ORIGINAL ARTICLE

Differential regional response of the bushy-tailed woodrat (*Neotoma cinerea*) to late Quaternary climate change

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ABSTRACT

Aim To reconstruct the regional biogeographical history of the bushy-tailed woodrat, *Neotoma cinerea* (Rodentia: Cricetidae), across its distribution using multiple sources of information, including genetic data, ecological niche models and the palaeorecord.

Location Western North America.

Methods We analysed complete cytochrome *b* gene (1143 bp) sequences from 182 specimens of *N. cinerea* using Bayesian and coalescent methods to infer phylogenetic relationships, time of major divergences, and recent demographic trends. For comparison, we developed clade-specific ecological niche models for groups of interest and analysed spatial trends of *N. cinerea* in the palaeorecord as well as temporal frequency trends across strata of individual palaeomiddens.

Results We found two largely allopatric clades within *N. cinerea*, with several regionally distinct subclades showing contrasting recent population dynamics. Niche models showed consistent habitat at the Last Glacial Maximum (LGM) and modern times in the Rocky Mountains and northern United States, while the Great Basin may have been markedly less suitable at the LGM than today. The palaeorecord showed great spatio-temporal variability in the presence of *N. cinerea*, but documents broad-scale patterns of occupancy and regional population trends.

Main conclusions The Quaternary dynamics and evolutionary history of *N. cinerea* appear to have been shaped by both vicariant events associated with geographical barriers and the availability of suitable habitat through time. Divergence of the two major clades dates to the Pliocene–Pleistocene transition, with clades separated by the Green and Colorado rivers and northern Rocky Mountain Pleistocene glaciations. We found largely concordant genetic, niche model and palaeorecord patterns suggesting long-term population stability in the Rocky Mountains, while extant clades in the Great Basin and far north appear to have expanded or re-expanded into these regions relatively recently. Furthermore, disjunct haplotype distributions, regional demographic history, and historical distribution of suitable habitat suggest that the Great Basin has been a particularly dynamic region.

Keywords

Divergence dating, ecological niche model, Great Basin, mitochondrial DNA, montane, *Neotoma cinerea*, palaeomidden, phylogeography, Quaternary, western North America.

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INTRODUCTION

Western North America is a biogeographically diverse region due to a combination of environmental and geological forces such as extreme climatic fluctuations (Grayson, 1993), glaciation (Conroy & Cook, 2000a; Runck & Cook, 2005), pluvial inundation (Johnson, 2002), and volcanism (van Tuinen *et al.*, 2008) in the presence of orogenesis and topographical complexity (Badgley, 2010). Taxa of this region have responded to these forces by a variety of means, typically categorized under three classes of mechanisms: geographical range shifts (e.g. Guralnick, 2007), elevational shifts (e.g. Moritz *et al.*, 2008), and *in situ* adaptation (e.g. Smith & Betancourt, 2006). Our understanding of biogeographical dynamics and modern taxonomic distributions is aided by this region's uniquely detailed record of past ecosystems in the form of palaeomiddens. These preserved collections of debris, including bones, plants and faecal material, are collected or deposited by woodrats (genus *Neotoma*) and can persist for tens of thousands of years, particularly in arid climates (Van Devender *et al.*, 1990). By recording detailed spatio-temporal community changes, the palaeorecord provides a powerful complement to phylogeographical and ecological niche modelling approaches by allowing independent confirmation of patterns of occupancy and abundance inferred from these other methods. For no other vertebrate is the palaeomidden record more complete than for the primary architect of these structures across much of this region, the bushy-tailed woodrat, *Neotoma cinerea* (Ord, 1815).

The palaeorecord of *N. cinerea* suggests that this species has responded to past climate change in different parts of its distribution through all three classes of demographic and evolutionary mechanisms. Geographically, the range of *N. cinerea* has shifted latitudinally via contraction in the south (Harris, 1984, 1993) and presumably expansion in the north with retreat of glaciers following the Last Glacial Maximum (LGM) *c.* 18,000 ^{14}C years before present (BP) as has been observed in other species (Conroy & Cook, 2000a; Lessa *et al.*, 2003; Runck & Cook, 2005; Galbreath *et al.*, 2009). This shift is also qualitatively predicted by ecological niche modelling of distributional changes since the LGM (*sensu* Waltari & Guralnick, 2009). Elevationally, upslope shifts in *N. cinerea* have been observed in the palaeorecord since the LGM, as expected for montane species through relatively warmer climatic periods (Guralnick, 2007; Waltari & Guralnick, 2009). Elevational range shift has also been observed in association with recent climate change (< 100 years) in the Sierra Nevada mountains of eastern California (Moritz *et al.*, 2008). Finally, the palaeorecord indicates that *N. cinerea* has responded to climate change through potential *in situ* adaptation via body size change (Smith *et al.*, 1995; Smith & Betancourt, 1998, 2006; Lyman & O'Brien, 2005) following an inverse relationship between body size and environmental temperature – in accordance with Bergmann's rule (Bergmann, 1847; Mayr, 1956).

Information concerning distributional and evolutionary responses from the palaeorecord and existing ecological niche models allow us to establish specific predictions of occupancy and abundance through time in two distinct regions of the contemporary *N. cinerea* range. (1) In recently deglaciated regions north of the geographical LGM limit we predict patterns consistent with population expansion, with the hypothesis that this species has undergone the same postglacial colonization inferred in other high-latitude, small mammal species of western North America. (2) South of the LGM limit we predict patterns consistent with population stability, with the hypothesis that *N. cinerea* has reacted to historical climate change through a combination of body size adaptation and relatively localized elevational shifts. Traditional sky island biogeographical theory of western North America posits that habitat may have been more widely available to montane species such as *N. cinerea* during the LGM (Brown, 1971; Waltari & Guralnick, 2009), leading to loss of habitat and demographic declines through the Holocene (Galbreath *et al.*, 2009). However, available niche models qualitatively suggest an increase in suitable *N. cinerea* habitat since the LGM (Waltari & Guralnick, 2009) and thus the potential for localized demographic expansion even in consistently occupied regions of the distribution. We test our predictions of contrasting regional occupancy and demographic patterns using genetic analyses of mitochondrial cytochrome *b* data, clade-specific ecological niche models that allow for differential response across the range of this widespread species, and examination of available palaeomidden records to identify occupancy and abundance across space and time.

MATERIALS AND METHODS

Data collection

We obtained tissues from recently collected specimens (*n* = 70), existing museum specimens (*n* = 91), and existing published and unpublished sequences (*n* = 21) (see Appendix S1 in Supporting Information). We extracted DNA using DNeasy Blood & Tissue Kits (Qiagen, Venlo, The Netherlands) and amplified the complete cytochrome *b* gene (cyt *b*, 1143 bp) using universal primers MVZ05 (Irwin *et al.*, 1991) and MVZ14 (Smith & Patton, 1993) in 15 µL reactions consisting of 1× AccuPrime Buffer II, 0.2 mM MgCl$_2$, 0.4 µM of each primer, and 1.5 units AccuPrime *Taq* DNA polymerase (Invitrogen, Carlsbad, CA, USA). After an initial denaturation at 94 °C for 2 min, we conducted polymerase chain reaction (PCR) via 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 68 °C for 1 min 30 s. We treated templates with ExoSAP-IT (USB Corp., Santa Clara, CA, USA), cycle sequenced with ABI BigDye Terminator v3.1 kits (Applied Biosystems Inc., Carlsbad, CA, USA), and cleaned extension products by gel-filtration (Edge BioSystems, Gaithersburg, MD, USA). We sequenced all templates in both directions using external universal primers MVZ05 and MVZ14, and as needed with internal primers MVZ16 (Smith & Patton, 1993) and cytb2a (Matocq *et al.*, 2007) to resolve ambiguous areas. We

assembled fragments in SEQUENCHER v4.2 (Gene Codes Corporation, Ann Arbor, MI, USA), aligned them by eye, and merged redundant haplotypes in MACCLADE v4.08 (Maddison & Maddison, 2005). We calculated molecular diversity statistics using ARLEQUIN v3.11 (Excoffier *et al.*, 2005) and uncorrected and corrected pairwise (*p*)-distances using PAUP* v4.0b10 (Swofford, 2002).

