

Using biogeographical history to inform conservation: the case of Preble's meadow jumping mouse

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Abstract

The last Pleistocene deglaciation shaped temperate and boreal communities in North America. Rapid northward expansion into high latitudes created distinctive spatial genetic patterns within species that include closely related groups of populations that are now widely spread across latitudes, while longitudinally 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 analysed molecular variation in zaptodid rodents to explore how past climate shifts influenced diversification in this group. By combining molecular analyses with species distribution modelling and tests of ecological interchangeability, we show that the lineage including the Preble's meadow jumping mouse (*Zapus hudsonius preblei*), a US 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 that is ecologically indistinct and extends to the far north. Of the 21 lineages identified, this Northern lineage has the largest geographical range and low measures of intralinear genetic differentiation, consistent with recent northward expansion. Comprehensive sampling combined with coalescent-based analyses and niche modelling leads to a radically different view of geographical structure within jumping mice and indicates the need to re-evaluate their taxonomy and management. This analysis highlights a premise in conservation biology that biogeographical history should play a central role in establishing conservation priorities.

Keywords: conservation prioritization, historical biogeography, phylogeography, species distribution modelling

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Introduction

Historical biogeography provides the spatiotemporal context to document geographical variability and to explore processes responsible for generating diversity (Hewitt 2000; Riddle & Hafner 2007; Wiens 2012). A growing body of knowledge from fossils (Polly 2003), DNA analyses (Lessa *et al.* 2003; Nullmeier & Hallatschek 2013) and species distribution models (SDMs; Bell *et al.* 2007; Carnaval *et al.* 2009) demonstrates poleward

shifts (Hewitt 1999, 2004) of biota since the last glacial maximum (LGM, 26.5–19.0 ka; Clark *et al.* 2009), 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 (Moritz *et al.* 2008; Galbreath *et al.* 2009). 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 (Lessa *et al.* 2003). Conversely, adjacent low-latitude populations are often genetically divergent, reflecting enduring spatial disjunction (Hampe & Petit 2005; Malaney *et al.* in press). Identifying distinct evolutionary lineages and their spatial distribution is central to understanding the

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processes that lead to biological diversification (Richardson & Whittaker 2010), but these units also are often the target of conservation action (Collen *et al.* 2011; Winter *et al.* 2013). Deciphering molecular signatures across the entire range of a species should be an essential first step towards executing effective conservation and management strategies, but this step requires broad sampling across multiple components (taxonomic, genetic, geographical, ecological) to ensure variation and historical signatures are rigorously assessed (Knowles 2009; Hickerson *et al.* 2010; Hey & Pinho 2012).

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 (Schwartz 2008; Wilcove & Master 2008; Wood & Gross 2008). Debate persists on how best to assess imperilment, but a foundational principle is to conserve diversity and processes responsible for diversification, often by identifying significant evolutionary divergence (Crozier 1997; Nee & May 1997; Stockwell *et al.* 2003; Willis & Birks 2006). Limited ranges and declining populations also are widely considered to heighten conservation concern (IUCN 2001; Bradshaw & Brook 2010). Conservation decisions often need to be made quickly and thus using available information, which can often be data sets based on a single character type (usually morphology) analysed before rigorous quantitative methods were widely available. Furthermore, morphologically based taxonomies may miss the details of phylogeographical variation (Riddle & Hafner 1999; Pryon & Burbrink 2009; Braby *et al.* 2012). Consequently, conservation efforts frequently rely on antiquated infraspecific taxonomy (i.e. subspecies) as the primary roadmap identifying diversity (Mace 2004; Gippoliti & Amori 2007), 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 geographical variation within species (Moritz 1994, 1995) and assess ecological interchangeability within and among lineages (Crandall *et al.* 2000; Fraser & Bernatchez 2001). Once lineages have been identified, populations should be further assessed to identify and accommodate localized adaptive features (Rader *et al.* 2005). To identify units of significant evolutionary divergence, lineage-based conservation depends on adequate sampling across genes and across the spatial and ecological breadth of diversity (Zwickl & Hillis 2002; Hird *et al.* 2010; Makowsky *et al.* 2010) to ensure evolutionary history is well established (Fujita *et al.* 2012). We implement conservation-phylogenetic methods (May 1990; Vane-Wright *et al.* 1991; Faith 2007; Winter *et al.* 2013) by integrating genetic and ecological approaches to assess whether genetic subdivisions are consistent

with previous jumping mice taxonomic hypotheses. Then, we develop conservation priorities that reflect a historical-biogeographical perspective (Ceballos & Brown 1995; Channell & Lomolino 2000; Whittaker *et al.* 2005; Richardson & Whittaker 2010) predicated on extinction threats of lineages. Conservation phylogenetic techniques have been developed (Isaac *et al.* 2007; Collen *et al.* 2011) to more objectively prioritize protection efforts. We explore the historical signatures (genetics and niches) of jumping mice lineages and simultaneously test alternative hypotheses (Knowles & Carstens 2007b; Richards *et al.* 2007) of evolutionary independence across this group.

Broadly, our aim is to highlight that unravelling biogeographical signatures of the past is an essential step in conservation efforts. More specifically, we examine whether geographical structure of evolutionary diversity is reflected in taxonomy (Kruttsch 1954; Holden & Musser 2005), which is the current foundation of the politically charged management of zapodid rodents in North America (Ramey *et al.* 2005; King *et al.* 2006). We use a coalescent-based approach (de Queiroz 2007; Fujita *et al.* 2012) to establish intraspecific relationships and then integrate phylogeographical structure, including historical demographic signals and spatial shifts, into conservation prioritization. With this approach, we reveal recent biogeographical histories (since LGM) including populations of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*, Fig. 1B) along the Front Range of Colorado and Wyoming (USFWS 1998, 2002) that are minimally diverged from populations extending far northward to western Canada and Alaska (Figs 1A and 2). Since 1998, controversy regarding the federal listing of this subspecies has led to rancorous debates in popular press (Johnson 2004; Heilprin 2006), science (Ramey *et al.* 2005, 2006, 2007; King *et al.* 2006; Martin 2006; Vignieri *et al.* 2006; Crifasi 2007), policy (Lackey 2007; Scott *et al.* 2007) and law (Doremus 2010). Conservation efforts for *Z. h. preblei* in the past were estimated at nearly \$172 million (Industrial Economics I 2002) and may cost an additional \$268 million in the next two decades (Industrial Economics I 2010; USFWS 2010). Our work extends previous efforts to test the distinctiveness of this subspecies (Ramey *et al.* 2005; King *et al.* 2006) by placing *Z. h. preblei* populations within an expanded context of zapodid variation. This approach uses lineage-based evolutionary divergence and tests of ecological variation across all infraspecific taxa, not just adjacent subspecies.

