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ORIGINAL ARTICLE

Phylogeography of a Holarctic rodent (*Myodes rutilus*): testing high-latitude biogeographical hypotheses and the dynamics of range shifts

Brooks A. Kohli[1,2]*, Vadim B. Fedorov[3], Eric Waltari[4] and Joseph A. Cook[1]

[1]Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131-1051, USA, [2]Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824-3534, USA, [3]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA, [4]Department of Biology, City College of New York, New York, NY 10031, USA

*Correspondence: Brooks A. Kohli, Department of Natural Resources and the Environment, University of New Hampshire, 56 College Road, Durham, NH 03824-3534, USA.
E-mail: bak2014@unh.edu

ABSTRACT

Aim We used the Holarctic northern red-backed vole (*Myodes rutilus*) as a model organism to improve our understanding of how dynamic, northern high-latitude environments have affected the genetic diversity, demography and distribution of boreal organisms. We tested spatial and temporal hypotheses derived from previous mitochondrial studies, comparative phylogeography, palaeoecology and the fossil record regarding diversification of *M. rutilus* in the Palaearctic and Beringia.

Location High-latitude biomes across the Holarctic.

Methods We used a multilocus phylogeographical approach combined with species distribution models to characterize the biogeographical and demographic history of *M. rutilus*. Our molecular assessment included widespread sampling (more than 100 localities), species tree reconstruction and population genetic analyses.

Results Three well-differentiated mitochondrial lineages correspond to geographical regions, but nuclear genes were less structured. Multilocus divergence estimates indicated that diversification of *M. rutilus* was driven by events occurring before *c.* 100 ka. Population expansion in all three clades occurred prior to the Last Glacial Maximum (LGM) and presumably led to secondary contact. Species distribution modelling predicted a broad LGM distribution consistent with population and range expansion during this period.

Main conclusions The biogeographical history of *M. rutilus* differs from other boreal forest-associated species. Well-differentiated clades and the existence of secondary contact zones indicate prolonged isolation and persistence in Eurasian and Beringian refugia. Dynamic demographic and distributional changes emphasize the impact of pre-LGM glacial–interglacial cycles on contemporary geographical structure. The Bering Strait was not a significant factor in the diversification of northern red-backed voles.

Keywords

Beringia, boreal mammals, contact zone, Eurasian Pleistocene refugia, historical demography, Holarctic, range-wide phylogeography, species distribution modelling, species tree.

INTRODUCTION

In northern high latitudes, recent environmental changes have greatly influenced species' distributions and genetic diversity (Webb & Bartlein, 1992). During the Quaternary, climatic oscillations led to shifting landscapes, with glacial cycles having increased in intensity and frequency in the late Pleistocene (Hofreiter & Stewart, 2009; Miller *et al.*, 2010). During cold periods, much of North America and Europe were ice-covered, low sea levels exposed more land, and regional climate patterns changed (Hopkins, 1967), altering species distributions and community structure (Hofreiter &

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Stewart, 2009). Some regions were ice-covered for extended periods (e.g. Canada and Scandinavia), whereas others experienced more localized montane glaciations or remained ice-free (e.g. northern Asia; Glushkova, 2001; Ehlers & Gibbard, 2007).

For many boreal species, isolation in multiple glacial refugia facilitated divergence and contributed to increased genetic diversity on a continental scale (Hewitt, 2004a; Stewart *et al.*, 2010). Refugial populations were important sources for the recolonization of large geographical areas after the glaciers receded. Large unglaciated regions (e.g. Beringia) were characterized by habitat heterogeneity, which led to isolation and *in situ* diversification and/or provided a conduit for dispersal (Hopkins *et al.*, 1982; Waltari *et al.*, 2007; Galbreath *et al.*, 2011). Compared with the relative wealth of knowledge about mammalian biogeographical history in Europe and North America, the intervening Asian region is under-studied; considering its immense span and largely ice-free status during Quaternary glacial cycles, however, north-central Asia must have played a critical role in structuring high-latitude biodiversity (Tarasov *et al.*, 2000; Ehlers & Gibbard, 2007; Binney *et al.*, 2009).

Two alternative historical biogeographical models have emerged from the relatively few phylogeographical studies of Asian boreal and Arctic mammals. The first consists of recent widespread expansion from a single refugium, with limited contemporary genetic differentiation across Asia or the Holarctic; this history is observed in many northern taiga (forest) species (Fedorov *et al.*, 2008; Korsten *et al.*, 2009). A contrasting model entails genetic structure partitioned among geographical subregions and often delineated by contemporary contact zones, a signal indicative of deep historical subdivision (Brunhoff *et al.*, 2003; Fedorov *et al.*, 2003; Galbreath & Cook, 2004). This second hypothesis postulates multiple refugia, such as those identified in Europe or Beringia, contributing to the recolonization of Eurasia. This model has primarily been described for tundra and grassland species (Fedorov *et al.*, 1999a; Brunhoff *et al.*, 2003; Hope *et al.*, 2011). A few putative Asian refugia also have been inferred based on fossils, palaeoecological reconstructions, and comparative molecular studies, most notably in the Ural Mountains and northern Mongolia (Markova *et al.*, 1995; Tarasov *et al.*, 2000; Todisco *et al.*, 2012), and south-east Siberia and the Amga River basin (Fedorov *et al.*, 2008; Hope *et al.*, 2011). Spatially extensive phylogeographical studies of Holarctic species are, however, needed to validate the hypothesized refugia and to clarify temporal aspects of diversification and expansion.

Study species and hypotheses

Holarctic species provide unparalleled insight into biogeographical processes and we present range-wide analyses of the northern red-backed vole, *Myodes rutilus* (Pallas, 1779), a species distributed from Scandinavia east to North America (Wilson & Reeder, 2005; Fig. 1). Although considered a boreal forest species, *M. rutilus* is also more commonly found in shrub tundra than most taiga mammals (Gromov & Polyakov, 1977).

Fossil and genetic studies support an Asian origin of *M. rutilus* during the Pleistocene (Gromov & Polyakov, 1977; Cook *et al.*, 2004). In North America, the absence of fossils until the Holocene and an extensive contact zone with the southerly *M. gapperi* suggests late-Pleistocene colonization eastwards through Beringia (Rausch, 1963). Populations spanning the Bering Strait exhibit close genetic relationships, although Asian populations are more structured (Frisman *et al.*, 2002; Iwasa *et al.*, 2002; Cook *et al.*, 2004). Previous studies were limited, however, in their geographical scope, number of genetic loci and sample size.

Northern red-backed voles are of interest for numerous evolutionary and epidemiological reasons. Near the edges of its range, introgression has been documented between *M. rutilus* and two mostly parapatric congeners: *M. gapperi* in North America (Runck *et al.*, 2009) and *M. glareolus* in Eurasia (Tegelström, 1987; Deffontaine *et al.*, 2005). Temporal estimates of these events generally coincide with post-glacial expansion after the Last Glacial Maximum (LGM), supporting the role of environmental change in hybridization. A dynamic history of exchange among species of *Myodes* also has implications for the evolution and persistence of zoonotic pathogens (Dekonenko *et al.*, 2003; Dragoo *et al.*, 2006; Haukisalmi *et al.*, 2007) and host–parasite coevolution (Hoberg *et al.*, 2012).