Phylogenetic analyses

We estimated phylogenetic relationships using several methods for comparison. Our reconstructions (neighbour joining, maximum parsimony and Bayesian inference) were based on complete cyt *b* sequences from *N. cinerea* and nine outgroups (Appendix S1). We performed neighbour-joining analysis in PAUP* v4.0b10 using uncorrected *p*-distances and assessed nodal support using 10,000 bootstrap replicates. We performed maximum parsimony heuristic searches via close-neighbour interchange in MEGA v4.1 (Tamura *et al.*, 2007) using all sites with equal weighting and assessed support using 1000 bootstrap replicates. For the Bayesian analyses, we used MODELTEST v3.7 (Posada & Crandall, 1998) to identify the general time-reversible model GTR + I + Γ as the most appropriate based on the hierarchical likelihood ratio test and Akaike information criterion (AIC). We performed Bayesian inference in MRBAYES v3.1.2 (Huelsenbeck & Ronquist, 2001) with decreased chain-heating temperature of 0.05 from the default 0.2 to aid in chain mixing; all other defaults including uniform priors for I and α were maintained. We conducted two independent runs of four chains each for 20,000,000 generations with sampling every 1000 generations, and removed the first 10% (2,000,000 generations) as burn-in from each run before summarizing in a majority-rule tree. Burn-in was determined by visually checking for likelihood stationarity in TRACER v1.4 (Rambaut & Drummond, 2007), as well as with Are We There Yet (AWTY) plots of topological convergence, including particularly the 'Compare' and 'Cumulative' analyses (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008). 'Compare' plots the posterior probabilities of all splits (nodes) between runs, and should show points along the diagonal to indicate that the posterior probabilities of each split were comparable between independent runs. 'Cumulative' plots the posterior probabilities of the most variable splits through time for each run, and should show overall stationary trends to indicate that the proper burn-in has been discarded.

Divergence time estimation

We estimated divergence dates of the major *N. cinerea* clades and subclades in BEAST v1.4.8 (Drummond & Rambaut, 2007) to consider whether these dates correlated with known biogeographical events. To develop a fossil-calibrated estimate of the rate of molecular evolution, we added additional outgroup taxa (Appendix S1) and reduced our intraspecific dataset to include one representative from each of the five major *N. cinerea* subclades. To calibrate the trees, we

constrained tribe Neotomini (woodrats of genera *Neotoma*, *Hodomys* and *Xenomys*; Reeder *et al.*, 2006) to monophyly and applied a uniform age prior of 10.3–13.6 million years ago (Ma) representing the oldest known woodrat fossil from the Clarendonian North American Land Mammal Age (Reynolds, 1991). We applied a Yule process speciation prior with the GTR + I + Γ model indicated by AIC in MODELTEST, and performed two analyses assuming a relaxed uncorrelated lognormal clock (Drummond *et al.*, 2006) and a strict clock, respectively. To test for deviance from a strict clock, we assessed the distribution of the relaxed clock coefficient of variation in TRACER v1.4 (Rambaut & Drummond, 2007); if the distribution of variation in branch rates includes zero, the rates are similar enough that a strict clock cannot be rejected (Drummond *et al.*, 2007). For each analysis we conducted two independent runs of 10,000,000 generations, with trees sampled every 1000 generations. We used TRACER v1.4 to determine a burn-in of 20% (2,000,000 generations) and to ensure all parameters of interest in the combined trace files had effective sample sizes (ESS) > 200. We also assessed topological convergence using AWTY plots as described above (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008). We combined independent runs for each analysis into maximum clade credibility trees using LOGCOMBINER v1.4.6 and TREEANNOTATOR v1.4.6 in the BEAST package.

From the strict clock analyses we derived a rate of molecular evolution and performed an intraspecific analysis to estimate dates of divergence for internal nodes; our dataset for this consisted of all intraspecific haplotypes including identical sequences. We assumed a Bayesian skyline coalescent tree prior allowing variable population size (Drummond *et al.*, 2005) and edited the BEAUTI v1.4.8 .xml file to apply the transitional model TIM + I + Γ indicated by AIC in MODELTEST. We conducted six independent runs of 20,000,000 generations sampled every 5000 generations. Results were assessed using TRACER v1.4 and AWTY, as above.

Demographic analyses

To test for evidence of recent demographic expansion, we performed tests of Tajima's *D*, Fu's F_S and mismatch distribution analyses as implemented in ARLEQUIN v3.11. For these analyses, we partitioned all haplotypes including identical sequences into eight clades and subclades based on monophyly, population size and overall support across all three phylogenetic reconstructions (see Results). Tajima's *D* compares two estimates of θ based on the number of segregating sites (θ_S) and the average number of mismatches between sequences (θ_Π). Negative values of *D* may be evidence of recent population expansion (Tajima, 1989a,b; Excoffier *et al.*, 2005). Fu's F_S compares the observed number of alleles (k_O) to the expected number of alleles (*k*) given an observed θ_Π, and negative values of F_S may similarly indicate recent population expansion. Interpretation of these statistics should be tentative as selective forces can create the same patterns, although Fu's F_S is considered to be more specifically indicative of

population expansion (Fu, 1997; Excoffier *et al.*, 2005). We based tests of Tajima's *D* and Fu's F_S on 1000 simulated samples generated by a coalescent algorithm assuming no selective pressure and constant population size. We also generated mismatch distributions, which may provide additional evidence of recent expansion based on the modality of the frequency of pairwise differences between samples. A ragged or multimodal distribution may indicate the influence of population stability and lineage sorting, while a unimodal distribution may indicate expansion according to the stepping-stone model (SSM; Rogers & Harpending, 1992; Schneider & Excoffier, 1999). We compared observed mismatch distributions to simulated distributions assuming a SSM null model based on 500 bootstraps.

Ecological niche modelling

We performed ecological niche modelling to estimate the extent of potentially suitable *N. cinerea* habitat during the modern climate and palaeoclimate at the LGM, with the goal of linking qualitative changes in habitat extent with genetic and palaeomidden information. Occurrence records to develop the models came from MaNIS (http://manisnet.org/, accessed 27 July 2007) and ARCTOS (http://arctos.database.museum/home.cfm, accessed 27 July 2007) databases, as well as available databases of individual museums not yet networked. Records were restricted to dates from 1950 to present and with ≤ 1 km coordinate uncertainty to reflect the time period and resolution of climate layers. Models for the entire species have been developed elsewhere (Waltari & Guralnick, 2009); we chose to develop models for major clades and subclades discovered in our phylogenetic analyses to investigate the potential for region-specific distributional dynamics through time. We determined clade membership based on molecular information or, where lacking, location within geographical clade boundaries; samples falling outside or along clade boundaries were discarded.

We downloaded 19 modern bioclimatic (BIOCLIM) variables at 30 arc-second (*c.* 1 km^2) resolution from WorldClim v1.4 (Hijmans *et al.*, 2005; http://www.worldclim.org) and extracted climatic data for each collection point using DIVA-GIS 7.1.7.2 (Hijmans *et al.*, 2001) to calculate pairwise Pearson correlation coefficients between variables. We discarded variables until all correlations were $|r| < 0.8$; this is a somewhat more lax threshold than applied elsewhere (Rissler *et al.*, 2006; Kumar & Stohlgren, 2009; Stephens & Wiens, 2009) but allowed us to use the same variables for each clade model and thus make the subclade models more comparable. Variables were discarded or retained based on ease of interpretation and biological relevance suggested by previous studies (Smith & Betancourt, 2003; King, 2008). Ten variables were included in these models: bio2 (mean diurnal temperature range), bio4 (temperature seasonality), bio8 (mean temperature of the wettest quarter), bio9 (mean temperature of the driest quarter), bio10 (mean temperature of the warmest quarter), bio11 (mean temperature of the coldest quarter), bio15 (precipitation seasonality), bio16 (precipitation of the wettest quarter), bio17 (precipitation of the driest quarter), and bio18 (precipitation of the warmest quarter). We developed models in MAXENT 3.3.1 (Phillips *et al.*, 2006) restricted to North America between 15–75° N and 60–165° W, excluded 25% of samples from model training for testing purposes, and replicated models with 10-fold cross-validation. These models were projected to the LGM (18,000 ^{14}C yr BP; 21,000 cal. yr BP) ECHAM3 palaeoclimate reconstruction (DKRZ, 1992; Lorenz *et al.*, 1996; available from http://mvzgis.wordpress.com/), involving the same set of BIOCLIM variables used for model development.

