs from previous research by using a comprehensive taxon sampling approach (all subspecies) and implementing a coalescent-based context that harnesses the strength of multiple independent molecular datasets to assess evolutionary relatedness and divergence times. Once the phylogeny is established, I use phylogenetically-informed species distribution modeling (SDM) to assess if ecological variation mirrors evolutionary divergence. The advantage of this approach is that it emphasizes evolutionary relationships and accounts for ecological differences within the broader context of *all* jumping mice while simultaneously assessing if taxonomy accurately reflects phylogeographic variation.

Jumping mice have received national attention and have been considered iconic for conservation definitions and actions implemented by the USFWS (Foulke et al. 2010). However, in chapter 3, I highlighted (Malaney and Cook in review) there are other, more divergent, jumping mice lineages that potentially face serious threats, but that currently have no conservation status. Consequently, I apply the General Lineage Concept to update the taxonomy of the North American jumping mice (Zapodidae) and identify 14 statistically significantly divergent lineages (genetic and niche) that should be elevated to species level (Fig 1 & 2). I also explore a hierarchical set of ideas to include Evolutionary Significant Units (ESUs) within species and Distinct Population Segments (DPSs) within ESUs. For example, *Z. h. preblei* may be considered a DPS in the Front Range, within a broader Northern lineage (ESU; Fig 3). However the Northern lineage is divergent from neighboring Northern Plains and Canadian Shield lineages (see Chapter 3) reflecting deeper histories and combined the three make up neo *Z. hudsonius*.

My dissertation data suggest two specific conclusions related to North American jumping mice taxonomy. First, the morphological-based jumping mice taxonomy significantly under represents geographic variation in both DNA and niches and fails to reflect evolutionary and biogeographic history; a type I error (Felsenstein 2008; Skalski et al. 2008). Second, conservation predicated on morphological-based taxonomic understandings (i.e. subspecies) is potentially missing alternative units important for preservation with a changing climate; a type II error (Brosi and Biber 2009). These results echo the need to reduce ambiguity associated with subspecies-level classification (Haig et al. 2006) given the poor philosophical backbone, inconsistent execution, trinomial handicap (requires frequent taxonomic revisions), and most important, explicit lack of historical perspective. Consequently, I advocate abandoning the subspecies taxonomic distinction and provide an empirical example of where hierarchical divisions (i.e., species → ESU → DPS) can be placed within a more-powerful integrative context. More broadly, my results reflect the perspective that a more objective, yet integrative, taxonomic scope is needed to aid in identifying imperiled organisms and better clarify conservation considerations that may enhance ESA decisions. Further, an integrative and hierarchical approach should facilitate communication related to the classification across the taxonomic continuum, more fully explore the processes of speciation, and undercut the species (and infraspecies) concept debate, that combined, may provide fewer impediments to conservation efforts.

In conclusion, my dissertation detected deep molecular divergence across *Z. princeps* and *Z. trinotatus* that is accentuated over the southern portion of current distributions in western North America, reflecting deeper, allopatric divergence (Fitzpatrick et al. 2009; Fitzpatrick and Turelli 2006; Wiley and Lieberman 2011). Conversely, *Z. hudsonius* reflects a signature of latitudinal fluctuations over the last glacial cycle and preliminary signals of repetitive secondary contact may suggest the homogenization hypothesis (Nosil 2008) resulting in shallower molecular phylogenetic signal. The wide range of jumping mice provides opportunities to test hypotheses related to incipient speciation using multi-locus models and coalescent techniques (Carstens et al. 2005; Lessa et al. 2003) and further refined questions related to environmental drivers of diversification. Refinement of the persistent allopatric hypothesis includes testing among specific vicariant speciation models but also serves as a working hypothesis to explore concerted signatures among co-distributed species. My data suggest geographic separation between southern lineages has been a dominant and persistent force shaping divergence in jumping mice and presumably other sympatric mammals. Whether these vicariant signatures are suggestive of a common process that is spatially and temporally shared across co-distributed mammals, versus simply idiosyncratic responses to fluctuating climate is explored and summarized next. These data place jumping mice divergence within the context of montane mammal diversification in North America.