Materials and methods

Our generalized workflow began with sequencing DNA from all jumping mice infraspecific taxa using samples

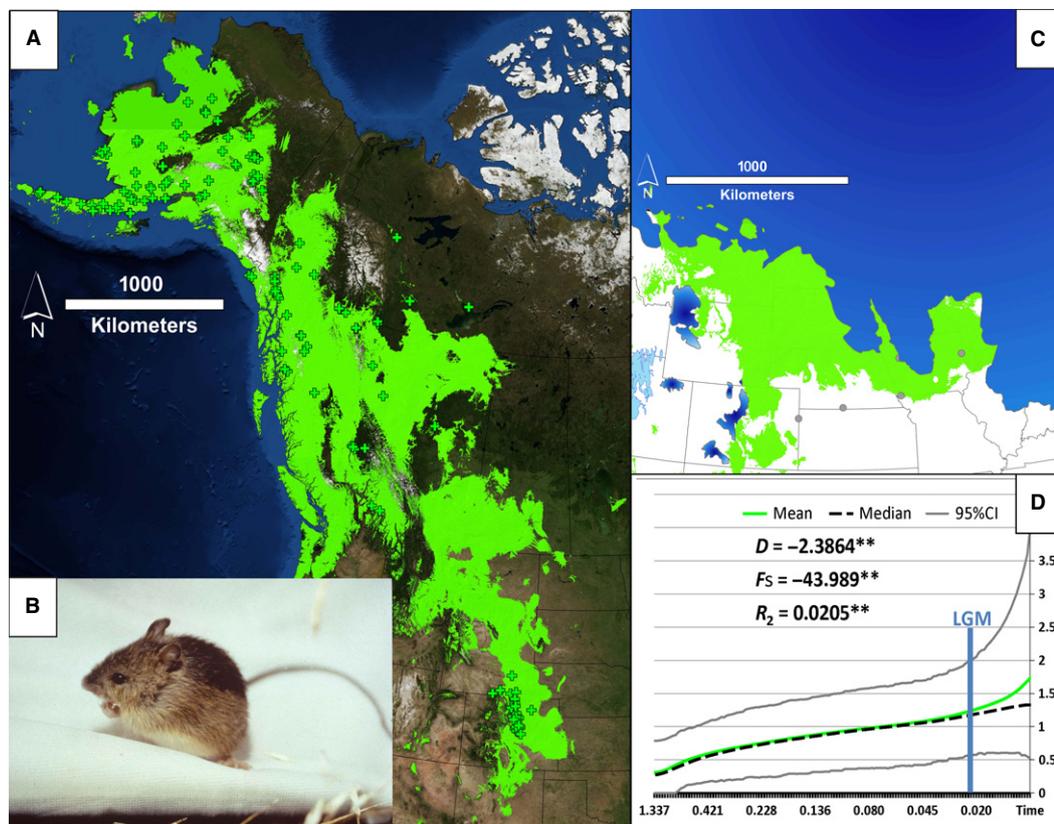


Fig. 1 (A) Potential contemporary distribution of the Northern lineage (includes USFWS threatened *Zapus hudsonius preblei*). (B) Photograph of Preble's meadow jumping mouse. (C) Species distribution model (SDM) for Northern lineage at the last glacial maximum (LGM). Note a significant expansion from 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-biogeographical process led to widespread and genetically similar populations that represent a low extinction threat of the lineage.

from natural history museums and targeted fieldwork (2007 and 2010). Single-gene and multilocus phylogeny reconstructions were used to identify coalescent-based lineages. Mutation–drift equilibrium summary statistics (mtDNA) and Bayesian skyline analyses were conducted to document historical demographic change for each lineage. Phylogenetically informed SDMs (Phillips *et al.* 2006; Franklin 2010; Scoble & Lowe 2010; May *et al.* 2011) were constructed from contemporary locality records and retrospectively applied to the past to identify potential paleodistributions (i.e. at LGM; Waltari *et al.* 2007). Fossils were integrated in phylogeny reconstructions and to independently confirm paleodistributions. Finally, evolutionary divergence, population size change (contemporary and historical), current range size, range size change since LGM and existing management units (e.g. Front Range jumping mice) were integrated to define extinction threats (Table S1, Supporting information), and each lineage was assigned

an updated regional IUCN score (IUCN 2003). IUCN scores were then converted using ranks-to-extinction probability transformations and applied to the lineage-based species-tree phylogeny to assess conservation priorities (Vane-Wright *et al.* 1991; Collen *et al.* 2011) across all jumping mice.

Genetic data

We obtained DNA sequences for 762 jumping mice across North America including type localities (i.e. topotypes) of subspecies. We extracted and sampled DNA from 430 individuals and sequenced the complete mitochondrial cytochrome *b* gene (*cytb*—1140 bp). To more fully explore genomic diversity, we also sequenced a subset of these samples for two nuclear introns and two nuclear exons. Partial introns included apolipoprotein B and glucocerebrosidase, and partial exons included breast cancer susceptibility (BCRA1) and the beta-myosin