Palaeorecord

We compiled palaeorecords of *N. cinerea* from midden and cave deposit strata databased through FAUNMAP (Graham & Lundelius, 2010), the USGS/NOAA North American Packrat Midden Database (http://esp.cr.usgs.gov/data/midden/), Grayson's supplementary data (Grayson, 2006; available from http://dx.doi.org/10.1016/j.quascirev.2006.03.004), and primary literature. All dates are presented in ^{14}C radiocarbon years BP unless otherwise noted. We relied on samples positively identified from other *Neotoma* species by molar, mandibular, or faecal pellet morphology or size, and augmented this dataset by interpreting presence of palaeomiddens as presence of *N. cinerea* in areas where congeners are unlikely (British Columbia, Montana and northern Wyoming). To illustrate broad spatio-temporal trends, we sorted records into four groups based on FAUNMAP and Grayson's (2006) divisions: 14,000 yr BP and older, representing full glacial and pluvial lake extents; 8000–14,000 yr BP representing the Pleistocene–Holocene transition marked by rapid glacial retreat (Dyke, 2004) and pluvial lake level drops (Benson, 2004); the comparatively arid middle Holocene 4000–8000 yr BP (Benson *et al.*, 2002); and the late Holocene 4000 yr BP and younger. To illustrate localized trends through time in the Great Basin region, we further examined a subset of palaeomidden profiles for which the most complete information including radiocarbon dates across multiple strata was available. We discarded strata with numbers of identified specimens (NISP) < 100 to help minimize spurious values attributable to sampling; when available and unless otherwise noted, the more specific percentage NISP (%NISP) of mammals was used. To summarize the data and make them comparable across temporal profiles, we binned strata into 1000 year intervals (0–1000 yr BP, 1000–2000 yr BP, etc.) and averaged across strata in each interval to produce the mean %NISP of mammals identified as *N. cinerea*.

RESULTS

We identified 120 unique cyt *b* haplotypes from 182 *N. cinerea* specimens (GenBank accession numbers JN593120–JN593237). Average nucleotide composition across all sites was A = 32.1%, C = 26.9%, G = 13.3% and T = 27.7%, and

the ratio of transitions to transversions was 4.1–1. Of 1143 nucleotides sites, 266 were variable including 79 singletons. Of 381 amino acid positions, 57 showed variability due to non-synonymous substitutions. Thirteen of these sites showed rare amino acid substitutions based on the empirically derived BLOSUM62 substitution matrix, which could reflect changes in protein functionality (Henikoff & Henikoff, 1992; Eddy, 2004); however, 10 of those 13 are at sites known to be variable in mammals and located in protein domains presumed to be of lower functional importance (Irwin *et al.*, 1991). The remaining three sites showed amino acid substitutions in only $n = 1$, 1 and 3 specimens respectively, confirming the rarity of these changes. Thus, *N. cinerea* cyt *b* sequences appear highly conservative with respect to functionality, and consistent with our understanding of the evolutionary constraints on this crucial gene.

Phylogenetic analyses

Trees constructed via all three phylogenetic methods were nearly identical in topology and largely comparable in nodal support. Two major clades with generally strong uncorrected neighbour-joining bootstrap (NJ), maximum parsimony bootstrap (MP), and Bayesian posterior probability (PP) support are evident: the Eastern clade and the Western clade (Fig. 1). There is moderate haplotype sequence divergence between these clades, with an average uncorrected *p*-distance of 6.5% (max = 7.6%, min = 5.4%), while distances within clades average 1.7% (max = 3.5%, min = 0.1%) in the Eastern clade and 2.6% (max = 4.6%, min < 0.1%) in the Western clade. Corrected divergence estimated using the GTR + I + Γ model was on average 8.8% (max = 10.8%, min = 6.9%) between the Eastern and Western clades.

Geographically, the Eastern clade is confined to regions east of the Colorado and Green rivers, while the Western clade is found across a broad area encompassing the majority of the species' range (Fig. 2). These clades are allopatric with the exception of one known location of sympatry in western South Dakota. There are five well-supported subclades within these major clades, including two in the Eastern clade (Southern Rocky Mountains, SRO; Middle Rocky Mountains, MRO), and three in the Western clade (Pacific Northwest, PNW; Northern, NOR; Intermountain, INT). Geographical distribution of the NOR subclade is complicated by two haplotypes found in the Sierra Nevada, disjunct from the remainder of the NOR clade; we refer to these as the Northern disjunct (NORd). Likewise, the Intermountain subclade has a major phylogeographical disjunct (INTd), a collection of five haplotypes that are paraphyletic and allopatric to the remainder of the INT subclade. We refer to the bulk of the INT subclade exclusive of this disjunct as Intermountain main (INTm).

Figure 1 Majority-rule Bayesian phylogram showing major clades and subclades of *Neotoma cinerea* in western North America, constructed using cytochrome *b* data and the GTR + I + Γ model. Major nodes are labelled with neighbour-joining bootstrap values (NJ), maximum parsimony bootstrap values (MP), and Bayesian posterior probabilities (PP), respectively. Abbreviations: WEST, Western clade; EAST, Eastern clade; INT, Intermountain subclade; INTm, Intermountain main; INTd, Intermountain disjunct; NOR, Northern subclade; NORd, Northern disjunct; PNW, Pacific Northwest subclade; MRO, Middle Rocky Mountains subclade; SRO, Southern Rocky Mountains subclade.
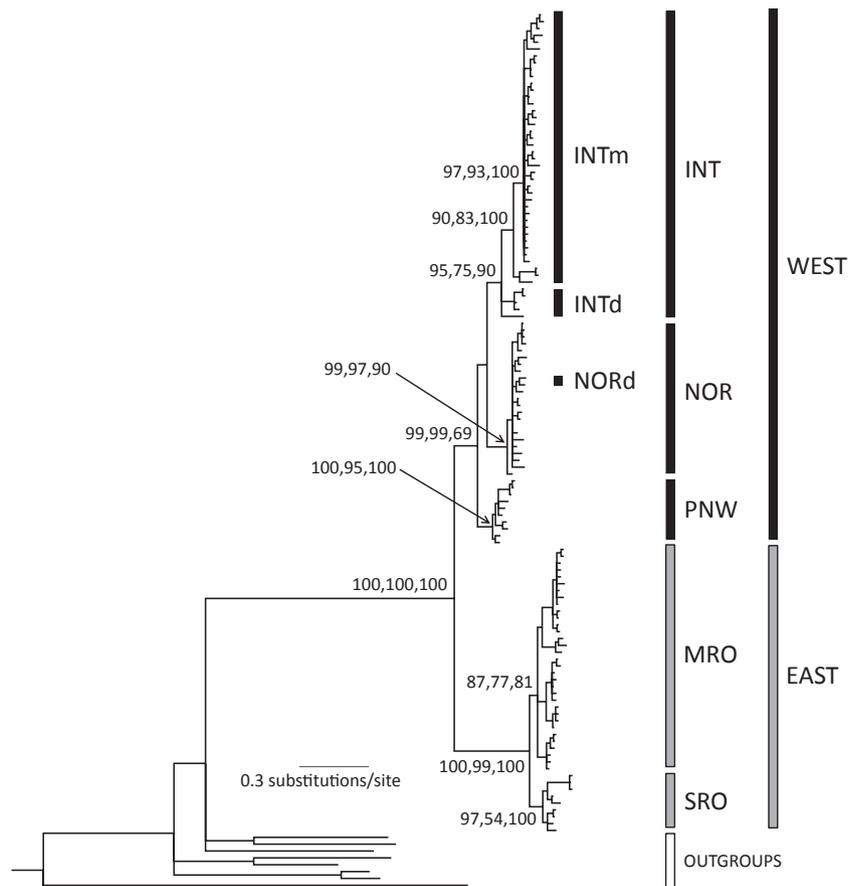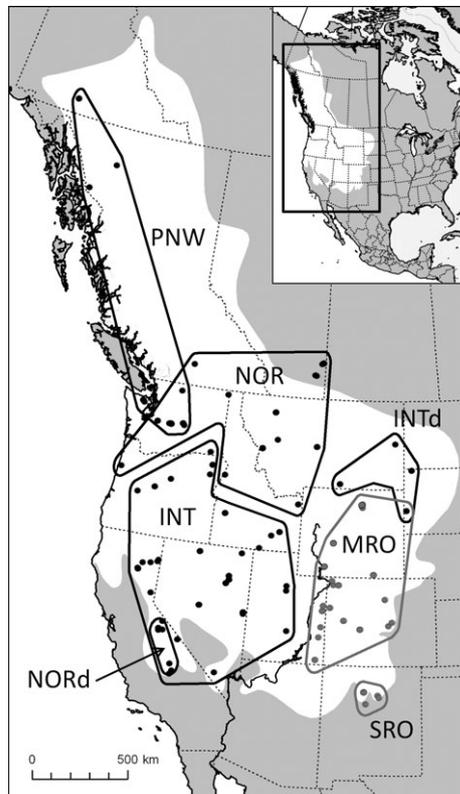
Figure 2 Extent and overlap of major *Neotoma cinerea* clades in western North America. Eastern clade points are marked with grey circles and bounded with heavy grey lines; western clade points are marked with black circles and bounded by heavy black lines. Major phylogenetic subclades are marked with abbreviations (see Fig. 1 for definitions). The range of *N. cinerea* (Hall, 1981) is shown in white, and the Green and Colorado rivers are represented by a heavy black line.