Comparative phylogeography

LINKING SIGNATURES ACROSS JUMPING MICE AND HIGHLIGHTING BIOGEOGRAPHIC PROCESSES OF DIVERGENCE IN NORTH AMERICAN BOREAL MAMMALS

Processes resulting in speciation or extinction and mechanisms of community assembly across the landscape have long fascinated biogeographers (Lomolino et al. 2006; Merriam 1895; Simpson 1940; Wallace 1876). Isolated systems have provided the foundations for biogeographic theory in identifying the principal processes of colonization versus extinction that both explain and predict factors affecting species richness of natural communities (Brown 1971; Lomolino et al. 1989; Lomolino and Davis 1997). Key factors contributing to the study of island biogeography include the spatial and temporal histories of organisms (Lomolino 1984; MacArthur and Wilson 1967) which suggests that some communities may be structured or persistent over the long-term. Conversely, fossil evidence suggests there were few historical communities that are analogs of today, implying populations and species distributions are dynamic and ephemeral (Graham et al. 1996) but not all agree (Lyons 2003). Comparative phylogeography is well suited to test specific hypotheses of spatial and temporal dynamics responsible for structuring communities, especially communities restricted to geographic regions such as the montane island systems of the West (Avise et al. 1987; Gutierrez-Garcia and Vazquez-Dominguez 2011; Hickerson et al. 2010). In general, these systems (Fig. 4) have been referred to as montane- or sky-islands (DeChaine and Martin 2005; Knowles 2000; McCormack et al. 2009).

Western North America has a diverse biota that is the product of complex evolutionary and environmental processes (Lomolino et al. 2006). A suite of boreal mammals (Fig. 4) are distributed from the ‘sky islands’ of the American southwest and Great Basin northward through most of mountainous western North America to northern Canada and Alaska (Hall 1981; McCormack et al. 2009; Merriam 1892). Given the vast range, variable topography and dynamic glacial history, this community is likely to have complex demographic signatures reflected in DNA because levels of connectivity and population sizes have changed (Hewitt 1999, 2001; Waltari and Guralnick 2009). My aim is to characterize and summarize the phylogeographic relationships among boreal mammals to provide a set of insights into the historical events responsible for triggering lineage diversification, the timing and directionality of lineage expansion or contraction, and phylogenetic congruence (or lack thereof) among mammals in major geographic areas in western North America.

Using phylogenetic techniques, I documented a consistent set of phylogenetic signatures across boreal mammals (Fig. 5) indicative of spatial breaks and temporal events that may have shaped the geographic distribution of genetic diversity. More specifically, northern populations are the result of post-Pleistocene re-colonization of deglaciated terrains (Hewitt 2004; Lessa et al. 2003; Runck and Cook 2005) and these populations are generally less disjunct, than southern peripheral populations that are isolated at higher elevations at lower latitudes (Brown 1971; Malaney et al. in press). I documented significant demographic expansion across all boreal mammals for the northern lineages, which is a common signature (Lessa et al. 2003). However, the isolated montane habitats within xeric western environments harbor populations of boreal associated mammals that reflect a deeper history of divergence (i.e., a signature of ancient vicariance). These community level analyses suggest that boreal mammals evolved over the last several glacial periods largely as a cohesive unit, with exceptions, rather than as independent species with idiosyncratic responses.