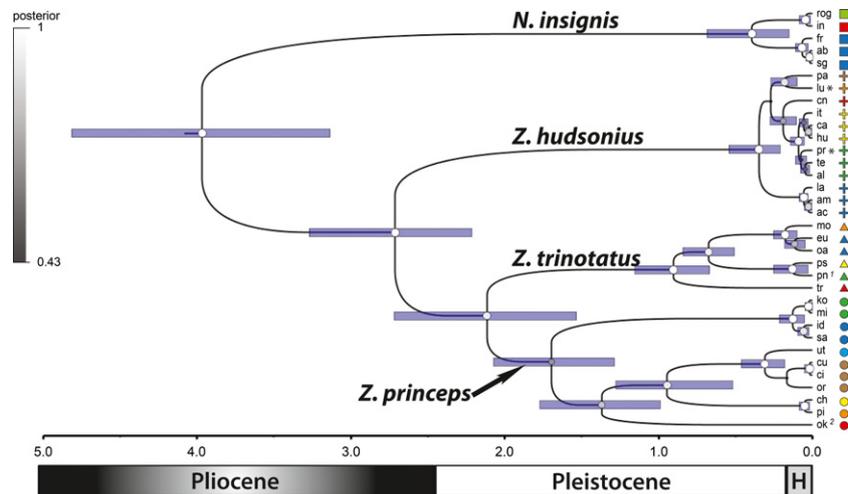


Fig. 2 Coalescent-based Bayesian multilocus species-tree phylogeny (Edwards 2009) for North American jumping mice. Open circles (○) at nodes represent >0.95 posterior probability (PP) and bars highlighting 95% highest posterior density interval (HPD) of divergence time. Tips reflect complete taxon sampling of 32 subspecies (two letter abbreviations) + 2 cryptic taxa (^{1,2}; see Himes and Kenagy 2013; Malaney *et al.* in press). Tip shapes represent 21 significantly divergent historical-biogeographical lineages and correspond with other Tables and Figures. Taxa of conservation concern (*) include the federally threatened subspecies (*Zapus hudsonius preblei*) and the federal candidate subspecies (*Z. h. luteus*). Timescales correspond with the chronology of Late Pliocene, Pleistocene and Holocene (H) epochs in North America.

heavy chain (MYH6). Additional mtDNA data were obtained from GenBank for the *cytb* gene from previous molecular studies including 332 samples of 1006 bp from King *et al.* (2006). Control-region data from Ramey *et al.* (2005) were not included in any analyses. Samples were partitioned by species: 31 *Napaeozapus insignis* (five subspecies), 455 *Z. hudsonius* (12 subspecies), 223 *Zapus princeps* (10 subspecies) and 53 *Zapus trinotatus* (four subspecies) to address conservation phylogenetic and historical-biogeographical questions and assess whether phylogeographical structure is reflected in the existing taxonomy (Krutzsch 1954; Hall 1981; Holden & Musser 2005; Fig. 2, Fig. S1, Supporting information). Polymerase chain reactions (PCRs) and cycle sequencing followed protocols previously established (Lyons *et al.* 1999; King *et al.* 2006; Malaney *et al.* in press), and heterozygous positions within the nDNA data sets were scored using the IUPAC nucleic acid code.

Specific nDNA alleles were identified using statistical methods with haplotypes inferred from multiallelic loci using a Bayesian framework via PHASE (Stephens *et al.* 2001; Stephens & Scheet 2005) in DNASP, v. 5.10.01 (Librado & Rozas 2009). 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, PP) were coded as missing data. Homologous sequences were aligned using MUSCLE, v. 3.7 (Edgar 2004), and validated visually. Individual contigs were deposited in GenBank (see Table S4,

Supporting information), and alignments are available on DRYAD (doi: 10.5061/dryad.rq412).

Phylogenetic analyses

We conducted phylogenetic analyses using a Bayesian inference (BI) framework for each locus with MRBAYES, v. 3.1.2 (Huelsenbeck & Ronquist 2005; Lakner *et al.* 2008). Aligned data sets were subjected to alternative models of sequence evolution in JMODELTEST (Posada 2008) where Bayesian information criterion (BIC; Posada & Buckley 2004) was used to determine the best-fit nucleotide substitution model (Table S3, Supporting information). Phylogenetic reconstructions were initiated with random trees, run with four chains (default heating values) for 5 million generations, with sampling every 5k generations. Convergence diagnostics were completed with the program AWTY (Nylander *et al.* 2007), and optimal parameter estimates were examined in TRACER (Drummond & Rambaut 2007). Nodal support (PP) was identified in the consensus of the residual trees with the first 5k trees discarded (Huelsenbeck & Imennov 2002), and three independent runs were performed to ensure replicated convergence, and trees were depicted with FIGTREE.

Tree-based methods may fail to reveal reticulate evolution (Posada & Crandall 2001) thought to be common in recent divergences Hudson & Bryant (2006), so we also conducted a phylogenetic statistical parsimony network analysis (Templeton *et al.* 1992) for each species and each gene using TCS, v. 1.21 (Clement *et al.*

2000). This analysis implements the statistical parsimony approach of Templeton *et al.* (1992) to further explore the relationship between incipient divergent haplotypes and facilitate a fuller investigation of the intraspecific gene genealogies. The King *et al.* (2006) data set required all *Z. hudsonius cytb* to be truncated by 134 bp for these analyses.

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 (McCormack *et al.* 2009), so we jointly estimated the phylogeny and divergence times with *BEAST (Heled & Drummond 2010) using a subset of the molecular data from each subspecies (topotypes). We used species-tree methods (McCormack *et al.* 2009) to assess whether phylogeographical structure is reflected by the morphologically based subspecies taxonomy of North American jumping mice (Kruttsch 1954). We sampled at least one representative topotype for each subspecies, but generally >3 representatives for all genes conforming to a multilocus, multispecies, coalescent-based framework (Fujita *et al.* 2012). Analyses were setup in BEAUTI, v. 1.7.0, and run with BEAST, v.1.7.0. Fossil validation points for divergences were used at several nodes (McCormack *et al.* 2011; Fig. 2) of the species tree from well-dated fossils of North American zapodids (Hibbard 1941; Klingener 1966; Kurtén & Anderson 1980; Hafner 1993; Ruez & Bell 2004; Harington 2011) and correspond to paleodistribution reconstructions (see below) and established estimates of spatiotemporal divergence. We used a strict molecular clock (0.05) for the mtDNA data set and estimated clocks for nDNA. Models of sequence evolution (Table S3, Supporting information) were used for each locus with remaining parameters set to default. Runs were conducted for 100 M generations, sampled every 10k, and we examined ESS values (>200) in TRACER and split frequencies across the Markov chain in AWTY (Nylander *et al.* 2007) indicating stabilization. We summarized all plausible trees to identify the single topology that best represents the posterior distribution using TREEANNOTATOR. Burn-in was set to 10% with 0.5 PP limit and mean node heights for divergence estimates. The final maximum clade credibility tree was depicted in FIGTREE.