We used range-wide, multilocus molecular analyses and species distribution models (SDMs) to explore how the environmental history of the northern high latitudes shaped the genetic diversity, demographics and distributions of boreal organisms. Previous phylogeographical assessments of boreal species, the fossil record and palaeoecological reconstructions provide a basis for spatial and temporal hypotheses set in the Palaearctic and Nearctic/Beringia.

Hypothesis 1 (H_1): Palaearctic biogeographical history

H_{1a} – The current Palaearctic distribution of *M. rutilus* is due to geographical expansion from a single LGM refugium in western Asia or Europe, as hypothesized for widespread Eurasian mammals (Korsten *et al.*, 2009). Populations across Eurasia are predicted to display little to no phylogenetic structure, low genetic diversity, signals of population expansion after the LGM, and greatly restricted LGM distribution compared to their current range.

H_{1b} – Populations of *M. rutilus* were isolated in multiple Eurasian refugia and subsequently expanded to their present continuous Palaearctic distribution. Initial divergence may correspond to the LGM or an earlier glacial period, as seen in other northern mammals (Fedorov *et al.*, 1999a; Brunhoff *et al.*, 2003; Hope *et al.*, 2011). Predictions associated with this multiple Eurasian refugia (MER) hypothesis and isolation over long periods include the presence of two or more lineages in Eurasia that may have diverged and expanded before the LGM, contact zones between divergent phylogroups and relatively high genetic diversity across the continent. The predicted LGM distribution of *M. rutilus* may be smaller than today, but not necessarily.

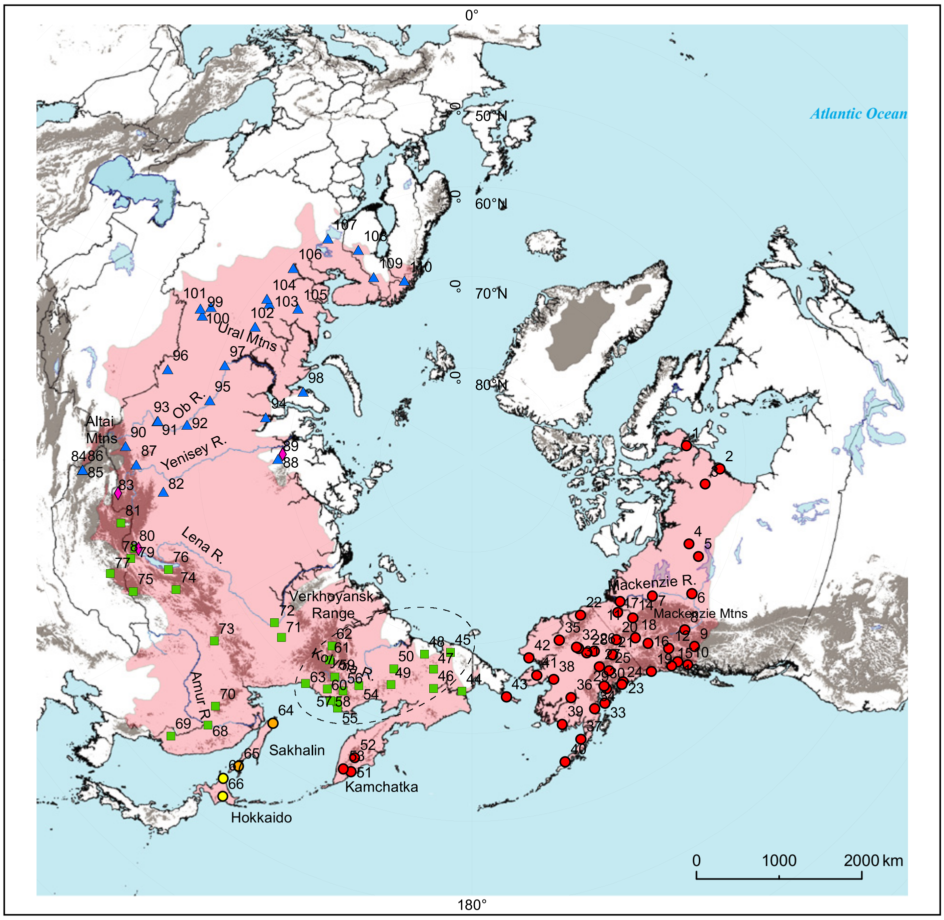

Figure 1 Distribution of *Myodes rutilus* (pink area, modified from IUCN and NatureServe range data; Linzey *et al.*, 2008; Patterson *et al.*, 2003) and sampling localities. Symbols correspond to cytochrome *b* clades/subclades (blue triangles, western clade; green squares, central clade; circles, eastern clade; red, Beringian subclade; orange, Sakhalin subclade; yellow, Hokkaido subclade). Populations containing both central and western haplotypes in central Siberia (79, 83 and 89) are shown as pink diamonds; these do not represent a separate clade. Localities are numbered sequentially from east to west (see Appendix S1). The individuals used for species-tree estimation were from localities 3, 11, 29, 41, 46, 48, 53, 61, 65, 67, 68, 77, 86, 98 and 100. The dashed ellipse centred on the Kolyma River indicates the region of presumed secondary contact identified by the nuclear gene *MLR*. Grey areas represent land above 1000 m elevation. The map uses a Lambert azimuthal equal-area projection.

Hypothesis 2 (H_2): Nearctic/Beringian history

H_{2a} – Nearctic populations of *M. rutilus* are post-glacial colonizers from Asia that rapidly expanded across Beringia during the LGM (Rausch, 1963; Cook *et al.*, 2004). This hypothesis predicts minimal differentiation from Asian populations, low genetic diversity and very recent population expansion (Waltari *et al.*, 2007). If phylogeographical structure is detected, the Bering Strait should be the primary barrier and divergence should date to the recent flooding of the Bering land bridge (*c.* 10 ka). Because no confirmed Nearctic *M. rutilus* fossils pre-date the Holocene (Rausch, 1963), the LGM distribution of *M. rutilus* in Beringia should be absent or greatly restricted compared to the present.

H_{2b} – Nearctic populations of *M. rutilus* are derived from a Beringian lineage that inhabited the region over several glacial cycles. North American and West Beringian populations are predicted to constitute a cohesive genetic lineage that diverged from Eurasian populations prior to the LGM. Recent assessment of red-backed vole populations within the historical boundaries of Beringia found that individuals from Kamchatka group with Alaskan populations and had been isolated from West Beringian populations for at least two glacial cycles (Hope *et al.*, 2012), suggesting possible substructure. Population expansion may be detected given the vast ice-covered area east of Beringia in North America that *M. rutilus* has recolonized since the LGM. Its persistence in Beringia would confer relatively high genetic diversity to modern Beringian and Nearctic populations unless a severe bottleneck occurred recently. Beringia should be included in the LGM distribution of the species.