In all taxa, I document a distinct east-west split that generally dates to Middle Pleistocene and precedes subsequent divergence of the Late Pleistocene. The southern clade is always closer to the eastern/continental clade than to the western/coastal clade and where present, tends to be older than eastern/continental clade. Continental clades extending into the Pacific Northwest generally originate from further east and not from southern or western clades. Pulses of diversification include a progression of an early eastern lineage, followed by a coastal and continental split further west, and a subsequent southwestern divergence. Timing of divergent splits is coincident with periodicity of Pleistocene cycling (Fig. 1D). Among the taxa I examined, all reflect cladogenic events coincident with warmer interglacial periods and not cooler glaciations. Given many species are known to maintain niche conservatism (Hadly et al. 2009; Wiens 2004; Wiens and Graham 2005), boreal mammals may have shifted to higher elevations during warmer interglacial periods reinforcing geographic variation during isolation coupled with reduced effective population sizes. Recolonizations of northern deglaciated (leading edge) areas are typically via populations that represent the continental clade from the Midwest. These northern populations tend to exhibit significant signatures of demographic and range expansion during the Holocene across boreal mammals. However, in other organisms within the region significant signatures of demographic expansion do not always coincide with range expansion reflecting a complex signature in

Northwestern North America (Brunsfeld et al. 2001; Carstens et al. 2005). A fundamental understanding of the processes shaping geographic variation is critical for addressing questions ranging from community assembly to speciation, and also applied to conservation management.

The deep mitochondrial divergence observed in some taxa would warrant species status with the lineage-based taxonomic framework (see taxonomic implications above), but should be tested with independent nuclear markers, and combined with niche models, morphology, and natural history criteria. However, these deeper signatures have conservation implications for boreal mammals as many clades are isolated at the highest elevations, and presumably relatively smaller population sizes. With projections of generally warmer conditions over the next century and dwindling high elevation montane and riparian habitats in the west (Ackerly et al. 2010), conservation efforts and monitoring programs should focus on the future of these species and lineages. Over the last century, mammals have generally moved to higher elevations (Moritz et al. 2008) and continued anthropogenic mediated climate change will likely force some species extinctions (Beever et al. 2010). Species that persist will likely face genetic erosion as observed in alpine organisms (Rubidge et al. 2012) with dwindling populations. Continued efforts to systematically monitor and preserve these deep evolutionary legacies within the ‘sky-islands’ of the west should be a management priority.

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FIGURES

Figure 1. Bayesian multilocus coalescent-based fossil calibrated molecular species-tree phylogeny of 14 North American jumping mice. Bars represent 95% credible intervals of divergence time. All nodes have ≥0.95 posterior probability and probability of speciation.