To define lineages, we use three forms of evidence common in phylogenetic studies. Specifically, we identified monophyly in the species tree, gene coalescences at the mtDNA and at least one nDNA gene, plus divergence time prior to the Holocene. For mtDNA independent (i.e. nuclear only) perspective, a *BEAST analysis was conducted with *cytb* excluded. Analogous parameterizations were retained except the BCRA gene

mutation rate was fixed at 0.005 with remaining loci relaxed (Fig. S5, Supporting information).

Demographic tests

Molecular diversity indices (Nei 1987) were calculated in DNASP and determined for each gene, by species and by lineage (mtDNA-Table 2) including segregating sites (S), number of haplotypes (N_h), haplotype (h) and nucleotide (π) diversity, and mean nucleotide differences (K).

Demographic equilibrium tests for the mtDNA data set were conducted for each lineage and included Tajima's D (Tajima 1989) Fu's F_s (Fu 1997) and R_2 test (Ramos-Onsins & Rozas 2002), and significance was assessed using a null distribution of 10 000 coalescent-based simulations. Demographic equilibrium tests (D , F_s , R_2) have high power for revealing change in N_e under a model of sudden expansion (Ramos-Onsins & Rozas 2002) where significant negative values of D and F_s and small positive values of R_2 are indicative of demographic 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' (Ewens 1972) 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 analysed changes in N_e through time using Bayesian skyline (mtDNA; Drummond *et al.* 2005) and extended Bayesian skyline analyses (multilocus; Heled & Drummond 2008). These coalescent-based approaches calculate the posterior distribution of N_e 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 data sets. 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 modelling

We used SDM to assess niche envelopes of each lineage with 2.5 min (~4 km) resolution, bioclimatic variables (Hijmans *et al.* 2005) from the WorldClim database (<http://www.worldclim.org>) for contemporary and LGM. Modelling procedures followed previous studies (Waltari *et al.* 2007; Waltari & Guralnick 2009) by clipping the coverages to the study area (species ranges + 300 km buffer; Anderson & Raza 2010). Niche

variables may be highly correlated and influence projections, so we used the 11 most biologically meaningful and uncorrelated coverages across North America (Bio1-3, 7-9, 15-19; Rissler & Apodaca 2007). Localities for each taxon were downloaded from MANIS (January 2011) and updated using Biogeomancer workbench (Guralnick *et al.* 2006). To account for sampling biases (Reddy & Davalos 2003) that may result in model overfitting, we discarded localities with $>0.5 \text{ km}^2$ uncertainty and filtered records so that only a single location was represented within 10 km^2 . Filtered locality data are available on DRYAD (doi: 10.5061/dryad.rq412). We partitioned localities by species-tree lineages (Fig. 2) rather than nominal subspecies to reconstruct SDMs for contemporary and ancestral conditions. One exception includes a finer-scale analysis of the Northern lineage to test whether *Z. h. preblei* is ecologically interchangeable with conspecifics (i.e. *Z. h. alascensis*, *Z. h. tenellus*; Table S3, Supporting information). Partitioned SDMs were used to inform regional IUCN rankings for each lineage (see below, Table S1, Supporting information).

Species distribution models were constructed using default settings in the program MAXENT, version 3.3.3a (Elith *et al.* 2006; Phillips *et al.* 2006), with 20 replicate runs and random background sampling within the 300 km buffer (Phillips *et al.* 2009). Species-specific parameter tuning is thought to enhance model performance (Anderson & Gonzalez 2011). Consequently, a preliminary analysis of model selection (Warren & Seifert 2011) was conducted, and results suggested the default settings in MAXENT were most appropriate for our wide-ranging and densely sampled data sets consistent with empirical performance evaluations (Phillips & Dudik 2008). When possible, localities with genetic data were used as the training data set. Some localities genotyped by Himes and Kenagy (2013) were used for *Z. trinotatus* but not for any genetic analyses. When insufficient genetic samples were available, we randomly reserved 20% of down-sampled MANIS localities as training data sets. Models used the pointwise bootstrap median of replicated runs with the 90% of the samples included as the projection criterion (Pearson *et al.* 2007). Given that changes in population size and range size are correlated (Excoffier *et al.* 2009; Arenas *et al.* 2012), we relate LGM and contemporary predicted SDM to historical and contemporary N_e that were then incorporated into IUCN rankings.

Niche conservatism is considered a continuum (Wiens & Graham 2005; Warren *et al.* 2008) where closely related taxa generally share niche space more frequently than randomly expected, but rarely are environmental envelopes identical. Ecological interchangeability is expected when niches are sufficiently similar (Rader *et al.* 2005). To detect the degree of ecological

interchangeability among jumping mice, we assessed niche overlap between pairs of lineages using two metrics: the *I* statistic (Warren *et al.* 2008) and relative rank (RR; Warren & Seifert 2011). 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 whether environmental envelope overlap is significantly different (one-tailed test) from a null expectation for populations within the Northern lineage. The niche identity test randomizes sample points and then reconstructs an expected degree of niche overlap from an underlying distribution. ENMTOOLS, v.1.3 (Warren *et al.* 2010), was used to assess niche overlap (*I*, RR) and conduct randomized tests (niche identity) using 100 pseudoreplicates for each analysis (Table S3, Supporting information).

Conservation prioritization

Regional IUCN rankings were updated for each lineage using established criteria (IUCN 2001, 2003) and applied to address both risk of extinction and conservation priority. Rankings are characterized by threats to extinction (Table S1, Supporting information), which simultaneously incorporates independent data sets. These data sets include current conservation concerns, phylogenetic distinctiveness, SDMs reflecting current range size and range size change since LGM, plus contemporary and historical change in population size. IUCN rankings included critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT) and 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 IUCN₁₀₀ (Mooers *et al.* 2008; Collen *et al.* 2011) ranks-to-extinction probability transformations with the TUATARA module (Maddison & Mooers 2007) in MESQUITE, v.2.75 (Maddison & Maddison 2009). There are several ranks-to-extinction transformations, but the IUCN₁₀₀ is thought to most accurately reflect threats to extinction within the next 100 years considering ongoing and future anthropogenic pressure (Mooers *et al.* 2008). In MESQUITE, conservation priority metrics were calculated using the Evolutionarily Distinct and Globally Endangered (EDGE; Isaac *et al.* 2007) score for each lineage with the IUCN₁₀₀ ranks-to-extinction transformation as the inverse weighting scheme (Table S1, Supporting information). For comparison, the unweighted May's Distinctness (May 1990) was used to offset any effects of using the IUCN₁₀₀ weighting scheme. A scatter plot was used to compare conservation priority measures (Fig. 3).