MATERIALS AND METHODS

Sampling and laboratory techniques

Specimens were primarily acquired from fieldwork over the past decade as part of the Beringian Coevolution Project, supplemented with museum specimens. We sequenced 1–5 individuals from 110 localities (Fig. 1) for a total of 220 individuals spanning the distribution of *M. rutilus*, including 11 of the 14 described subspecies (Gromov & Polyakov, 1977; Hall, 1981; see Appendix S1 in Supporting Information). Another 92 mitochondrial sequences (mtDNA) were obtained from GenBank (Appendix S1). We sequenced four independent loci, including the mtDNA cytochrome *b* gene (*cytb*: 761–1143 bp) and three nuclear gene (nDNA) loci: 1059 bp of the first exon of interphotoreceptor retinoid binding protein gene (*IRBP*), 205 bp of mineralocorticoid receptor exon 3 (*MLR*), and 926 bp of v-ets erythroblastosis virus E26 oncogene homologue 2 (*ETS2*). Completed sequences were deposited in GenBank (accession numbers KJ765124–KJ765331 and KJ789404–KJ789620; see Appendix S2 for detailed sequencing methods). Other species of *Myodes* were included in all phylogenetic analyses as well as putatively polyphyletic species of *Alticola* (Lebedev *et al.*, 2007) in gene-tree analyses. Species of two other arvicolid genera, *Microtus* and *Dicrostonyx*, were included as outgroups (see Appendix S1 for more details).

Phylogeny reconstruction

Sequence alignment was completed with MEGA 5 (Tamura *et al.*, 2011) and validated by eye. Sequences of *cytb* (761–1143 bp) were partitioned by codon position. For nDNA, a subset of individuals was sampled from each mtDNA clade (Table 1) to maximize geographical breadth. MrModeltest 2.3 (Nylander, 2004) determined the best model of evolution for each gene and *cytb* codon position based on the Akaike information criterion (Table 1). Gene trees were reconstructed using MrBayes 3.2.1 (Huelsenbeck & Ronquist, 2001); runs were conducted for 12–50 million generations (Table 1), sampling every 1000, with four independent chains and a burn-in of 25%.

Species trees and divergence dates

BEAUti was used to set up runs for BEAST 1.7.4 (Drummond & Rambaut, 2007) using the *BEAST algorithm, a Bayesian MCMC multilocus coalescent technique for estimating species tree relationships (Heled & Drummond, 2010). The individual histories of genes may affect the reconstruction of phylogenies, but by estimating a species tree from multiple, independent loci, discord among gene trees may be reconciled. We include mitochondrial and nuclear loci to provide independent perspectives of the species' evolutionary history. A subset of individuals representing each mitochondrial clade and subclade identified in preliminary mtDNA analysis was selected for species tree analysis. Datasets for each genetic locus were unlinked across all partitions and the priors for models of evolution were informed by subset-specific outcomes from MrModeltest. Samples were assigned to clade, subclade or outgroup as determined by the *cytb* phylogeny. Groups for *Myodes rutilus* and *Myodes* were created but monophyly was not forced. Based on a Russian fossil dated to at least 2.6 Ma (Repenning *et al.*, 1990), an exponential prior (offset 2.6 Ma, median 3.148 Ma, 95th percentile 4.967 Ma) was placed on the node representing the most recent common ancestor (MRCA) of *Myodes*. These parameters were selected because the fossil represents a hard minimum estimate and the subfamily to which *Myodes* belongs is known from *c.* 5 Ma, providing a meaningful soft upper bound (Ho & Phillips, 2009). No appropriate fossils for reliably dating internal nodes are available for the genus (Ho *et al.*, 2008). Bayes-factor tests revealed no significant difference between clock models, indicating no departure from a constant evolutionary rate, so a strict clock was applied to *cytb* and the substitution rate was allowed to be estimated, as were the rates for each nuclear gene. Nuclear-locus clock models were assessed using the *ucld.stdev* parameter from preliminary runs in which the uncorrelated relaxed log-normal clock prior was applied and the resulting distribution examined, as recommended in the program documentation (Drummond *et al.*, 2007). As a result, a strict clock prior was applied in the final runs for all genes except *ETS2* (log-normal uncorrelated relaxed clock prior). A Yule tree prior was applied with piecewise linear and constant root. Proper ploidy was assigned to each locus and UPGMA (unweighted pair-group method with arithmetic mean) starting trees were selected. Two identical runs of 300–500 million MCMC generations were conducted for each analysis to achieve sufficient sampling (effective sample sizes > 200), and convergence was assessed using Tracer (Rambaut & Drummond, 2007).

Divergence-date estimates were generated simultaneously with species trees in BEAST. Only divergence dates generated for the species tree are reported (Sánchez-Gracia & Castresana, 2012).

Table 1 Gene sampling and information for Holarctic, range-wide sampling of *Myodes rutilus*. Models of evolution were determined by MrModeltest.

Gene	*n* (gene tree)	*n* (species tree)	Length (bp)	Model of evolution	MCMC generations
ETS2	69	33	926	GTR+I+Γ	50 million
IRBP	57	33	1059	GTR+I+Γ	50 million
MLR	76	33	205	HKY+I	12 million
Cytb	312	33	761–1143	GTR+I+Γ	50 million
pos1				K80+I+Γ	
pos2				HKY+I	
pos3				GTR+I+Γ	

Population genetics

Traditional summary statistics and measures of divergence were used to assess genetic variability and characterize the structure within *M. rutilus*. Population genetic parameters were calculated using Arlequin 3 (Excoffier *et al.*, 2005) and DnaSP 5.10 (Librado & Rozas, 2009) for each nuclear gene and a subset of *cytb* sequences (n = 281; 783 bp). Individuals were assigned to groups based on mtDNA identity, hereafter referred to as mtDNA clades. Genetic diversity indices were calculated for each clade and each gene to characterize the variation at each locus. Uncorrected sequence divergence within and between mtDNA clades was calculated for each gene using MEGA. Standard errors were estimated by 1000 bootstrap replicates. Analysis of molecular variance (AMOVA) was computed in ARLEQUIN to identify how variation was partitioned among individuals, populations and clades.

Demographic history

To elucidate population size trends and the timing of events, several demographic methods were applied. Potential signals of demographic expansion were analysed using Fu's F_S (Fu, 1997) and R_2 (Ramos-Onsins & Rozas, 2002), and were calculated in DNASP using 10,000 coalescent simulations to test significance. Mismatch distributions of *cytb* sequences were constructed in DNASP and a goodness-of-fit test was applied to test whether the observed data fitted a model of recent expansion (Slatkin & Hudson, 1991; Rogers & Harpending, 1992). Temporal changes in population size were estimated using a multilocus method implemented in BEAST, the extended Bayesian skyline plot (EBSP; Heled & Drummond, 2008). Because fossil dates were unavailable for intraspecific analysis, we applied a mean *cytb* strict clock rate (4.56% Myr^{-1}) derived from a BEAST run consisting of only *cytb* samples from *M. rutilus* to eliminate bias from outgroups. Rates for nuclear loci were estimated based on the mitochondrial rate and clock models were applied to each locus according to appropriate test results, described above. The EBSP coalescent tree prior was applied, and all other parameters mirrored those from the species tree construction where appropriate. For each major mitochondrial clade, the analysis was run twice for MCMC chain lengths of 50 million (east and central) or 100 million (west) generations, and assessed for stationarity and convergence accordingly.