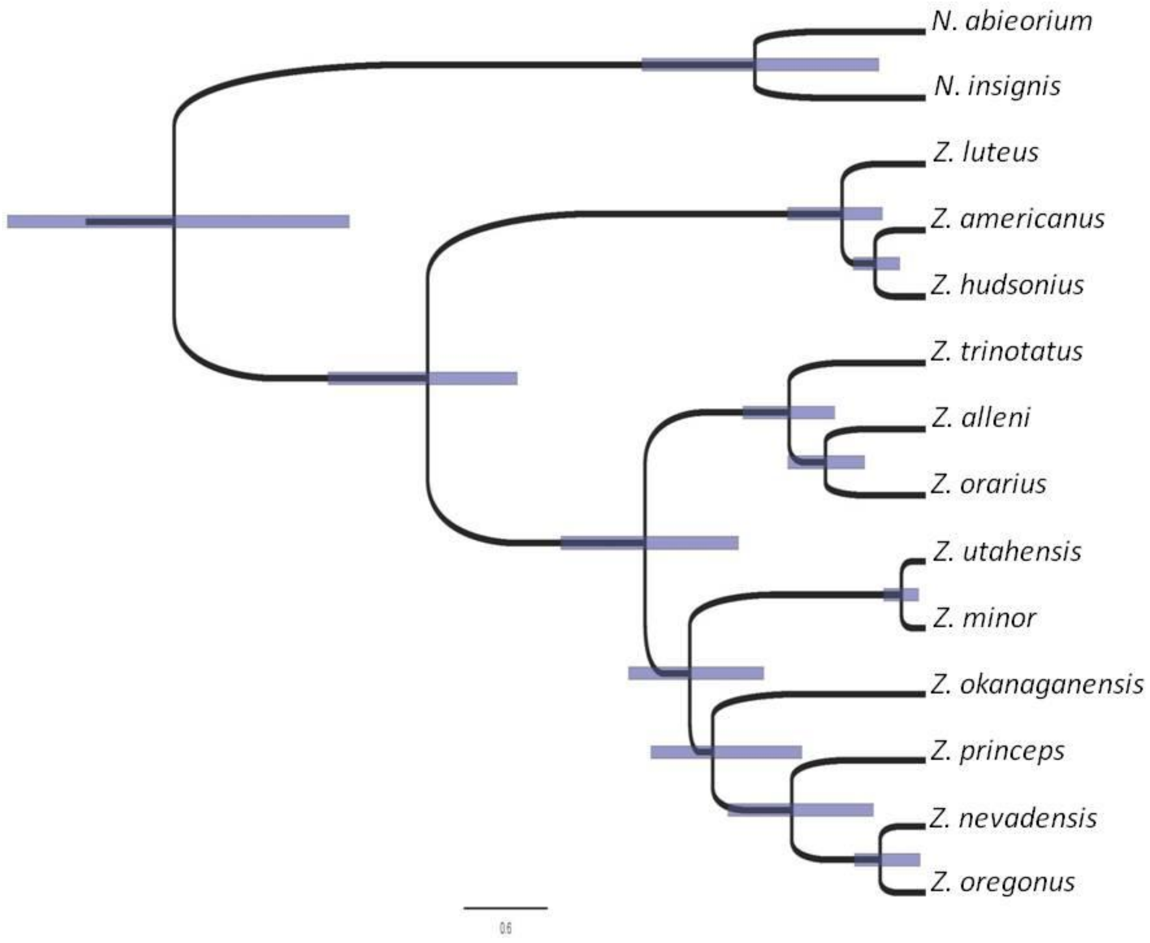


Figure 2. Reproduced from Malaney and Cook (in review). [A] Northern lineage (ESU), mtDNA cytochrome *b* gene haplotype network via statistical parsimony that was [B] spatially and taxonomically sampled. In this dataset, Southern populations may be considered a Distinct Population Segment (DPS) due to geographic separation from Northern populations (DPS). Intervening areas (?) need further sampling to test if this system represents a widespread set of populations or geographically Northern and Southern isolates (DPS).