Divergence time estimation

The interspecific analysis using a relaxed uncorrelated lognormal clock showed a coefficient of variation distribution abutting zero, akin to a failure to reject the null hypothesis of a strict molecular clock (Drummond *et al.*, 2007); we therefore report the results of the strict clock analysis. The strict clock rate was estimated at an average 1.764×10^{-2} substitutions per site per million years; by multiplying by 2 to represent divergent lineages, and 100 to present as a percentage, this rate is comparable to about 3.5% corrected sequence divergence per million years. This is within the widest range of divergence rates (2–10%) applied as rodent cyt *b* molecular clocks, but considerably lower than the 6–10% rate often inferred for smaller rodents such as voles and mice (Conroy & Cook, 2000b; Harris *et al.*, 2000; Brunhoff *et al.*, 2003; Degner *et al.*, 2007; Ahmed *et al.*, 2008). Our calculated rate may be slightly low and thus estimating divergence dates to be relatively old; for instance, the time since the most recent common ancestor (TMRCA) for the neotomine–peromyscine complex was 14.86 Ma [95% highest posterior density (HPD) 12.07–17.98 Ma], older than reported estimates of *c.* 8–14 Ma (Engel *et al.*, 1998; Steppan *et al.*, 2004; León-Paniagua *et al.*, 2007). However, we present results based on our calculated clock because independent, fossil-calibrated rates of cyt *b* evolution are rare in rodents. When applied to the intraspecific analysis, this rate estimated the divergence date between the Eastern and Western clades as 2.77 Ma (95% HPD of 2.17 to 3.41 Ma); the TMRCA for other major clades and subclades are reported in Table 1.

Spatial and demographic analyses

Following the phylogenetic tree results, groups defined for demographic expansion tests included the five major subclades noted (Fig. 1; Table 1). To better illustrate trends in the INT subclade, we analysed both the INT subclade and INTm subclade excluding the disjunct taxa. Tajima's *D* and Fu's F_S results were largely in agreement, although only the NOR ($P_D = 0.010$, $P_F = 0.015$), INT ($P_D = 0.008$, $P_F < 0.001$), and INTm ($P_D = 0.004$, $P_F < 0.001$) subclades showed values that were statistically significant (D $\alpha = 0.05$; F_S $\alpha = 0.02$). The mismatch distributions suggest recent expansion for all

Table 1 *Neotoma cinerea* summary statistics including number of samples (*n*); number of haplotypes (*k*); number of segregating sites (*S*); expansion test results for Tajima's *D* and Fu's F_S; and time since the most recent common ancestor (TMRCA) with 95% highest posterior density (HPD) for major clades and subclades in western North America.

Clade	N	k	S	D (P-value)	F_S (P-value)	TMRCA Ma (95% HPD)
Total	182	120	266	0.16 (0.665)	−23.89 (0.001)*	2.77 (2.17–3.41)
Eastern	71	42	117	−0.89 (0.204)	−7.19 (0.065)	0.85 (0.61–1.09)
Southern Rocky Mountains (SRO)	10	9	38	0.22 (0.641)	−0.87 (0.259)	0.43 (0.27–0.60)
Middle Rocky Mountains (MRO)	61	33	79	−0.54 (0.309)	−4.72 (0.112)	0.62 (0.46–0.80)
Western	111	78	203	−0.90 (0.182)	−23.63 (0.001)*	1.27 (0.97–1.58)
Pacific Northwest (PNW)	11	10	32	−0.52 (0.325)	−2.31 (0.093)	0.29 (0.19–0.41)
Northern (NOR)	37	23	69	−1.87 (0.010)*	−6.56 (0.015)*	0.33 (0.22–0.46)
Intermountain (INT)	63	45	129	−1.84 (0.008)*	−19.85 (< 0.001)*	0.82 (0.61–1.04)
Intermountain main (INTm)	57	40	102	−1.97 (0.007)*	−20.62 (< 0.001)*	0.53 (0.38–0.70)

*Statistically significant at D $\alpha = 0.05$ and F_S $\alpha = 0.02$.
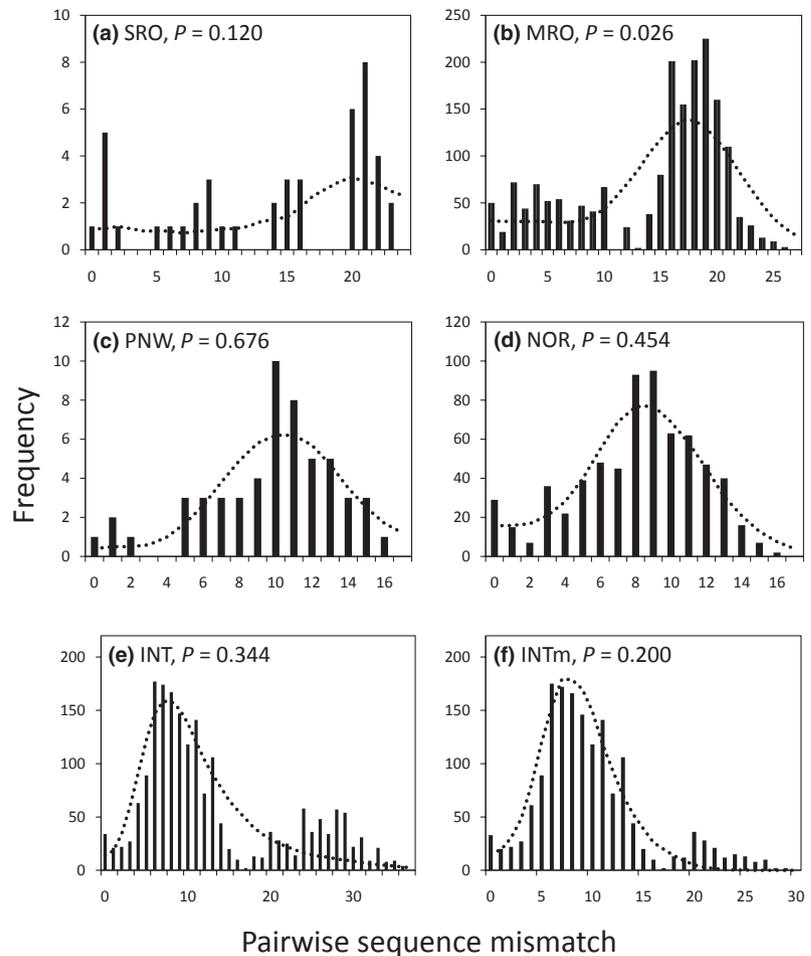
Figure 3 Mismatch distributions for major *Neotoma cinerea* subclades in western North America. Observed data are shown as bars. Simulated data representing the null stepping-stone model (SSM) of population expansion are shown as dotted lines, and *P*-values indicate deviations from the SSM expectation. (a) Southern Rocky Mountains (SRO), (b) Middle Rocky Mountains (MRO), (c) Pacific Northwest (PNW), (d) Northern (NOR), (e) Intermountain (INT), (f) Intermountain main (INTm).

subclades based on conformity to the SSM (Fig. 3), with the exception of the MRO subclade (*P* = 0.026); the SRO subclade shows a strongly multimodal pattern suggestive of no recent expansion, but failed to reach the significance threshold perhaps due to the small sample size, *n* = 10. Apparent biomodality in the INT subclade is due to inclusion of the disjunct taxa, as analysis of the INTm subclade shows a more strongly unimodal pattern consistent with population expansion.