Species distribution modelling

To independently test biogeographical hypotheses, SDMs for *M. rutilus* were generated under LGM and modern conditions using MAXENT 3.3.3k (Phillips *et al.*, 2006). For SDM development, we used current and LGM monthly climate data at 2.5′ (4-km) spatial resolution. LGM climate data were based on two general circulation model simulations: the Community Climate System Model (CCSM3) (Collins *et al.*, 2006) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; Hasumi & Emori, 2004; http://www.pmip2.cnrs-gif.fr/). SDMs were based on a subset of 19 bioclimatic variables in the WorldClim data set (Hijmans *et al.*, 2005) that characterize dimensions of climate that are considered particularly relevant in determining species distributions, and georeferenced species occurrence points of *M. rutilus*. Because of the difficulties of projecting species distributions in space and time (Anderson & Gonzalez, 2011; Peterson *et al.*, 2011; Merow *et al.*, 2013), we used a series of techniques to ensure models were not overly fitted to the present conditions, but were rather estimates of fundamental niches (Peterson *et al.*, 2011). To avoid the inclusion of regions where a species is absent for non-climatic reasons (Anderson & Raza, 2010), particularly the presence of congeners, our present-day SDMs were developed in masks using a specific extent of 42–77° N and 20° E–80° W. We reduced the 19 bioclimatic variables by removing highly correlated variables (Pearson's correlation coefficient, $r^2 > 0.8$). Species-specific parameter tuning often enhances model performance (Anderson & Gonzalez, 2011); we therefore optimized regularization values (Warren & Seifert, 2011) using the model-selection process in ENMTOOLS 1.3 (Warren *et al.*, 2010). Summary maps created in ARCGIS 9.3 show MAXENT predictions for the present day and LGM, the latter under CCSM and MIROC climate models (see Appendix S2 for detailed methods).

RESULTS

Phylogenies and phylogeography

A total of 312 individuals are included in the mtDNA gene tree (Appendix S1), which reveals strong support for three geographically structured clades (Figs 1 & 2). A western clade includes populations from northern Europe, western Siberia and western Mongolia. A central clade ranges from central Siberia and Mongolia to south-eastern Siberia and the Bering Strait. An eastern clade consists of all Nearctic samples and East Asian localities from Hokkaido, Sakhalin and Kamchatka. Sister relationships among these monophyletic groups are uncertain (Fig. 2).

The three widespread clades are effectively parapatric, overlapping only narrowly (Fig. 1). Representatives of the western and central clades meet near the Yenisei River. Three localities contain both central and western clade individuals. Contact between the eastern and central clades is inferred in north-eastern Siberia, as individuals from Kamchatka group with North American samples rather than adjacent Siberian populations. Only the eastern clade shows strong structure, with three subclades; two are East Asian (Hokkaido and Sakhalin, hereafter East Asian island subclades), and a third encompasses eastern Beringia, north-western Canada and Kamchatka (Fig. 2). Samples from Kamchatka are interspersed among North American samples of the Beringian group.

In contrast to mtDNA, nDNA gene trees are not sharply structured (see Appendix S3) and variability ranges from highest in *ETS2* to lowest in *MLR* (Table 2). The single informative *MLR* site distinguishes two groups with alternative alleles: one allele is found in all Nearctic populations and three north-east Siberian populations (localities 44, 53 and 62); the other is homozygous in all other populations west of the Kolyma River, including the East Asian islands. Heterozygous individuals are, however, found in north-eastern Siberia near the Verkhoyansk Range and Kolyma River region (Fig. 1; localities 45–49, 54, 59, 61 and 63). All individuals in these populations have central-clade *cytb* haplotypes.

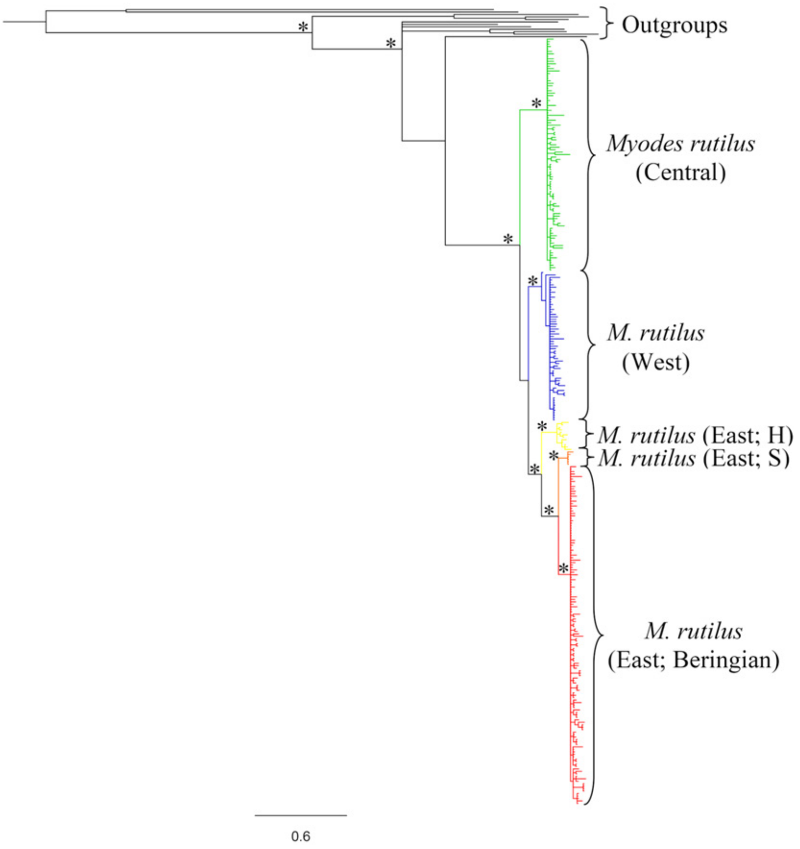

Figure 2 Bayesian cytochrome *b* (*cytb*) gene tree for 312 individuals of *Myodes rutilus* (761–1143 bp). Colours correspond to *cytb* clade colours in Fig. 1. *Microtus pennsylvanicus*, *Dicrostonyx groenlandicus* and other species of *Myodes* were included as outgroups (see Appendix S1 for details). Asterisks indicate posterior probabilities > 0.95 at major nodes. H, Hokkaido; S, Sakhalin.

Species trees and divergence dates

Clades delineated by mtDNA analyses are not strongly supported in the species tree (Fig. 3) but the monophyly of *M. rutilus* is supported (Fig. S1). The estimated time to the MRCA (TMRCA) for *M. rutilus* clades is greater than 100 ka, with a relatively narrow 95% credible interval (CI), indicating low error in estimates of the TMRCA of *M. rutilus* (Fig. 3). Larger error is evident in deeper relationships, probably due in part to the low sample sizes for the outgroup taxa. As such, our interspecific divergence estimates may not be as reliable as those found in a recent systematic assessment of the tribe Myodini (Kohli *et al.*, 2014), in which sampling was much more comprehensive and special attention was given to interspecific divergence estimates.

Population differentiation and demographic history

Myodes rutilus is characterized by geographically structured clades, sequence divergence and population expansion. *Cytb* exhibits high genetic diversity (Table 2), with sequence divergence between clades and subclades ranging from 0.012 to 0.033 (Table 3). East Asian island haplotypes are most similar to each other, whereas the central clade shows its highest divergence from the eastern (Beringian) clade and Sakhalin subclade. Nuclear sequence divergence is much lower than *cytb* (Table 3). AMOVA results attribute nearly 85% of *cytb* variation to among-group variation (Table 3) and reveal significant underlying nuclear structure that corresponds to *cytb* clades.