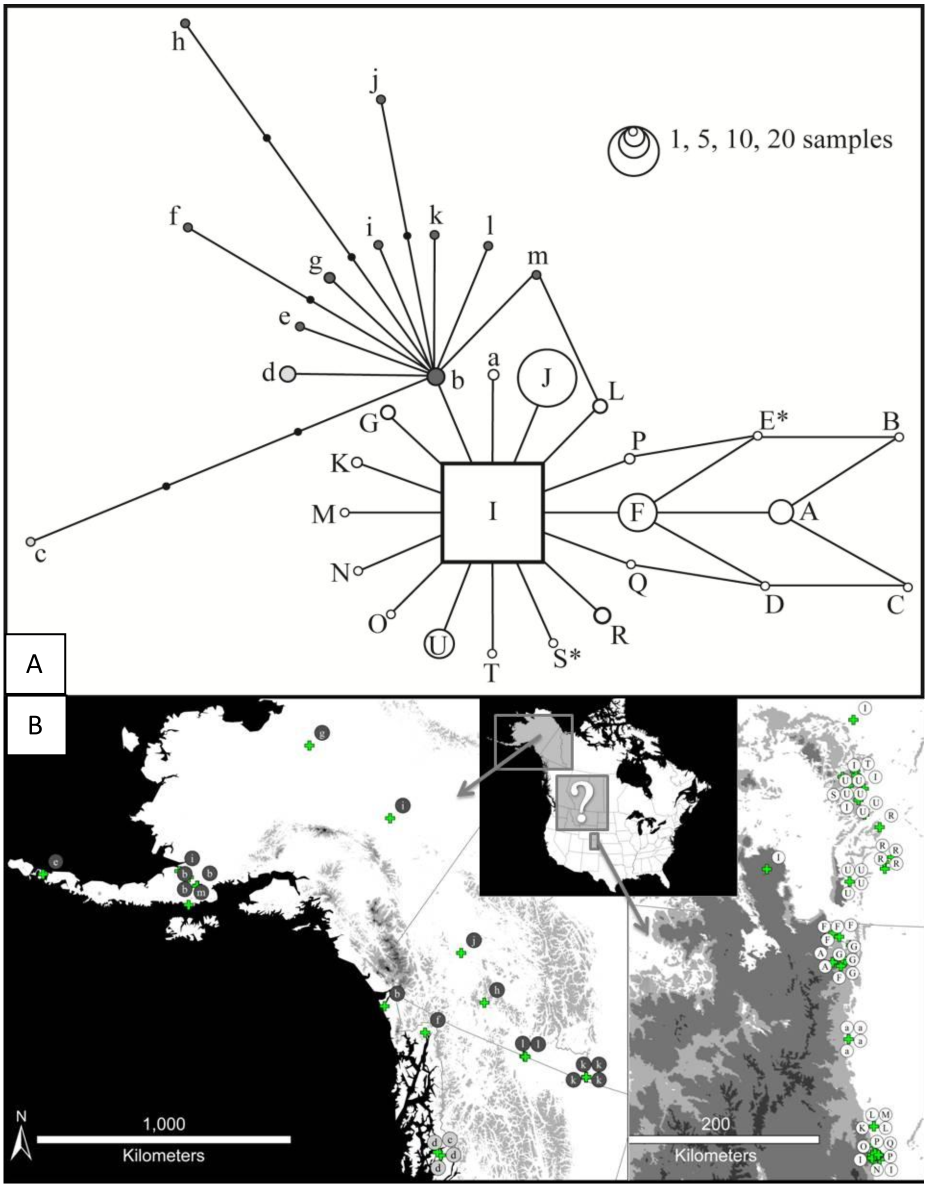


Figure 3. Species distributions for each proposed taxonomic species (see Fig. 1). All models have significantly different niches. [A] Blue = *N. abietorum*, Red = *N. insignis*; [B] Blue = *Z. americanus*, Green = *Z. hudsonius*, Brown = *Z. luteus*; [C] Black = *Z. okanaganensis*, Orange = *Z. princeps*, Yellow = *Z. utahensis*, Pink = *Z. minor*, Purple = *Z. nevadensis*; [D] Spruce = *Z. alleni*, Grey = *Z. orarius*, Navy = *Z. trinotatus*.