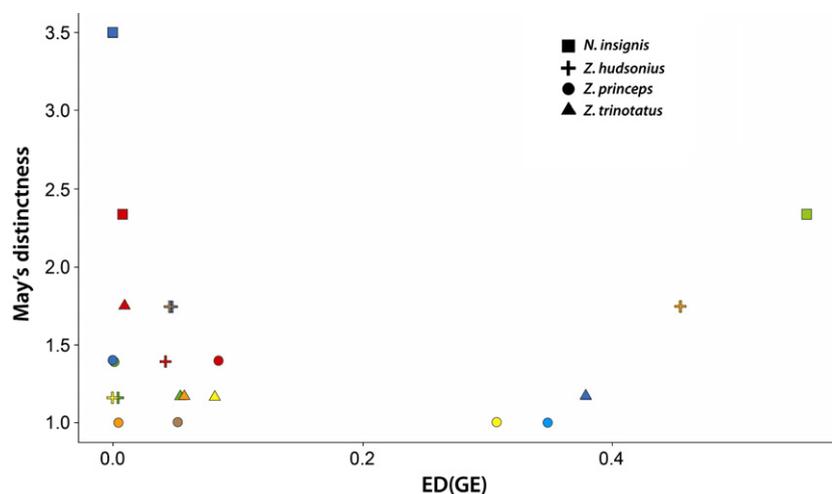


Fig. 3 Conservation prioritization (Evolutionarily Distinct + Globally Endangered—EDGE vs. May's Distinctness) scores contrasted for 21 divergent North American jumping mice lineages. The lineage that includes the federally threatened taxon (*Zapus hudsonius preblei*—green cross) is among the lowest conservation priorities using the IUCN₁₀₀ ranks-to-extinction probability transformation (Isaac *et al.* 2007; Mooers *et al.* 2008).

Results

Sampling

Range-wide samples that represented all extant zaptodid taxa were obtained (i.e. complete taxon sampling, 32 subspecies of four extant species), and we then sequenced multiple genetic loci and inferred niche space to assess whether phylogeographical structure accurately reflects the taxonomy (Krutzsch 1954; Holden & Musser 2005). We simultaneously tested the genetic structure against the existing taxonomy and set the historic framework with a species-tree phylogeny (Carstens & Knowles 2007; Knowles & Carstens 2007a; Degnan & Rosenberg 2009; Heled & Drummond 2010). Then, by sampling niches using phylogenetically informed SDMs (Kozak *et al.* 2008; Franklin 2010), we explored potential contemporary and paleodistributions (Waltari *et al.* 2007) and to assess ecological interchangeability (Crandall *et al.* 2000; Rader *et al.* 2005; Warren *et al.* 2008) across all jumping mice lineages.

Phylogenetic analyses

Bayesian gene-tree analyses of individual loci produced alternate estimates of divergence (Fig. S1, Supporting information) and varying degrees of stochastic coalescent events among lineages. The mtDNA data set had the strongest phylogenetic signal and support values (posterior probabilities ≥ 0.95) identifying 12 clades as deeply divergent and 20 statistically divergent haplotype networks. 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 (Fig. S1, Supporting information).

Intraspecific genetic variation varied among jumping mice for the mtDNA and nDNA data sets. *Napaeozapus insignis* had 28 mtDNA haplotypes with two statistically significant networks (14 steps). Within the *Z. hudsonius* *cytb* data set (1006 bp), there were 102 haplotypes across five networks (12 steps). Intraspecific genetic variation in *Zapus princeps* reflected eight networks (14 steps) and 176 haplotypes and five networks (14 steps) across 31 haplotypes in *Z. trinotatus*.

Within the Northern lineage (see below—includes *Z. h. preblei*), we failed to detect haplotype H from King *et al.* (2006), but their reported sample (YG-9801) is identical to A when using statistical parsimony and phylogenetic reconstruction. We documented four errors in reporting data from King *et al.* (2006). In Douglas Co. Colorado, both haplotypes C and I were reported, but all available data sets reflect only haplotype J at this locality. GenBank does not return haplotypes E or S, but the F and V that were reported to GenBank actually have two distinct haplotypes each (asterisk in Fig. S4, Supporting information). We detected the widespread I haplotype from two new locations plus one previously undetected haplotype in Colorado. Twelve closely related haplotypes were detected in the far north that range from 1 to 4 bp divergent from the central haplotype, and their divergence is comparable to variation within *Z. h. preblei* (i.e. Front Range populations are 1–3 bp divergent, Fig. S4, Supporting information). Further, there are no nDNA bp changes between Front Range populations and those in the far north.

Species-tree estimation and divergence

The taxonomy-based species tree reflected strong support for 21 phylogeographical 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 (Fig. S2, Supporting information). Instead, far northern (geographically distant) subspecies (i.e. *Z. h. alascensis*, *Z. h. tennellus*, and far western populations of *Z. h. hudsonius*) form a closely related clade with Front Range *Z. h. preblei* (Fig. 2). This widespread lineage diverged from the Southern Plains lineage (*Z. h. campestris*, *Z. h. hudsonius*, *Z. h. intermedius*) at the end of the last glacial period. This new understanding of shared biogeographical 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 multilocus techniques, with signatures for both generally concordant (Table 2, Fig. S3, Supporting information). Ten lineages experienced significant shifts in N_e . The Northern lineage experienced the most pronounced historical demographic expansion signatures with a nearly 100× increase in effective population size (Table 2, Fig. 1D, Fig. S3B, Supporting information), while the Uinta lineage reflected historical demographic declines (Fig. S3C, Supporting information). This lineage also highlights the fallacy of depending on summary statistics alone which fail to detect recent (since LGM) declines. Other lineages show no signal of significant departure from historical population equilibrium (e.g. Southwestern lineage).

Species distribution modelling

Climate-based SDMs were predicted for each lineage and reflect geographically restricted populations with varying degrees of niche overlap, but generally overprediction was minimal (Fig. S2, Supporting information). One exception is the Northern Cascade and Southern Cascade lineages that show niche overlap ($I = 0.875$, $RR = 0.929$), but deep phylogenetic divergence (middle Illinoian; Fig. 2). Reconstructed SDMs fail to predict separation at the Columbia River. Relative influences of environmental parameters are typically lineage specific (Table S2, Supporting information) 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 (Warren *et al.* 2008) for populations partitioned by subspecies within the Northern lineage suggest there are minimal environmental (e.g. temperature and precipitation) differences across this wide range (Table 3).