Multiple tests support significant population expansion for all clades except Sakhalin, which had a small sample size. All three main clades have strongly significant F_S and R_2 values (Table 2) and unimodal mismatch distributions that corroborate rapid expansion. According to the EBSP results, the central and eastern clades initiated population growth *c.* 50 ka and have continued growing to the present day (Fig. 4). In contrast to all other tests of major clades, the western-clade EBSP shows population stability rather than growth. A smaller sample size and the invariability of *MLR* (which caused that gene to be excluded from the western-clade EBSP analysis) is likely to have influenced the western-clade EBSP result. All other demographic tests support rapid population expansion of the western clade.

Species distribution models

Present-day and LGM SDMs, optimized to indicate the potential distribution, show nearly continuous suitable conditions across Eurasia and Beringia, and LGM predictions are only more restricted than at present because of direct ice coverage (Fig. 5). The two models of LGM conditions are similar, although the MIROC model predicts highly suitable habitat extensively across Central Asia (see Appendix S3 for supplementary results).

Table 2 Population genetic summary statistics based on 783 bp of cytochrome *b* and each nuclear gene investigated for *Myodes rutilus*. Sample size (n), number of segregating sites (S), number of haplotypes (H), haplotype diversity (Hd), average number of nucleotide differences (k), nucleotide diversity (π), and two estimators of recent population expansion, Fu's F_S and Ramos-Onsins & Rozas' R_2 are presented.

Gene/group	n	S	H	Hd	k	π	F_S	R_2
ETS2	69	54	50	0.870	7.59	0.0083	−26.437**	0.0655
IRBP	57	44	22	0.666	4.80	0.0047	−4.397	0.0525
MLR	76	4	5	0.536	0.59	0.0029	−1.046	0.0761
Cytb	281	138	169	0.982	14.66	0.0202	−175.640**	0.0518
Cytb clade/subclade								
Western	43	45	29	0.950	3.30	0.0043	−27.701**	0.0291**
Central	87	65	51	0.886	2.53	0.0031	−74.812**	0.0166**
Eastern / Beringian	135	72	80	0.978	3.84	0.0050	−119.830**	0.0246**
Sakhalin	5	3	3	0.700	1.20	0.0015	−0.186	0.2667
Hokkaido	11	18	11	1.000	4.29	0.0055	−7.781**	0.0985*

*$P < 0.05$, **$P < 0.0001$.

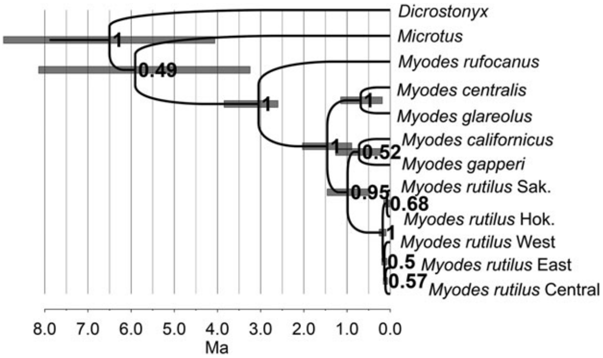

Figure 3 Species tree of *Myodes rutilus* clades and related outgroup species based on all genes, constructed using *BEAST. The time scale shows time from past to present (left to right) in millions of years ago. Posterior probability is shown to the right of nodes. Grey error bars show the 95% credible intervals around estimates of the mean time to the most recent common ancestor (TMRCA). (See Appendix S3 for estimates derived from nDNA and mtDNA separately).

DISCUSSION

Biogeographical history of *Myodes rutilus*

Holarctic species such as *M. rutilus* provide a spatially comprehensive perspective on how biogeographical processes affected northern species through the late Quaternary. Molecular signatures and SDMs of northern red-backed voles are consistent with Pleistocene vicariance rather than continental-scale dispersal from a single glacial refugium. In the comparatively under-studied region of Asia, we identified three lineages that have been separated for multiple glacial cycles, consistent with the MER hypothesis. Nearctic populations reflect dispersal from Beringia into previously glaciated areas by a lineage with deep Beringian history rather than recent (LGM) dispersal across the Bering land bridge. The three *M. rutilus* clades are parapatrically distributed over the Holarctic, reflecting the importance of independent refugia in the colonization of subarctic habitats around the Northern Hemisphere (Fig. 1). Such a history is distinct from most Eurasian boreal species that each apparently dispersed to their current wide Palaearctic distributions from a single refugial source (see Fedorov *et al.*, 2008; Korsten *et al.*, 2009; and references therein). Greater genetic divergence and structure in *M. rutilus* is more similar to tundra or grassland species whose modern phylogeographical structure reflects greater influence from vicariance than dispersal (Fedorov *et al.*, 1999a; Brunhoff *et al.*, 2003). These results suggest that pre-LGM vicariance events generated Holarctic structure in northern red-backed voles and underscore the idiosyncratic response of species to major environmental perturbations (Stewart, 2009; Hope *et al.*, 2011).

Genetic divergence among lineages was initiated before or during the penultimate glaciations (300–130 ka). Temporally, these results coincide with signals of deeper divergence found in other amphi-Beringian species (Hope *et al.*, 2012). Poor resolution in nDNA gene trees and species trees is likely to reflect incomplete lineage sorting and lower substitution rates than those of mtDNA. Large historical population sizes prior to vicariance or gene flow between geographical regions also may have increased the genetic variation and contributed to longer nuclear sorting times. Despite the discrepancy between mtDNA and nDNA phylogenies (Appendix S3), the divergence dates derived from combined data reveal that gene flow was limited for at least the last 100 kyr, allowing divergence to accrue (Fig. 3), and strongly supporting MER and long-term Beringian persistence.

LGM SDMs are consistent with palaeoecological work that has described the extent and location of forest communities in northern Asia during glacial periods (Tarasov *et al.*, 2000; Brubaker *et al.*, 2005; Binney *et al.*, 2009) as well as fossils of *M. rutilus* from the Ural Mountains and Transbaikalia (Markova *et al.*, 1995). A relatively widespread LGM distribution is consistent with clade expansion beginning before the LGM (Fig. 4). Refugial locations during previous late Pleistocene glacial periods are presumably nested within the LGM predicted range.

Table 3 Analysis of molecular variance (AMOVA) results of variation partitioning in *Myodes rutilus*. Populations were pooled into groups based on assignment to reciprocally monophyletic *cytb* groups.

Locus	Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Cytb	Among groups	4	1806.922	10.384*	84.37
	Among populations within groups	65	241.476	0.672*	5.46
	Within populations	197	246.582	1.252*	10.17
	Total	266	2294.980	12.308	
ETS2	Among groups	4	37.334	0.336*	8.58
	Among populations within groups	33	119.694	0.025	0.63
	Within populations	70	249.083	3.558	90.80
	Total	107	406.111	3.919	
IRBP	Among groups	4	138.051	2.204*	47.42
	Among populations within groups	32	94.901	0.515*	11.07
	Within populations	44	84.900	1.930*	41.51
	Total	80	317.852	4.649	
MLR	Among groups	4	13.183	0.214*	57.68
	Among populations within groups	34	4.672	−0.016	−4.24
	Within populations	53	9.167	0.173*	46.56
	Total	91	27.022	0.371	

*$P < 0.05$.