Ecological niche modelling

We developed niche models for three groups (Eastern MRO + SRO, *n* = 80; NOR, *n* = 20; INTm, *n* = 78) based on sufficient sample sizes and areas of geographical interest. All models performed well, showing high area under the curve (AUC) values for the receiver operating characteristic (ROC) curves. AUCs are measures of overall accuracy in assigning presence and absence and range from zero to one, with one indicating perfect accuracy. AUCs for each clade expressed as mean of ten replicate models ± standard deviation are as follows: MRO + SRO 0.981 ± 0.007; NOR, 0.944 ± 0.023; INTm, 0.984 ± 0.003. These models also passed all 11 Maxent test statistic standards for significantly better performance than random.

Modern and projected LGM palaeoclimate models did not show substantial qualitative differences for the Eastern SRO + MRO clade, with discontinuous but highly probable areas of occupancy both east and west of the Green and Colorado rivers (Fig. 4); this includes large areas in the Intermountain West where the Eastern clade is not currently found (Fig. 2). The NOR subclade likewise showed little difference between modern and LGM models, with highly probable habitat in the Pacific Northwest, Great Basin, central Rocky Mountains and Sierra Nevada, although the current range of that subclade is restricted to northern United States and southern Canada. In contrast, the INTm subclade showed dramatic differences between the modern and LGM models. The modern model suggests suitable habitat primarily across the Great Basin where this group is currently found, whereas the LGM model indicates that habitat was historically restricted to areas at the northern and southern edges of this region.

Palaeorecord

We compiled over 500 strata palaeorecords of *N. cinerea* representing 131 unique localities. Spatio-temporal sampling of palaeomiddens is highly variable, yet broad geographical
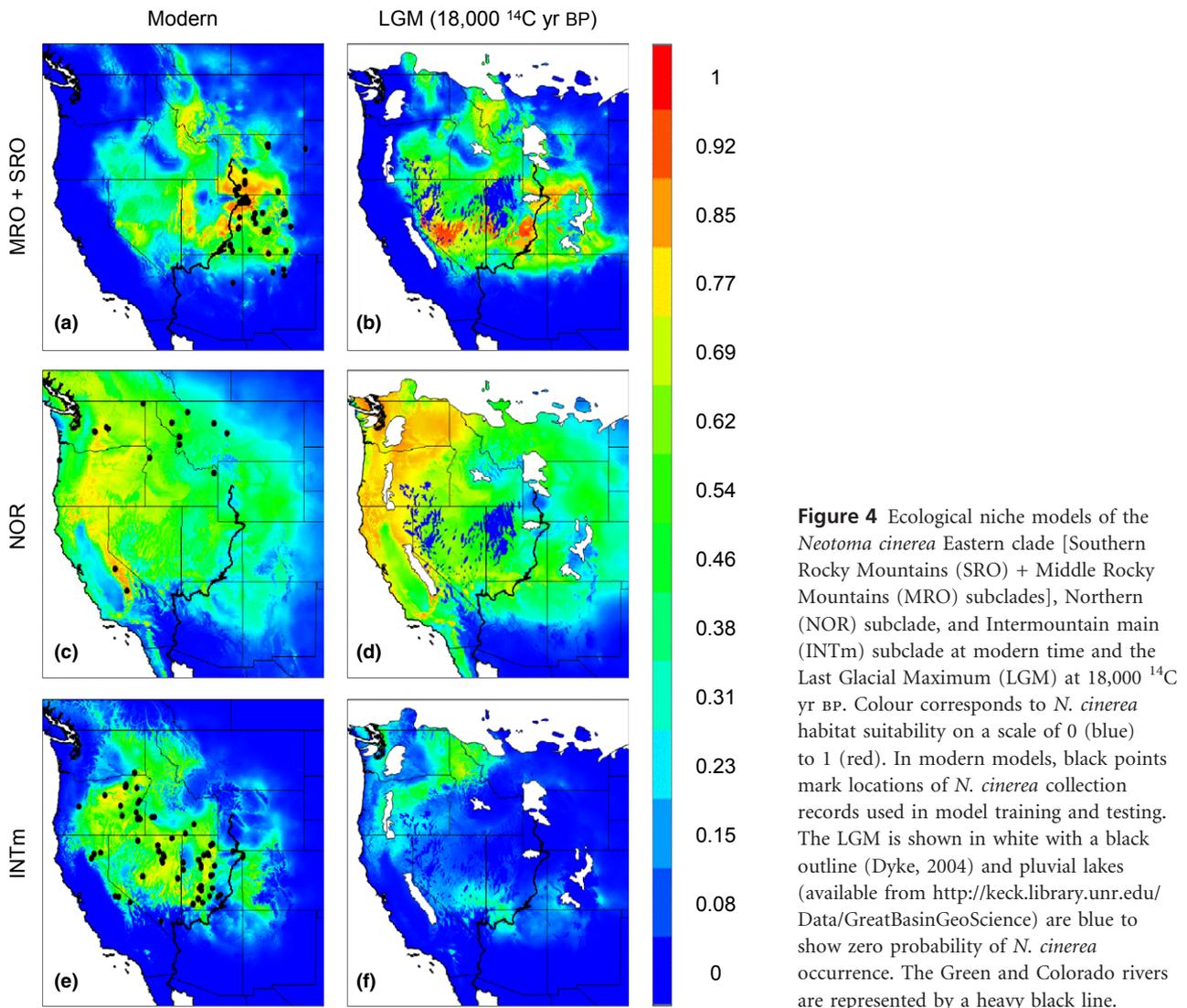
Figure 4 Ecological niche models of the *Neotoma cinerea* Eastern clade [Southern Rocky Mountains (SRO) + Middle Rocky Mountains (MRO) subclades], Northern (NOR) subclade, and Intermountain main (INTm) subclade at modern time and the Last Glacial Maximum (LGM) at 18,000 ^{14}C yr BP. Colour corresponds to *N. cinerea* habitat suitability on a scale of 0 (blue) to 1 (red). In modern models, black points mark locations of *N. cinerea* collection records used in model training and testing. The LGM is shown in white with a black outline (Dyke, 2004) and pluvial lakes (available from http://keck.library.unr.edu/Data/GreatBasinGeoScience) are blue to show zero probability of *N. cinerea* occurrence. The Green and Colorado rivers are represented by a heavy black line.

distributional trends were seen particularly at the southern and northern range boundaries. As noted elsewhere (Harris, 1984, 1993), records of *N. cinerea* occur south of the current range limit until *c.* 8000 yr BP (Fig. 5) suggesting localized extirpation and range contraction after that time. Consistent with a northward distributional shift, records occur in northern regions (Alberta, British Columbia, Montana, Washington) more frequently through the time series, with the exception of records in south-western Alberta, which date to > 23,000 yr BP (Fig. 5a).

Trends showing localized declines in the number of *N. cinerea* through time from *c.* 8000–12,000 yr BP through the mid-Holocene 4000–8000 yr BP are evident in a subset of palaeomiddens (Fig. 6). Declines were seen in Hidden Cave in west–central Nevada (based on total %NISP; Grayson, 1985); Danger Cave (Grayson, 1987, 1988), Hogup Cave (Durrant, 1970), and the well-sampled and described Homestead Cave (Grayson, 2000a) in north-west Utah; and Camels Back Cave in west–central Utah (Schmitt *et al.*, 2002; Schmitt & Lupo, 2005). A similarly timed decline is seen at Pintwater Cave in

southern Nevada (Hockett, 2000), although no records < *c.* 7000 yr BP are available and thus the trajectory of the trend through modern times is unknown. Two palaeomidden profiles showed different patterns: Gatecliff Shelter in central Nevada (Grayson, 1983) showed consistently high numbers, with a potential decline in the late Holocene *c.* 2000 yr BP, and Wilson Butte Cave in southern Idaho (Gruhn, 1961) showed a trend of markedly increasing numbers of *N. cinerea* (based on small mammal %NISP).