Conservation prioritization

Key metrics (Table S1, Supporting information; Bradshaw & Brook 2010) that elevate conservation ranking include evolutionary distinctiveness, comparatively low N_e (Table 2, Fig. S3, Supporting information), population declines (historical or contemporary), spatial declines (Table 1), nonoverlapping niches (i.e. ecologically different; Table S2, Supporting information) and existing management concerns (e.g. *Z. h. preblei*). We defined the risk of extinction for all lineages by first establishing evolutionary distinctiveness (Fig. 2). Evolutionary distinctiveness for each lineage was considered by three lines of evidence (species-tree monophyly + mtDNA and at least one nDNA coalescent event + divergence time) then calculating effective population sizes (N_e ; Table 2, Fig. S3, Supporting information), population declines (historical and contemporary), spatial shifts in distribution (Table 1) and overlap in niche space (i.e. ecological interchangeability) among lineages. Risks of extinction ranged from LC (0.0001) to critically endangered (0.999) and were applied in a phylogenetic context to identify conservation priorities. The lineage that includes the federally threatened subspecies *Z. h. preblei* has a low conservation priority score using this approach (Fig. 3), while other lineages without protection are identified as high priority or have a high extinction threat of an evolutionarily divergent lineage.

Discussion

This study highlights how historical biogeography can be used to lay a foundation for conservation action. Across the spectrum of diversity and using comprehensive infraspecific taxon sampling of jumping mice, we document 21 lineages. Some lineages are deeply divergent and have high conservation priority, under a variety of well-established conservation criteria such as small range size, declined ranges since LGM, historically shrinking effective population sizes and/or ongoing anthropogenic pressure that has reduced contemporary populations/ranges. Conversely, most

Table 1 Lineages with associated subspecies, range area (km²) and furthest distributed range (km) using 90% minimum presence threshold for contemporary and last glacial maximum (LGM) median species distribution models (see Fig. 1 and Fig. S2, Supporting information) and updated regional IUCN₁₀₀ scores (IUCN 2003; Isaac *et al.* 2007; Mooers *et al.* 2008) following the ranks-to-extinction probability transformation

Species and lineage	Subspecies	Current km ² area	LGM km ² area	Km range	IUCN ₁₀₀
<i>Napaeozapus insignis</i>					
Acadian 	<i>insignis</i>	499 470	687 711	1486	0.01
Allegheny 	<i>roanensis</i>	450 840	645 627	926	0.667
Canadian 	<i>abietorum fructectanus saguenayensis</i>	990 523	204 610	2329	0.001
<i>Z. hudsonius</i>					
Appalachian 	<i>academicus americanus ladas</i>	907 822	53 898	2744	0.1
Can. Shield 	<i>canadensis</i>	1 505 480	989 855	2080	0.1
Northern 	<i>alascensis preblei tenellus</i>	2 421 006	914 388	4701	0.01
N. Plains 	<i>campestris hudsonius intermedius</i>	2 166 740	1 020 983	2559	0.001
S. Plains 	<i>pallidus</i>	430 561	789 993	958	0.1
Southwestern 	<i>luteus</i>	208 817	429 565	787	0.999
<i>Zapus princeps</i>					
Boreal 	<i>idahoensis saltator</i>	710 746	131 824	2624	0.001
Great Basin 	<i>cinereus curtatus oregonus</i>	206 593	536 630	877	0.1
Great Plains 	<i>minor kootenayensis</i>	624 282	525 904	1703	0.001
La Sal 	<i>chrysogenys</i>	36 [†]	N/A	13	0.667
Okanogan 	Un-described*	38 523	60 880	220	0.1
S. Rockies 	<i>princeps</i>	204 470	473 724	1031	0.01
Uinta 	<i>utahensis</i>	89 441	190 592	596	0.667
<i>Z. trinotatus</i>					
Coastal 	<i>eureka orarius</i>	7861	38 909	481	0.667
N. Cascade 	<i>trinotatus</i>	115 012	356 987	577	0.01
S. Cascade 	<i>montanus</i>	83 659	322 589	473	0.1
N. Sierra 	<i>Z. p. pacificus</i>	29 675	66 584	449	0.1
S. Sierra 	<i>Z. p. pacificus*</i>	14 781	68 989	361	0.1

*Cryptic and undescribed taxa (Himes and Kenagy 2013; Malaney *et al.* in press).

[†]Range area based on georeference and associated uncertainty (Guo *et al.* 2008).

lineages have relatively low conservation priority, including the federally listed *Z. h. preblei*. This taxon is part of the wide-ranging Northern lineage, composed of closely related populations that presumably expanded north- and westward following the last deglaciation of North America. This widespread set of populations has 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 demographic declines (Waples 1991, 1998; Pennock & Dimmick 1997; Winter *et al.* 2013). We suggest that management plans for species-of-concern should, at a minimum, require comprehensive sampling of a species range coupled with phylogeographical 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 (Faith 2007) set within a broader lineage-based context that

explicitly integrates historical signatures (e.g. demographic and spatial shifts) and provides a more objective means of prioritizing management efforts (Vane-Wright *et al.* 1991). Finally, museums harbour an irreplaceable wealth of spatiotemporal data for deciphering changing conditions and informing conservation (Moritz *et al.* 2008; Rubidge *et al.* 2012).

Comprehensive sampling reveals intraspecific diversity

A requisite, but often overlooked, first step in any conservation study is establishing the systematic relationships and geographical limits of the taxon of concern (Bradshaw & Brook 2010). A key assumption in systematics is complete taxon sampling (Poe & Swofford 1999; Zwickl & Hillis 2002; Wiens & Morrill 2011) to distinguish among alternative phylogeographical hypotheses (Avice *et al.* 1987; Hewitt 2001; Hickerson *et al.* 2010). Using comprehensive taxon sampling, assessing geographical variation across multiple genes (Brito & Edwards 2009; Edwards 2009) and implementing an integrative approach that includes niche characterization

Table 2 Species and infraspecific taxa, lineage-based molecular diversity indices for 762 mtDNA samples (*cytb* gene)

Species [†] and lineage	N	S	N _h	h	π	K	D	F _s	R ₂
<i>Napaeozapus insignis</i>	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 [‡]		2						
Canadian■	15	29	13	0.971	0.0064	7.2571	-1.0068	-4.661**	0.1007
<i>Z. hudsonius</i>	455	178	102 [§]	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 [‡]		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
<i>Zapus princeps</i>	223	313	130 [§]	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 [‡]		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*
<i>Z. trinitatus</i>	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 [‡]		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*

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 R₂. *P < 0.05, **P < 0.01.