Myodes rutilus persisted in at least three refugia leading to spatially defined mitochondrial lineages in Beringia (eastern clade) and two distinct regions in north-central Asia (central and western clades; Figs 1 & 2). Beringia, the probable eastern-clade refugium, was central to diversification within *M. rutilus*. Beringia's role as a critical refugium and centre of diversification is known for a variety of northern plants (Abbott & Brochmann, 2003; Brubaker *et al.*, 2005) and animals (Hewitt, 2004b; Galbreath *et al.*, 2011), but has been identified less often as a source for expansion into both North America and Eurasia (Waltari *et al.*, 2007). Besides serving as the source for post-glacial colonization of North America, the persistence of the Beringian clade in Kamchatka led to multiple *M. rutilus* lineages existing in north-eastern Siberia. The close phylogenetic association of East Asian Island populations and the presence of a Beringian subclade suggest historical connections that extended westwards from Beringia along the Pacific Rim. SDMs indicate a corridor of suitable conditions along the Pacific coast during the LGM from the East Asian islands to southern Beringia (Fig. 5). Although the Kuril Islands appear to provide an alternative connection, a deep ocean trench prevented dispersal even during lowest Quaternary sea levels (Pietsch *et al.*, 2003). Divergence estimates indicate that a split between Beringian and East Asian island subclades occurred before rising sea levels isolated these islands from continental Asia *c.* 8–10 ka (Dobson, 1994).

Multiple Eurasian lineages as divergent as those observed in northern red-backed voles have rarely been documented for other boreal forest species. Our results provide strong evidence for two Asian refugia, one presumably located near the Ural Mountains or western Mongolian mountain ranges, and the other in the Far East. These refugia both contributed to widespread colonization of Eurasia. Supporting the probable western-clade refugium, fossils from the Ural Mountains indicate the persistence of *M. rutilus* in the region throughout the last 130 kyr, including among 'non-analogue' assemblages containing forest and tundra species (Gromov & Polyakov, 1977; Markova *et al.*, 1995; Borodin, 1996). Further east, the Altai Mountains and western Mongolia were mostly ice-free during the LGM, harbouring vegetation similar to that seen in contemporary landscapes (Tarasov *et al.*, 2000), suggesting that the western clade may have maintained a broad distribution. Importantly, this highly dynamic region may not lend itself to straightforward interpretations of biogeographical patterns, as exemplified by the Siberian larch (*Larix sibirica*), a widespread boreal tree (Semerikov *et al.*, 2013). Far East Asia represents another complex centre of evolutionary processes and diversification for boreal plants (Polezhaeva *et al.*, 2010; Semerikova *et al.*, 2011) and animals (Fedorov *et al.*, 2008; Hope *et al.*, 2010), including cases of hybridization and historical range shifts. Although several boreal forest species exhibit phylogenetic discontinuities in south-east Siberia, the importance of East Asian lineages in the widespread colonization of Asia on the scale seen for *M. rutilus* is uncommon. Preliminary examinations of the diversity and distribution of cestode parasites of *Myodes* voles also imply expansion from an East Asian centre of diversification (Galbreath *et al.*, 2013).

Until recently, relatively simplistic biogeographical hypotheses for Holarctic or trans-Eurasian mammals were perpetuated, consisting of recent expansion from glacial refugia, or more often, a single refugium (Korsten *et al.*, 2009). Although some species may exhibit such a history, range-wide assessments of Holarctic species such as *M. rutilus* are providing evidence that northern Asia was temporally and spatially dynamic throughout Quaternary glacial cycles, lending support to more complex hypotheses of persistence, diversification and colonization, such as the MER hypothesis. Deep divergence and contact zones between Asian *M. rutilus* lineages reflect the role of this critically under-studied region in the generation and persistence of northern biodiversity. As with studies in Europe, North America and more recently

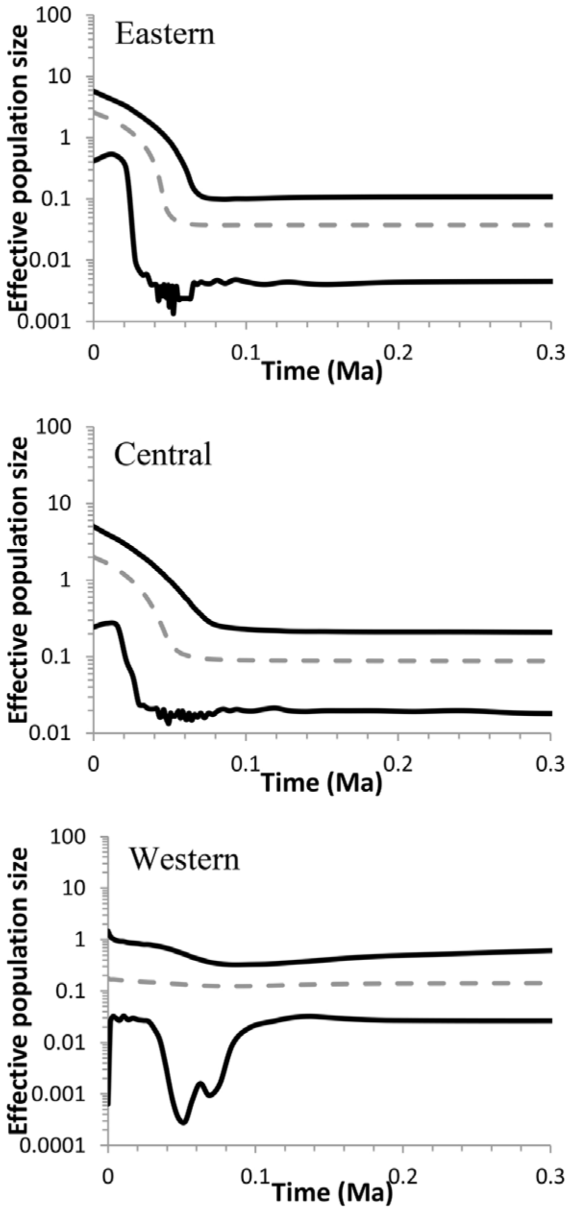

Figure 4 Extended Bayesian skyline plots (EBSP) for major cytochrome *b* clades of *Myodes rutilus*. The dashed line in the EBSP is the median estimated population size and solid lines are the 95% credible interval. The *y*-axis is logarithmic.

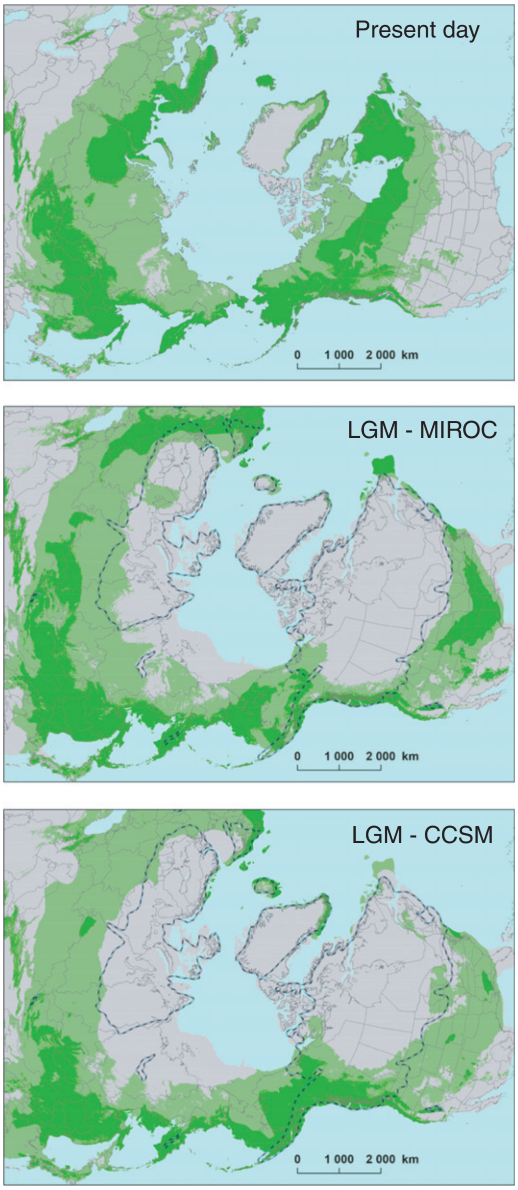

Figure 5 Species distribution models for *Myodes rutilus* for present-day and two Last Glacial Maximum scenarios. The light and dark shades of green represent suitable conditions for *M. rutilus* based on two thresholds (0.231 and 0.498, respectively). The blue and black dashed outline represents glacial coverage at LGM, although the full extent of ice is debated (see Svendsen *et al.*, 2004). The maps use a Lambert equal-area projection.