DISCUSSION

Divergence and comparative phylogeography

Our phylogenetic analyses identified two largely allopatric clades within *N. cinerea*, which are spatially consistent with groups previously identified based on classical morphological techniques (e.g. Merriam, 1893, 1894). Given the consistency of our mtDNA phylogenetic results with past analyses and our recent re-examination of morphology (A.D. Hornsby & M.D.
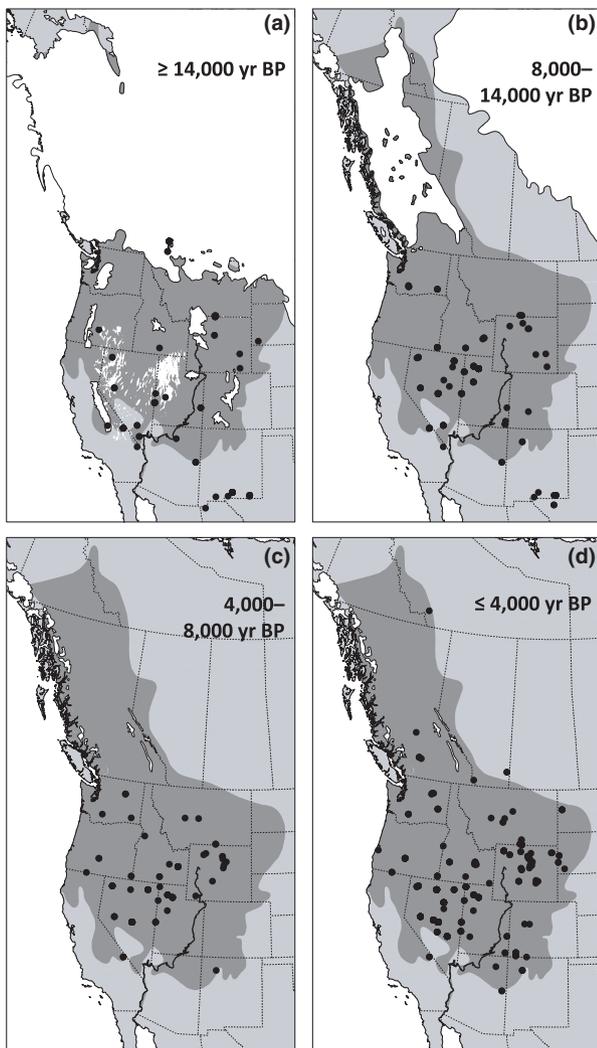
Figure 5 Spatial patterns of *Neotoma cinerea* palaeomidden records (black points) in western North America at four time intervals since the Last Glacial Maximum (LGM). Glaciers are shown in white with black outlines and represent the ice extent at the median age of each panel, with the exception of panel (a) showing the LGM at 18,000 ^{14}C yr BP (*c.* 21,000 cal. yr BP; Dyke, 2004). White regions without outlines represent pluvial lakes, the heavy black line represents the Green and Colorado rivers, and the darker grey region represents the modern *N. cinerea* range (Hall, 1981).

Matocq, in prep.) we are confident that mtDNA variation reflects a major divergence in the history of this taxon, although future examination of nuclear loci will undoubtedly refine our results.

The divergence time between the Eastern and Western clades falls near the Pliocene–Pleistocene transition at 2.58 Ma (Gibbard *et al.*, 2010), and allopatry may have been initiated and maintained through this time by major biogeographical barriers in two specific regions. In the north, onset of major Rocky Mountain glaciations may have divided the clades beginning at the Pliocene–Pleistocene transition and continuing cyclically during Pleistocene glacial periods. Glaciers

covered high elevation areas in the Yellowstone region of north-west Wyoming, and periglacial alpine permafrost was widespread from Colorado through western and central Wyoming, western Montana, and eastern and central Idaho (Péwé, 1983; Dyke, 2004). These conditions probably impeded *N. cinerea* regional habitation, and are reflected elsewhere as low probabilities of *N. cinerea* occurrence in the full-species palaeoclimate model (Waltari & Guralnick, 2009). Further south, the Green River and upper Colorado River may separate the major clades via dispersal limitation. This is a similarly effective barrier in other small mammals (Findley & Anderson, 1956; Riddle *et al.*, 2000; Wilson *et al.*, 2005; Patton *et al.*, 2008), and there is no evidence that Pleistocene avulsions of the lower Colorado River have allowed contact or mixing of the *N. cinerea* clades in this region (e.g. Jezkova *et al.*, 2009).

Swenson & Howard (2004, 2005) showed that boundaries such as contact zones, hybrid zones and phylogeographical breaks are spatially clumped across mammalian, avian and plant taxa. The occurrence of suture zones supports the intuitive prediction that the same geographical and climatological constraints, such as barriers to dispersal and expansion from refugia, may manifest as similar patterns of variation across taxa (Swenson & Howard, 2004, 2005). One of the major suture zones in western North America involves a continuous series of roughly east–west splits along the Rocky Mountains from New Mexico to central British Columbia (Swenson & Howard, 2005), spanning much of the latitudinal range of *N. cinerea* and roughly dividing the two major clades found here. Similar splits are found along this suture zone, particularly in the Rocky Mountains from Idaho and Montana through the Yellowstone region in north-west Wyoming, in other small mammal taxa including *Tamias* (*Neotamias*) *ruficaudus* and the *T.* (*N.*) *ameonus-ruficaudus* group (Good & Sullivan, 2001; Good *et al.*, 2003; Hird & Sullivan, 2009), *Spermophilus armatus* (van Tuinen *et al.*, 2008), and *Microtus longicaudus* (Conroy & Cook, 2000a; Spaeth *et al.*, 2009).