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

[‡]Sample size <5 and thus not tested for demographic indices.

[§]Smaller values are due to the reduced (1006 bp) data set of King *et al.* (2006)—missing data excluded.

(Franklin 2010; Scoble & Lowe 2010), we uncovered 21 divergent lineages across North American jumping mice (Fig. 2). Generally, lineages differed in niche space (Table S2, Supporting information) and these are interpreted as ecologically unexchangeable. For example, the Uinta lineage (*Z. p. utahensis*) is sufficiently distinctive based on genetic and niche variation to warrant specific status via classic measures (Baker & Bradley 2006; Raxworthy *et al.* 2007; Rissler & Apodaca 2007) and within a generalized lineage context (de Queiroz 2007; Fujita *et al.* 2012). Similarly, using this approach, and accounting for limited morphological variation (Krutzsch 1954), *Z. h. preblei* may be considered synonymous with *Z. h. alascensis* and *Z. h. tenellus*. Further, Ramey *et al.* (2005) concluded and validated by an independent review (Arbogast *et al.* 2006) that there were few morphological differences between *Z. h. campestris*, *Z. h. intermedius* and *Z. h. prebeli*. Our multilocus molecular data sets concur with King *et al.* (2006) that the Northern lineage is evolutionarily distinct from Northern Plains jumping mice. Additional tests will be required before

hypotheses of infraspecific taxonomic synonymy can be implemented.

Considering the deep divergences of some lineages and shallow divergences of others, a revised taxonomy of the group is needed but is outside the context of this study. However, we suggest that jumping mice taxonomy (Hall 1981; Holden & Musser 2005) under-represents species-level variation with both phylogenetic and niche data sets reflecting substantial unrecognized differentiation. Consequently, in the interim, management should focus on lineages as the requisite backdrop to conservation action. Populations along the Front Range (King *et al.* 2006) should be carefully compared with recently diverged northern populations, and several other deeply divergent zapodid lineages require further assessment and monitoring.

Both the morphologically based taxonomy (Krutzsch 1954; Holden & Musser 2005) and previous molecular studies of Preble's jumping mice (Ramey *et al.* 2005; King *et al.* 2006) assumed that spatially adjacent subspecies were most closely related, leading to limited

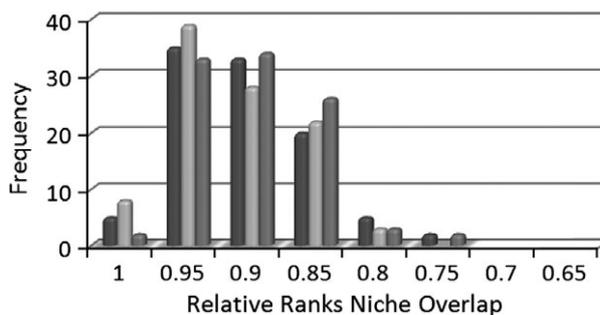
sampling of taxa (1/2 subspecies) and geographical breadth (<1/3 *Z. hudsonius* range) as the basis for the federal listing (Crifasi 2007). In this case, spatially proximal subspecies are not necessarily closely related. *Zapus h. preblei* was described in 1954 based on four adult specimens (Krutzsch 1954). Although diagnostic morphological characters (Krutzsch 1954) 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 geographical distance from the southern Rocky Mountain populations. Instead, taxonomic evaluation of the jumping mice (Ramey *et al.* 2005, 2007; King *et al.* 2006; Vignieri *et al.* 2006) 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-biogeographical context, as a first step in evaluating conservation status (Moritz 1995, 2002; Avise 2008; Colleen *et al.* 2011) or exploring other processes (Crandall *et al.* 2000; Rader *et al.* 2005). Further, observations of morphological similarity across jumping mice were part of the basis for a proposal to remove recognition of all *Z. hudsonius* subspecies (Jones 1981), 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 and showed no statistically significant abiotic ecological differences (Table 3). Taxonomic re-evaluation should include a set of tests that encompasses the emerging historical-biogeographical perspective and more finely assesses hypotheses of both evolutionary independence and adaptive variation.

Signatures of diversification and demography

Bayesian skyline analyses were used to assess historic demographic signals (Fig. 1D) and integrated with niche-based approaches to reveal spatial shifts since the LGM (latitudinal, longitudinal or elevational) that can be characterized as four general models. (i) *Demographic* (Lessa *et al.* 2003; Excoffier *et al.* 2009) and *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 (Ramos-Onsins & Rozas 2002) with comparatively lower nucleotide diversity, increased haplotype diversity (Excoffier *et al.* 2009) and recent population increases (Fig. S3, Supporting information; Drummond *et al.* 2005; Heled & Drummond 2008). Further, each lineage reflects spatial expansion from disjunct late Pleistocene ancestral ranges (Fig. 1C, Table 1, Fig. S2, Supporting

Table 3 Measures of niche overlap (ecological exchangeability), Warren's *I* and relative ranks (RR) between subspecies comprising the Northern lineage

Northern lineage taxa pairs	<i>I</i>	RR
<i>Z. h. alascensis</i> vs. <i>Zapus hudsonius preblei</i>	0.7493	0.9665
<i>Z. h. alascensis</i> vs. <i>Z. h. tenellus</i>	0.8657	0.9604
<i>Z. h. preblei</i> vs. <i>Z. h. tenellus</i>	0.8444	0.9669



Values near 1.0 are considered identical or highly interchangeable vs. near 0.0 are considered completely different or not interchangeable. Significance (niche identity) tests were conducted with 100 pseudoreplicates of randomized localities for paired taxa, but no comparison was significantly different, suggesting that niche space is analogous across all taxa pairs (graph). Jumping mice populations along the Front Range appear to be ecologically exchangeable with populations in the far north.

information). (ii) *Demographic and Spatial Contraction* (Arenas *et al.* 2012). 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 reduction 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 (Malaney *et al.* in press). (iv) *Demographic Stability but Spatial Shift* (Malaney *et al.* 2012). Finally, the Coastal, Southern Plains and the Southwestern lineage shifted from ancestral ranges, but experienced no significant demographic change. The commonality of these four signatures should be evaluated in other north temperate organisms (Carstens & Richards 2007; Gutierrez-Garcia & Vazquez-Dominguez 2011).