Beringia, deciphering the locations and roles of poorly-understood refugia will illuminate specific phylogeographical patterns of Asian species and bridge the geographical knowledge gap between better-understood areas.

Expansion and contact zones

Demographic tests reveal rapid expansion for all three major clades (Table 2, Fig. 4), beginning as early as 50 ka for the central and eastern clades and corresponding to the start of a warm interstadial period between the last two glacial advances (Svendsen *et al.*, 2004). Population growth continued through the LGM, as suggested by SDMs that show that *M. rutilus* was probably not highly restricted during this time. Because *M. rutilus* inhabits shrub tundra, its overall distribution was less limited than other species that were strictly associated with boreal forest during cold periods.

Secondary contact along the Yenisei River between the central and western clades is consistent with relatively recent contact resulting from central clade expansion *c.* 50 ka (Figs 1 & 4). The only sampling localities containing multiple mtDNA lineages are in this narrow region. The Yenisei River defines the border between two subspecies of *M. rutilus* based on dental morphology (Gromov & Polyakov, 1977), and represents the only case where subspecies assignments correspond to mtDNA lineages. Other broadly distributed species, such as shrews, exhibit phylogeographical breaks at the Yenisei River (Hope *et al.*, 2010) and around other prominent geographical features, including the Ural Mountains and the Ob River to the west (Hewitt, 2004b).

A second potential contact zone, identified by variation in *MLR*, exists in the Kolyma River region in north-eastern Siberia (Fig. 1), a suture zone for Holarctic taxa (Fedorov *et al.*, 1999a,b; Galbreath & Cook, 2004; Hewitt, 2004b). Historical contact between the central and eastern clades occurred near the Kolyma River, presumably due to expansion of the central clade from the west some time after 50 ka. Before this (*c.* 80–55 ka), the Verkhoyansk Range was heavily glaciated and is likely to have prevented contact, but these glaciers were much less extensive during the LGM (Bespalyy, 1984). Contact apparently led to a regional displacement of the eastern clade except from the isolated Kamchatka peninsula, which appears to have sheltered a relict population of eastern-clade *M. rutilus*. Brown bears (*Ursus arctos*) also maintained distinct lineages in Kamchatka (Korsten *et al.*, 2009), substantiating the relative inaccessibility of the peninsula for millennia. Furthermore, many trans-Beringian species have close genetic ties across the Bering Strait, emphasizing the role of pre-LGM events rather than contemporary barriers in structuring modern high-latitude biodiversity (Hewitt, 2004b; Hope *et al.*, 2012). The absence of central-clade haplotypes in Alaska and St Lawrence Island in the Bering Strait imply that central-clade expansion in north-eastern Siberia occurred after the flooding of the Bering land bridge, although incomplete lineage sorting may also explain this apparent break in *M. rutilus*.

The dynamic and idiosyncratic biogeographical history of northern red-backed voles demonstrates the role of distinct Asian refugia in high-latitude diversification and recolonization during the late Pleistocene. *Myodes rutilus* shares with other northern species spatiotemporal aspects of its history that reflect the imprint of common biogeographical processes (Hope *et al.*, 2012), but this species also responded independently. As we continue to study biogeographical processes across northern Asia, we will gain a more comprehensive view of evolution and diversification in the Northern Hemisphere.

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REFERENCES

Abbott, R.J. & Brochmann, C. (2003) History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology*, **12**, 299–313.

Anderson, R.P. & Gonzalez, I., Jr (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecological Modelling*, **222**, 2796–2811.

Anderson, R.P. & Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, **37**, 1378–1393.

Bespalyy, V.G. (1984) Late Pleistocene mountain glaciation in northeastern USSR. *Late Quaternary environments of the Soviet Union* (ed. by A.A. Velichko), pp. 31–33. University of Minnesota Press, Minneapolis.

Binney, H.A., Willis, K.J., Edwards, M.E., Bhagwat, S.A., Anderson, P.M., Andreev, A.A., Blaauw, M., Damblon, F., Haesaerts, P. & Kienast, F. (2009) The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database. *Quaternary Science Reviews*, **28**, 2445–2464.

Borodin, A.V. (1996) Quaternary small mammal faunas from the west Siberian plain. *Acta Zoologica Cracoviensia*, **39**, 75–81.

Brubaker, L.B., Anderson, P.M., Edwards, M.E. & Lozhkin, A.V. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography*, **32**, 833–848.

Brunhoff, C., Galbreath, K.E., Fedorov, V.B., Cook, J.A. & Jaarola, M. (2003) Holarctic phylogeography of the root vole (*Microtus oeconomus*): implications for late Quaternary biogeography of high latitudes. *Molecular Ecology*, **12**, 957–968.

Collins, W.D., Bitz, C.M., Blackmon, M.L., Bonan, G.B., Bretherton, C.S., Carton, J.A., Chang, P., Doney, S.C., Hack, J.J., Henderson, T.B., Kiehl, J.T., Large, W.G., McKenna, D.S., Santer, B.D. & Smith, R.D. (2006) The Community Climate System Model version 3 (CCSM3). *Journal of Climate*, **19**, 2122–2143.

Cook, J.A., Runck, A.M. & Conroy, C.J. (2004) Historical biogeography at the crossroads of the northern continents: molecular phylogenetics of red-backed voles (Rodentia: Arvicolinae). *Molecular Phylogenetics and Evolution*, **30**, 767–777.

Deffontaine, V., Libois, R., Kotlík, P., Sommer, R., Nieberding, C., Paradis, E., Searle, J. & Michaux, J.R. (2005) Beyond the Mediterranean peninsulas: evidence of central European glacial refugia for a temperate forest mammal species, the bank vole (*Clethrionomys glareolus*). *Molecular Ecology*, **14**, 1727–1739.

Dekonenko, A., Yakimenko, V., Ivanov, A., Morozov, V., Nikitin, P., Khasanova, S., Dzagurova, T., Tkachenko, E. & Schmaljohn, C. (2003) Genetic similarity of Puumala viruses found in Finland and western Siberia and of the mitochondrial DNA of their rodent hosts suggests a common evolutionary origin. *Infection, Genetics and Evolution*, **3**, 245–257.

Dobson, M. (1994) Patterns of distribution in Japanese land mammals. *Mammal Review*, **24**, 91–111.