While phylogeographical patterns such as intraspecific divergences may be primarily attributable to large-scale vicariant forces with small-scale stochastic processes such as lineage sorting, they may also be explained through differences in species' ecologies which affect individualized reactions to climate and terrain. Unlike many taxa, including several species of small mammals, *N. cinerea* does not show a split along one of the other major suture zones in North America which divides coastal and continental groups through Washington and Oregon (Arbogast *et al.*, 2001; Brunsfeld *et al.*, 2001; Demboski & Cook, 2001; Carstens *et al.*, 2005; Galbreath *et al.*, 2009; Chavez & Kenagy, 2010; Shafer *et al.*, 2010). This split in other taxa presumably arose during uplift of the Cascade and Sierra Nevada mountains *c.* 2–5 Ma and the subsequent aridification of the Columbia Basin (Brunsfeld *et al.*, 2001; Shafer *et al.*, 2010). Although *N. cinerea* is classically considered a montane species (Brown, 1971), it is found in relatively arid regions and thus may not show this coastal–continental split because it can inhabit or effectively
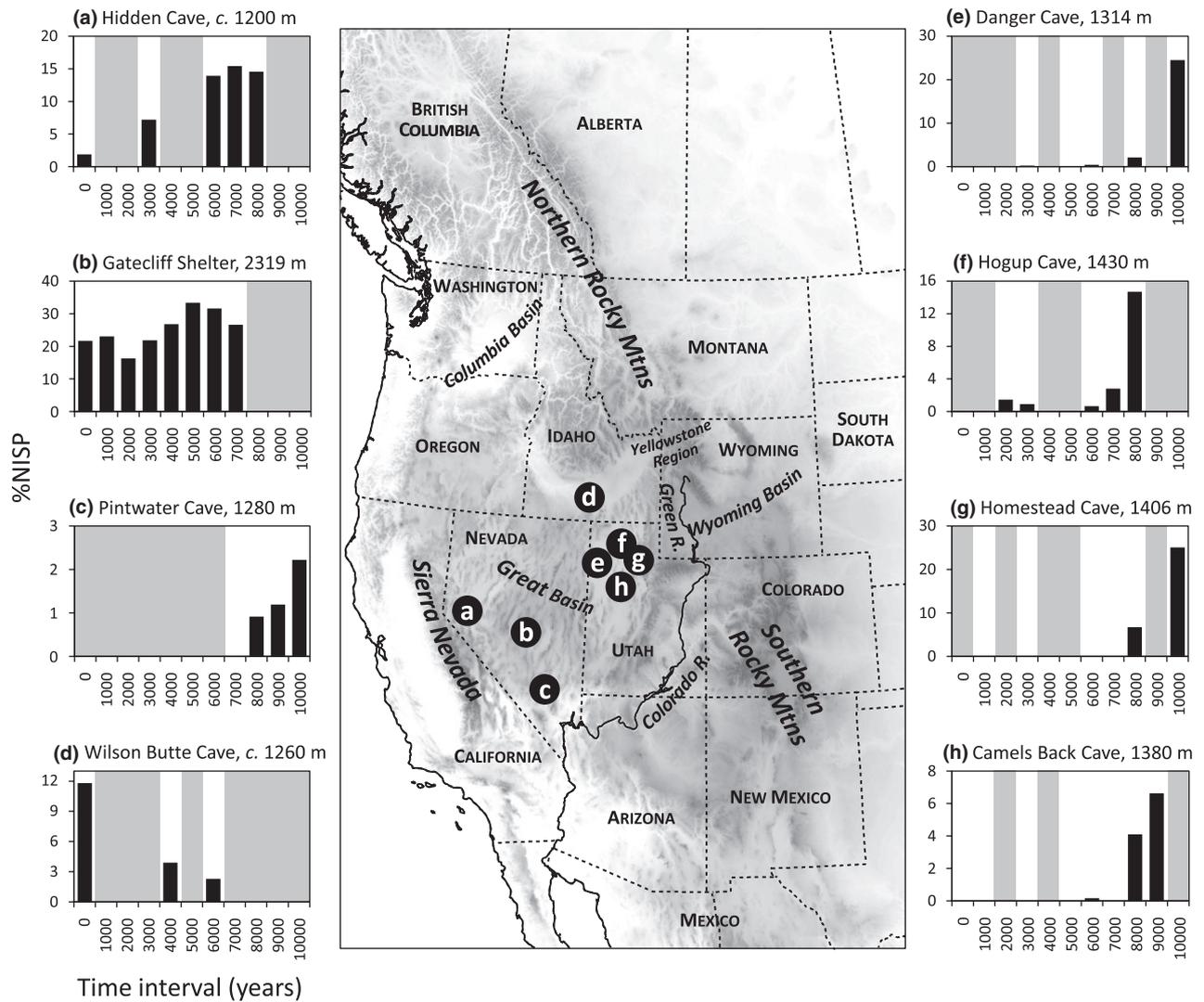
Figure 6 Temporal patterns of *Neotoma cinerea* palaeomidden records through the Holocene at localized points in the Great Basin. The *x*-axis is divided into 1000-year bins labelled by minimum age; bins for which no data were available are shaded grey. The *y*-axis displays the average percentage number of identified specimens (%NISP) of mammals identified as *N. cinerea* with the exception of (a) Hidden Cave, which is based on the %NISP of total specimens and (d) Wilson Butte Cave, which is based on the %NISP of small mammals. The location of each palaeomidden and regional topography (higher elevations as darker grey) are shown on the centre panel.

disperse through basin areas that would more completely restrict other forest and montane species. Indeed, *N. cinerea* appeared in the Columbia Basin as it became warmer and drier through the Pleistocene–Holocene transition (Lyman & Livingston, 1983) and is found there in modern times. *Neotoma cinerea* also does not appear to have been split or restricted as other species by the relatively low and flat Wyoming Basin (Demboski & Cook, 2001; Wilson *et al.*, 2005) or by high elevations in north–central Colorado (Wilson *et al.*, 2005; Galbreath *et al.*, 2009), and the absence of these splits in *N. cinerea* compared to other montane species may be attributable to its flexibility in habitat and denning behaviours. For instance, *Tamiasciurus hudsonicus* is obligate to forested habitats (Steele, 1998), making the unforested Wyoming Basin a major barrier and the site of a phylogeographical break; *N. cinerea* is found in both forested and unforested habitats

(Smith, 1997) and thus is not restricted in the same fashion. Likewise, *Ochotona princeps* is obligate to higher elevation rock and talus habitats (Smith & Weston, 1990), which may have been heavily glaciated in north–central Colorado intermittently through the Pleistocene to cause a phylogeographical break. Although *N. cinerea* is generally highly reliant on rocky outcrops, it is more flexible in its structural requirements and will den among boulders, crevices, lava flows, and even in trees, which could allow persistence in the absence of talus or other specific rock formations (Carey, 1991; Smith, 1997).

Biogeographical history: deglaciated north

Northern regions of the *N. cinerea* range that were recently deglaciated are currently inhabited by the PNW and NOR subclades, which probably expanded into much of these areas

following the LGM. In the far north across Canada, our inferences regarding the PNW subclade are limited by sparse sampling ($n = 11$), although the unimodal mismatch distribution suggests recent colonization. Along with this mismatch pattern, previous niche models (Waltari & Guralnick, 2009) and the absence of a distinct clade in northern Canada suggest that *N. cinerea* did not expand into northern regions from high-latitude glacial refugia after the LGM.

At the southern LGM limit across the northern contiguous United States, all demographic tests suggest recent expansion of the NOR subclade. We infer that this expansion occurred following the LGM because much of this region was glacial or periglacial in the LGM (Péwé, 1983) and because the modes of the PNW and NOR mismatch distributions are comparable, with the same degree of divergence suggesting expansion in similar timeframes. In contrast, the NOR subclade niche model suggests that habitat like that of its modern range was similarly distributed at the LGM compared to today, which could suggest recent population stability since the LGM. The niche model and disjunct distribution of NORd haplotypes in the Sierra Nevada may also indicate a previously broader distribution of this clade along this mountain range, and even through the Great Basin, as recently as the LGM.

The palaeomidden record in this region is more consistent with the hypothesis of recent colonization inferred from genetic patterns than large-scale stability suggested by the niche model. Some of the oldest *N. cinerea* records are in south-west Alberta between 23,000 and 50,000 yr BP (Fig. 5a; Burns, 1991), dating to a relatively warmer late-Wisconsinan interstadial period prior to the glacial growth starting *c.* 33,000 cal. yr BP (25,000 ^{14}C yr BP) which climaxed in the LGM (Clark *et al.*, 2009). Lack of records in the period 4000–23,000 yr BP suggests regional extirpation in the far north through the LGM. Similarly, there are no records of *N. cinerea* in the northern states of Washington, Idaho and most of Montana for sites dating to ≥ 14,000 yr BP, and the appearance of records further north through time (Fig. 5b–d) is suggestive of wide scale recolonizations following glacial retreat. This culminated in the recolonization of Canada and the oldest post-LGM Canadian records of < 4000 yr BP in Alberta and British Columbia and < 2500 yr BP farther north in the Northwest Territories (Fig. 5d).

Biogeographical history: Rocky Mountains

In contrast to subclades of the deglaciated North, the Eastern clade of the Rocky Mountains appears to have occupied most of its modern range for tens of thousands of years based on concordant demographic, niche model and palaeomidden evidence. The lack of strong signs of demographic expansion in the SRO and MRO subclades is consistent with ecological niche model results, which show comparable patterns in the range and suitability of habitat from the LGM to today (Fig. 4). Although the modern and LGM models suggest that suitable habitat exists in the Great Basin and northern Rocky Mountains, the Eastern clade is not found there and, thus, may

not be in species–climate equilibrium, perhaps due to dispersal limitation by aforementioned glacial and river barriers (Nogués-Bravo, 2009).