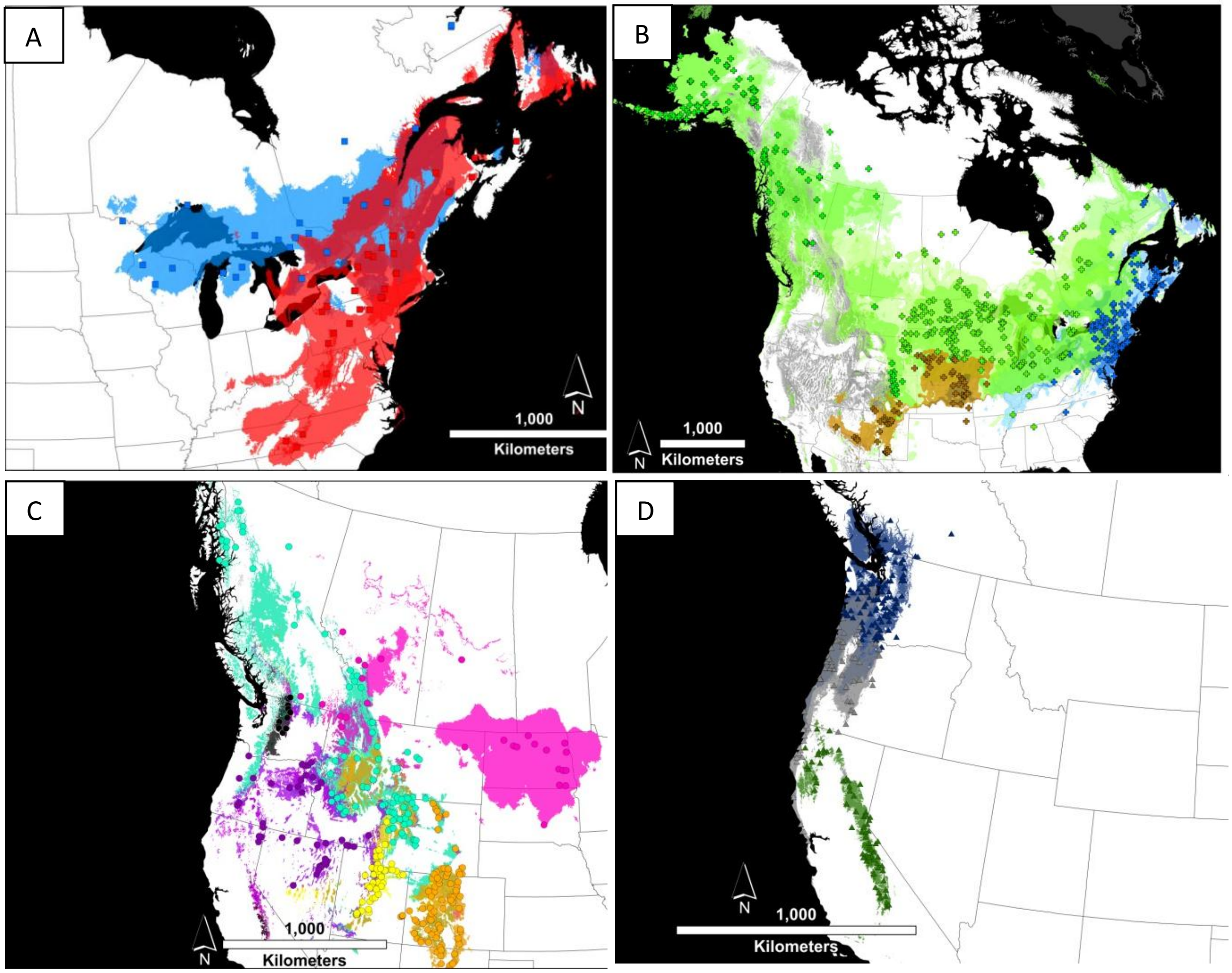


Figure 4. [A] Major biotic communities of North America with emphasis on boreal (dark green) and cold temperate forests (olive) distributed in the West. [B] Generic geographic ranges of 10 boreal mammals illustrating the broad overlap and opportunity to test for concordant patterns of geographic variation in molecular data among taxa. [C] Glaciated areas of North America at Last Glacial Maximum with potential refugial areas (highlighted in red) presented in the literature and tested here with comparative phylogeography. [D] Pulses of diversification for 8 species though glacial cycles of the Quaternary tested in a Bayesian framework with relaxed molecular clock and calibrated with fossils (glacial chart from Wikipedia December 2010). Bar heights correspond to number of cladistic events. Example: 6 cladistic events during the Sangamon interglacial.