The Northern lineage is representative of Model (i). This 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 high haplotype diversity (*h*)

coupled with low nucleotide diversity (π) and the fewest nucleotide differences (K). Together (Table 2), these metrics are suggestive of recent demographic growth (Lessa *et al.* 2003; Excoffier *et al.* 2009). Further, populations across this wide range appear ecologically interchangeable (i.e. occupy equivalent niche space, Table 3). Fossils dated to the Late Pleistocene from the Great Plains coincide with the paleodistribution models (Fig. 1C, Fig. S2 Supporting information; Kurtén & Anderson 1980) with the hind-cast narrow range agreeing with low-density ancestral effective population sizes (Table 2, Fig. 1D, Fig. S3 Supporting information). Collectively, these signatures suggest that 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 (Ramey *et al.* 2005; King *et al.* 2006; Vignieri *et al.* 2006) and northward to Alaska. Northward expansion signatures were detected in six other jumping mice lineages (Table 2), mirroring a common process (Hewitt 2000, 2004; Lessa *et al.* 2003; Excoffier *et al.* 2009). However, no other zapodid reflects demographic expansion metrics near the magnitude ($\sim 100\times$) of the Northern lineage (Table 2; Fig. S3, Supporting information).

Conservation prioritization

Over 75% (16/21) of jumping mice lineages rank higher in the EDGE conservation priority than the Northern lineage (Fig. 3). Furthermore, the seven lineages (Acadian, Appalachian, Boreal, Canadian, Great Plains, Northern and 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; Fig. S3, Supporting information). Combined, these metrics and regionally updated IUCN scores suggest that these lineages are LC. Despite these metrics and careful consideration of the ongoing management concerns along the Front Range of Colorado and Wyoming, we instead used the near threatened criterion (Fig. 3) for the Northern lineage.

In contrast to Model (i), lineages that are endemic to southern mountains and mesic coasts have remained relatively stable over glacial cycles (Model iv) or moved to higher elevations (Model ii & iii). Signatures of these histories are preserved as accrued genetic variation and ecological differentiation. These signatures demonstrate that climate-mediated demographic histories (Hugall *et al.* 2002; Moritz *et al.* 2005; Carnaval *et al.* 2009) are

mirrored in genes and niches. The five 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 IUCN₁₀₀; Mooers *et al.* 2008). The Allegheny (*N. i. roanensis*) lineage, two populations of the narrow-ranged La Sal lineage (*Z. p. chrysoyensis*), the historically contracting Uinta lineage (*Z. p. utahensis*) and relict populations of the Coastal lineage in California (*Z. t. eureka* + *Z. t. orarius*) have no protective status. Thus, existing management plans primarily targeting *Z. h. preblei* may be missing key and divergent units of evolutionary and biogeographical 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 that are projected to worsen (Thomas *et al.* 2004). Shrinking mesic habitats at lower latitudes are due to the synergy (Mantyka-Pringle *et al.* 2011) between climate change (McDonald & Brown 1992; Thomas *et al.* 2004; Ackerly *et al.* 2010) and anthropogenic fragmentation (Andren 1994) that may precipitate jumping mice declines (Frey & Malaney 2009; Malaney *et al.* 2012). Conversely, high-latitude lineages of zapodids are the result of expanded ranges during the warming phase of the Holocene epoch (Lessa *et al.* 2003) and generally have lower extinction risk because of more limited human use of these landscapes.

Collectively, these data may counter the proposed listing of *Z. h. preblei* under the ESA (ESA 1973; Haig *et al.* 2006) based on traditional measures of extinction threat such as rarity and limited range size of an ecologically and genetically discrete taxon (Rabinowitz 1981; Yu & Dobson 2000). Conservation efforts targeting jumping mice within the Front Range of Colorado and Wyoming (USFWS 2003) should be carefully re-evaluated in the light of the projected wide distribution of the Northern lineage. Localized population declines, as reported for *Z. h. preblei* (USFWS 2002; Meaney *et al.* 2003; Trainor *et al.* 2007), are problematic for mesic-associated organisms throughout the xeric environments of the west (Frey & Malaney 2009). Analyses herein identified other lineages with higher conservation priority, reinforcing the premise that management efforts should first identify and preserve the most ecologically and evolutionarily divergent units (May *et al.* 2011). Furthermore, these results suggest management action should not rely principally on antiquated taxonomy (Gippoliti & Amori 2007), but instead emphasize ecological distinction and evolutionary history.

Specimen-based conservation remains undervalued

Finally, we highlight 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 develop SDMs (Graham *et al.* 2004; Elith *et al.* 2006) 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 the understanding of how phenotypes are interacting with changing conditions. Analyses that are spatiotemporally anchored by fossil specimens further underscore the value of integration across independent data sets to build robust taxonomies (Fujita *et al.* 2012) and falsifiable measures of diversity, critical for any conservation effort (Isaac *et al.* 2004).

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Both authors conceived the ideas, contributed to the analyses and interpretation of the results and wrote the manuscript.

Data accessibility

DNA sequences: GenBank accessions are linked to the Arctos Database see online Supporting information.

Sequence alignments and down-sampled SDM sample locations: Dryad entry doi: 10.5061/dryad.rq412.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Bayesian gene trees with posterior probabilities indicated on branches next to supported nodes (●).

Fig. S2 Subspecies (32 taxa) taxonomy and species distribution models (current & LGM) for 21 lineages of North American jumping mice (see Table 1).

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.

Fig. S4 (A) Northern lineage, mtDNA cytochrome *b* gene haplotype network via statistical parsimony (Templeton *et al.* 1992; Clement *et al.* 2000). 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.

Fig. S5 Species tree without mtDNA dataset.

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.

Table S2 (a–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.

Table S3 Molecular data, character variation, and nucleotide substitution model selected using Bayesian Information Criterion (BIC) for 92 samples of North American jumping mice.