The lack of conspicuous changes in range boundaries of the Eastern clade niche model is mostly consistent with the palaeomidden record. At the northern boundary of this clade, records of *N. cinerea* are relatively old, including > 40,000 yr BP in southern Montana (Fig. 5a; Wells, 1983). Additional records from northern Wyoming suggest that *N. cinerea* occupied these areas consistently through and since the LGM (Fig. 5b–d; Mead, 1982; Lyford, 2001; Smith & Betancourt, 2006); thus, populations in this region may have persisted roughly *in situ* through numerous Pleistocene stadial/glacial cycles. At the southern boundary, the palaeomidden record suggests a retraction of the range from southern New Mexico at the LGM to central New Mexico currently (Hall, 1981; Harris, 1984, 1993), although this is not reflected by the niche model. This lack of large scale range boundary shifts is consistent with the expectation that, as a montane species, *N. cinerea* reacted to climate change primarily through elevational rather than latitudinal range shifts (Guralnick, 2007) and/or that it reacted to climate via demonstrated patterns of body size change (Smith *et al.*, 1995; Smith & Betancourt, 2006). One curiosity in this region is the paraphyletic INTd subclade, which may have originally dispersed to the middle Rocky Mountains during a warmer Pleistocene interglacial period, and subsequently became isolated from the remainder of the INT clade by the same cycles of Rocky Mountain glaciation that restricted the Eastern clade through the LGM (Péwé, 1983).

Biogeographical history: Great Basin

The Great Basin is of particular interest from a biogeographical perspective because it has undergone marked climatic changes since the LGM (Grayson, 1993), with well-documented concurrent shifts in plant (e.g. Nowak *et al.*, 1994) and small mammal communities (e.g. Grayson, 2000b, 2006). These climatic shifts include glaciation and widespread pluvial lake coverage during the LGM, aridification through the Pleistocene–Holocene transition at 10,000 cal. yr BP, and a period through the mid-Holocene 5000 to 8000 cal. yr BP that was relatively warmer and drier than seen today (Grayson, 1993, 2000a). Arid conditions have also aided in the preservation of hundreds of palaeomiddens in the Great Basin, allowing more detailed inference of presence and demographic trends than are possible in other regions.

The Great Basin is inhabited solely by the INTm subclade today, which shows very strong patterns consistent with recent expansion. As the mode of the mismatch distribution is similar to those of the PNW and NOR subclades (Fig. 3), we believe the INTm subclade may have colonized much of this region in the same post-LGM timeframe during the Pleistocene–Holocene aridification. The niche model suggests that habitat similar to that of the current INTm range was very sparse in the Great Basin during the LGM (Fig. 4). This region was

concurrently riddled with pluvial lakes, reaching their greatest extent 14,000–17,000 yr BP (Benson, 2004). These lakes may have restricted dispersal of small, non-volant animals such as *N. cinerea*, so their emptying or drying could have opened habitat and corridors for dispersal. For example, as Lake Lahontan in north-west Nevada receded sharply around 14,000 yr BP to form the modern Pyramid Lake, elevations previously under water were quickly colonized by *Neotoma* (potentially *N. cinerea*) within 1000 years of drying (Benson *et al.*, 1995). This pattern could have occurred across much of the Great Basin as pluvial lakes receded.

An alternative hypothesis to account for the strong expansion signatures in the INTm subclade, although not mutually exclusive, is of wide scale colonization more recently as the Great Basin rebounded from the warm and arid mid-Holocene. As noted elsewhere (Grayson, 2006), and as evident in the palaeomidden profiles, *N. cinerea* went through dramatic demographic declines at multiple points across the Great Basin around the early- to mid-Holocene 7000–8000 yr BP (Fig. 6). In some instances it is evident that these declines were mirrored by phenotypic changes as *N. cinerea* reacted to Holocene conditions by dwarfing and then through extirpation and replacement by the more desert-adapted *N. lepida* (Smith & Betancourt, 2003; Lyman & O'Brien, 2005; Smith *et al.*, 2009). Extirpation through this time may have been widespread but does not appear to have been complete, as records of *N. cinerea* suggest populations persisted in areas such as Gatecliff Shelter in central Nevada (Grayson, 1983); this site in particular may have been suitable through the mid-Holocene, relative to the other sites, as it is at least 800 m higher in elevation and presumably maintained a cooler climate. Because *N. cinerea* is found across the Great Basin today, including at some of the sites showing decline or extirpation, such as Homestead Cave, recolonization in many areas may have occurred quite recently in the late Holocene (Grayson & Madsen, 2000). Wilson Butte Cave in particular shows markedly increasing numbers from *c.* 4000 yr BP through today (Fig. 6; Gruhn, 1961), the appropriate timeframe to show evidence of late Holocene demographic expansion. Despite the strong evidence of recent expansion and relative homogeneity of the INTm subclade haplotypes, there are higher levels of allozyme heterozygosity in *N. cinerea* across the Great Basin than in either the eastern or western ranges bounding it (Mewaldt & Jenkins, 1986). This supports the possibility that recolonization was staged from several points, which may include source populations at the edges of the Great Basin as well as populations within the Great Basin that persisted through the mid-Holocene.

Palaeomiddens only rarely provide insight prior to the LGM, but we suspect that extirpations and recolonizations like those inferred from Holocene records could have occurred serially through Pleistocene glacial and interglacial periods. These dynamics may have involved different clades than those currently found in their respective regions today. For instance, assuming different and stable climatic niches through time, the niche models suggest the NOR subclade may have occupied the Great Basin during the LGM prior to the INTm subclade, which may have had little suitable habitat across that region and time. After the LGM, the NOR subclade may have been replaced by the INTm through a variety of processes including competition, differential dispersal, mitochondrial introgression, or other stochastic forces. Our analyses cannot distinguish whether any such potential lineage replacements were due to differences in fundamental climatic tolerances between lineages or merely to stochastic processes, and such comparisons would best be addressed in conjunction with tests of niche similarity (e.g. Warren *et al.*, 2008). However, the genetic expansion signature of the INTm subclade across the Great Basin, coupled with limited LGM availability of the climate envelope this subclade currently inhabits, suggest that climate-associated, deterministic processes may have contributed to subclade dynamics through time.

CONCLUSIONS

Our combination of analyses of phylogenetic and population genetic patterns, palaeodistributions estimated by clade-specific niche models, and palaeorecord trends provides a robust, if yet initial, view of the biogeographical history of *N. cinerea*. Our study demonstrates the strength of developing an integrated dataset that captures different timeframes, including the Pliocene–Pleistocene transition, the late Pleistocene and the Holocene.

Evolutionary diversification of this taxon is the result of a dynamic history that includes long-term geographical barriers to dispersal in addition to periods of widespread fluctuation in suitable habitat. Consistent with our predictions for this species, we found signals of population extirpation and post-LGM expansion in northern regions. Also consistent with our predictions is a general signal of stable occupation in a large portion of the non-glaciated part of the range, especially in the Rocky Mountains, where we expected that the majority of response would have been at a localized level through body size change and/or elevational shifts. In contrast to our expectation of overall stability in non-glaciated regions, we uncovered a strong signal of expansion across the Great Basin. The genetic pattern of recent demographic expansion is supported by the clade-specific ecological niche model, which emphasizes the notion that distinct evolutionary lineages within species may have different niche associations, and thus, unique responses to past and future climatic shifts.

While niche models incorporating a series of bioclimatic variables are an informative approach to quantifying niche, it should be noted that, because *N. cinerea* is usually reliant on the availability of rocky outcrops for denning (Smith, 1997), large regions of climatically suitable habitat shown herein are probably unsuitable as measured by this other niche parameter (e.g. central California; Fig. 4). Likewise, a major assumption of ecological niche modelling, niche stability (Nogués-Bravo, 2009), may be poorly met by this species considering its presumed quick *in situ* reaction to past

climate change through body size evolution (Smith *et al.*, 1995, 2009; Smith & Betancourt, 2006). Models that include additional requirements such as rocky outcrops (or proxies such as depth to bedrock) and evolutionary parameters such as the capacity to change body size, will refine the results we present here.

Our understanding of the biogeographical history and development of phylogeographical pattern in this species will expand with advances in ancient DNA techniques (e.g. Prost *et al.*, 2010), habitat modelling that includes important non-climatic variables, information from variable regions of the nuclear genome, and the continued integration of demographic and distributional modelling. Given its unique link to the palaeomidden record and its broad distributional expanse, *N. cinerea* continues to provide an exceptional model for biogeographical investigations of western North America.

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SUPPORTING INFORMATION

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

Appendix S1 DNA samples used for phylogenetic and population genetic analyses.

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BIOSKETCHES

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