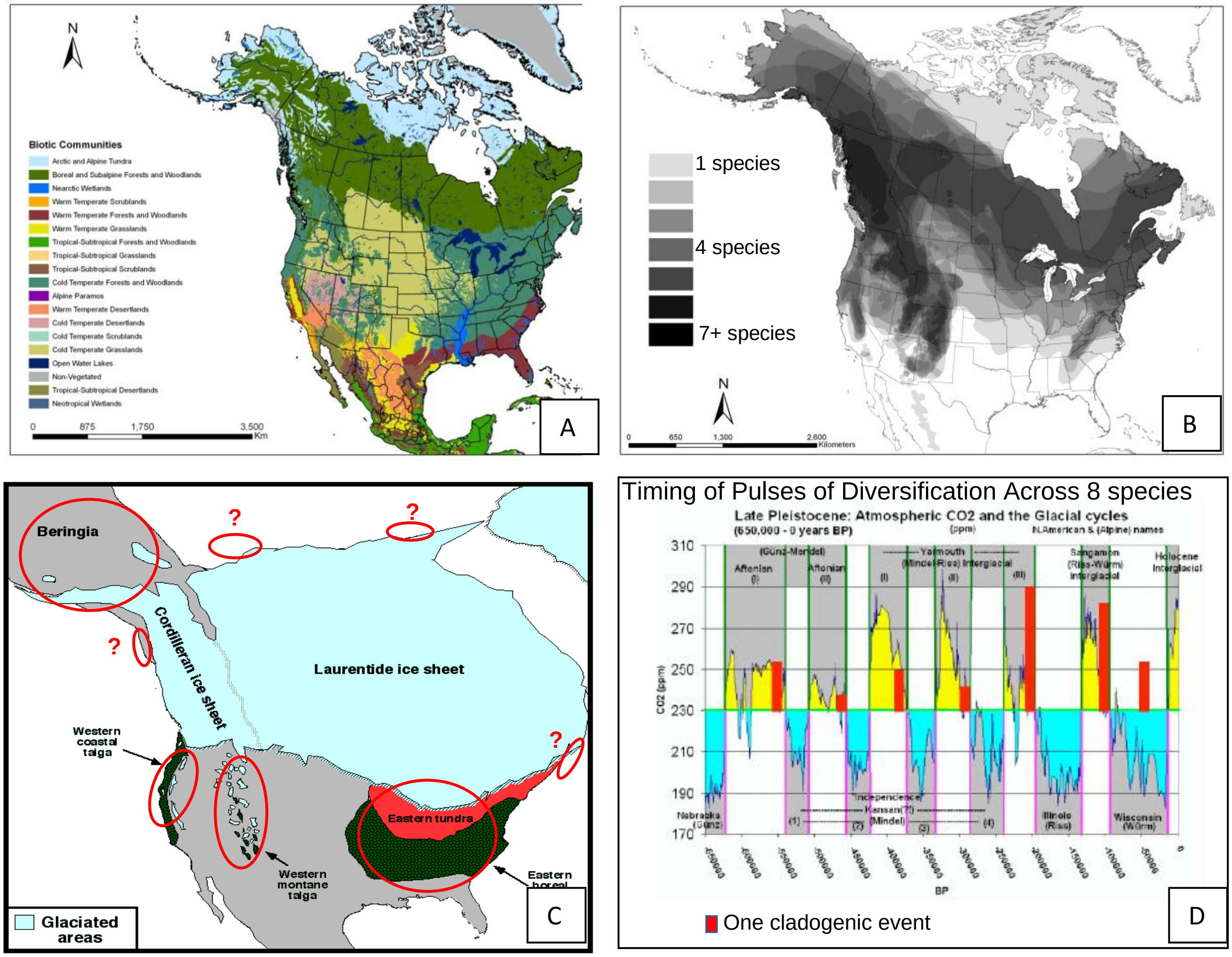
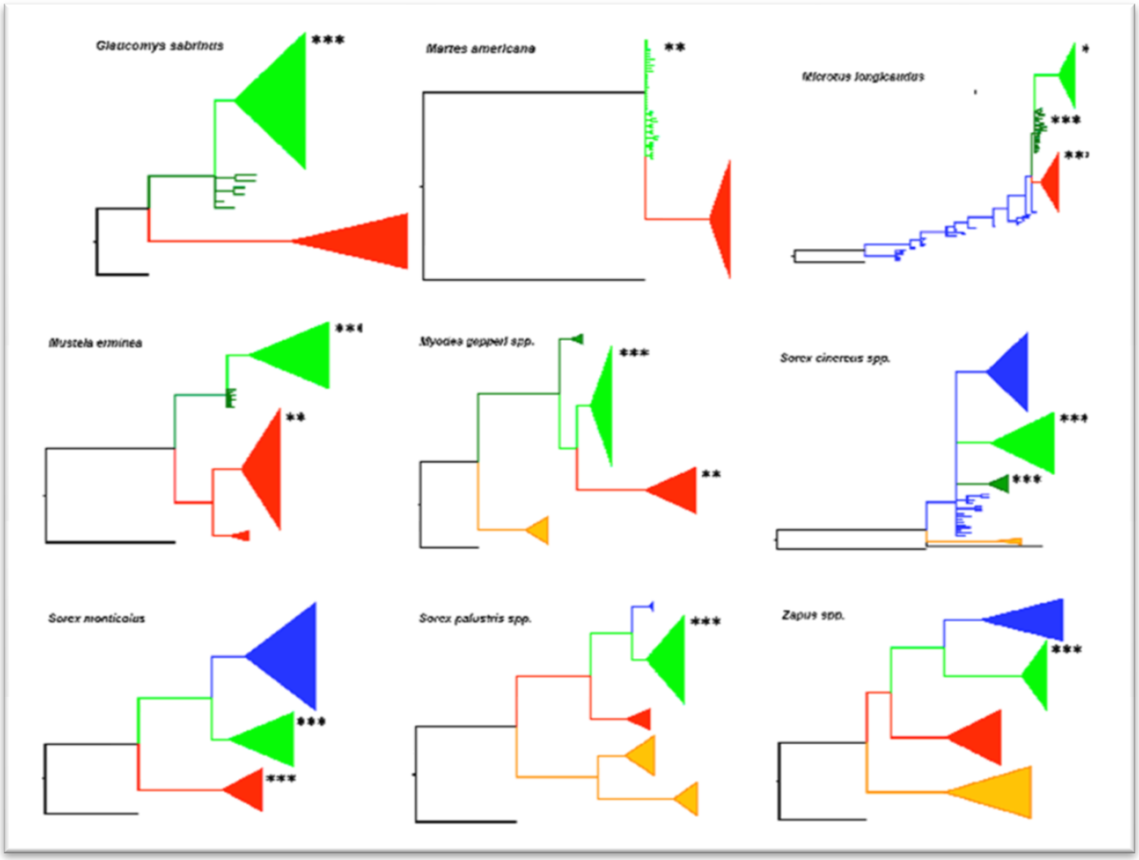


Figure 5. Mitochondrial DNA (cytochrome-*b* gene) genealogies for 9 boreal mammals in western North America. Major clades correspond with specific geographic regions: Green = Midwest/Continental, Red = West/Coastal, Blue = Southwest, Orange = Eastern. Eastern lineages are typically a separately described species (ex. *Zapus hudsonius* = eastern lineage). Certain species are lacking good range-wide sampling (ex. *Mustela erminea* & *Myodes gapperi* lack SW sequence data). Distinct east-west splits generally precede other splits. Exceptions: *Sorex cinereus* has no evident western coastal clade; *Microtus longicaudus* has a basal southern clade. Southern clade is always closer to the eastern/continental clade than to the western/coastal clade and where present, tends to be older than eastern/continental. Continental clades extending into the Pacific Northwest generally originate from further east and not from southern or western clades (see GLSA, MUER, SOCI, MILO, MYGA). Pulses of diversification 1) Eastern lineage, 2) Costal and Continental in West, 3) Southwestern with divergence timing coincident with periodicity of Pleistocene cycling. Recolonization and expansion of the continental clade from the Midwest and clades occupying deglaciated areas exhibit significant expansion (stars).


Glaucomys sabrinus
Martes americana
Microtus longicaudus
Mustela erminea
Myodes gapperi spp.
Sorex cinereus spp.
Sorex monticolus
Sorex palustris spp.
Zapus spp.