Dragoo, J.W., Lackey, J.A., Moore, K.E., Lessa, E.P., Cook, J.A. & Yates, T.L. (2006) Phylogeography of the deer mouse (*Peromyscus maniculatus*) provides a predictive framework for research on hantaviruses. *Journal of General Virology*, **87**, 1997–2003.

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

Drummond, A.J., Ho, S.Y.W., Rawlence, N. & Rambaut, A. (2007) *A rough guide to BEAST 1.4.* University of Edinburgh, Edinburgh, UK.

Ehlers, J. & Gibbard, P.L. (2007) The extent and chronology of Cenozoic global glaciation. *Quaternary International*, **164**, 6–20.

Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Fedorov, V., Fredga, K. & Jarrell, G. (1999a) Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian Arctic. *Journal of Evolutionary Biology*, **12**, 134–145.

Fedorov, V., Goropashnaya, A., Jarrell, G.H. & Fredga, K. (1999b) Phylogeographic structure and mitochondrial DNA variation in true lemmings (*Lemmus*) from the Eurasian Arctic. *Biological Journal of the Linnean Society*, **66**, 357–371.

Fedorov, V.B., Goropashnaya, A.V., Jaarola, M. & Cook, J.A. (2003) Phylogeography of lemmings (*Lemmus*): no evidence for postglacial colonization of Arctic from the Beringian refugium. *Molecular Ecology*, **12**, 725–731.

Fedorov, V.B., Goropashnaya, A.V., Boeskorov, G.G. & Cook, J.A. (2008) Comparative phylogeography and demographic history of the wood lemming (*Myopus schisticolor*): implications for late Quaternary history of the taiga species in Eurasia. *Molecular Ecology*, **17**, 598–610.

Frisman, L.V., Kartavtseva, I.V., Pavlenko, M.V., Kostenko, V.A., Suzuki, H., Iwasa, M., Nakata, K. & Chernyavskii, F.B. (2002) Gene-geographical variation and genetic differentiation in red-backed voles of the genus *Clethrionomys* (Rodentia, Cricetidae) from the region of the Sea of Okhotsk. *Genetika*, **38**, 655–664.

Fu, Y.-X. (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, **147**, 915–925.

Galbreath, K.E. & Cook, J.A. (2004) Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. *Molecular Ecology*, **13**, 135–148.

Galbreath, K.E., Cook, J.A., Eddingsaas, A.A. & DeChaine, E.G. (2011) Diversity and demography in Beringia: multilocus tests of paleodistribution models reveal the complex history of arctic ground squirrels. *Evolution*, **65**, 1879–1896.

Galbreath, K.E., Ragaliauskaite, K., Kontrimavichus, L., Makarikov, A.A. & Hoberg, E.P. (2013) A widespread distribution for *Arostrilepis tenuicirrosa* (Eucestoda: Hymenolepididae) in *Myodes* voles (Cricetidae: Arvicolinae) from the Palearctic based on molecular and morphological evidence: historical and biogeographic implications. *Acta Parasitologica*, **58**, 441–452.

Glushkova, O.Y. (2001) Geomorphological correlation of late Pleistocene glacial complexes of western and eastern Beringia. *Quaternary Science Reviews*, **20**, 405–417.

Gromov, I.M. & Polyakov, I.Y. (1977) *Fauna of the USSR: Mammals, Vol. 3, No. 8. Voles (Microtinae)*. Smithsonian Institution Libraries and the National Science Foundation, Washington, DC.

Hall, E.R. (1981) *The mammals of North America*, 2nd edn. John Wiley & Sons, New York.

Hasumi, H. & Emori, S. (2004) *K-1 coupled GCM (MIROC) description*. Center for Climate System Research, University of Tokyo, Tokyo.

Haukisalmi, V., Hardman, L.M., Hardman, M., Laakkonen, J., Niemimaa, J. & Henttonen, H. (2007) Morphological and molecular characterisation of *Paranoplocephala buryatiensis* n. sp. and *P. longivaginata* Chechulin & Gulyaev, 1998 (Cestoda: Anoplocephalidae) in voles of the genus *Clethrionomys*. *Systematic Parasitology*, **66**, 55–71.

Heled, J. & Drummond, A.J. (2008) Bayesian inference of population size history from multiple loci. *BMC Evolutionary Biology*, **8**, 289.

Heled, J. & Drummond, A.J. (2010) Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, **27**, 570–580.

Hewitt, G.M. (2004a) The structure of biodiversity – insights from molecular phylogeography. *Frontiers in Zoology*, **1**, 4.

Hewitt, G.M. (2004b) Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 183–195.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Ho, S.Y.W. & Phillips, M.J. (2009) Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology*, **58**, 367–380.

Ho, S.Y.W., Saarma, U., Barnett, R., Haile, J. & Shapiro, B. (2008) The effect of inappropriate calibration: three case studies in molecular ecology. *PLoS ONE*, **3**, e1615.

Hoberg, E.P., Galbreath, K.E., Cook, J.A., Kutz, S.J. & Polley, L. (2012) Northern host–parasite assemblages: history and biogeography on the borderlands of episodic climate and environmental transition. *Advances in Parasitology*, **79**, 1–97.

Hofreiter, M. & Stewart, J. (2009) Ecological change, range fluctuations and population dynamics during the Pleistocene. *Current Biology*, **19**, R584–R594.

Hope, A.G., Waltari, E., Dokuchaev, N.E., Abramov, S., Dupal, T., Tsvetkova, A., Henttonen, H., MacDonald, S.O. & Cook, J.A. (2010) High-latitude diversification within Eurasian least shrews and Alaska tiny shrews (Soricidae). *Journal of Mammalogy*, **91**, 1041–1057.

Hope, A.G., Waltari, E., Fedorov, V.B., Goropashnaya, A.V., Talbot, S.L. & Cook, J.A. (2011) Persistence and diversification of the Holarctic shrew, *Sorex tundrensis* (Family Soricidae), in response to climate change. *Molecular Ecology*, **20**, 4346–4370.

Hope, A.G., Takebayashi, N., Galbreath, K.E., Talbot, S.L. & Cook, J.A. (2012) Temporal, spatial and ecological dynamics of speciation among amphi-Beringian small mammals. *Journal of Biogeography*, **40**, 415–429.

Hopkins, D.M. (1967) *The Bering land bridge*. Stanford University Press, Redwood City, CA.

Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (1982) *Paleoecology of Beringia*. Academic Press, New York.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Iwasa, M.A., Kartavtseva, I.V., Dobrotvorsky, A.K., Panov, V.V. & Suzuki, H. (2002) Local differentiation of *Clethrionomys rutilus* in northeastern Asia inferred from mitochondrial gene sequences. *Mammalian Biology*, **67**, 157–166.

Kohli, B.A., Speer, K.A., Kilpatrick, C.W., Batsaikhan, N., Damdinbaza, D. & Cook, J.A. (2014) Multilocus systematics and non-punctuated evolution of Holarctic Myodini (Rodentia: Arvicolinae). *Molecular Phylogenetics and Evolution*, **76**, 18–29.

Korsten, M., Ho, S.Y.W., Davison, J., Pahn, B., Vulla, E., Roht, M., Tumanov, I.L., Kojola, I., Anderson-Lilley, Z. & Ozolins, J. (2009) Sudden expansion of a single brown bear maternal lineage across northern continental Eurasia after the last ice age: a general demographic model for mammals? *Molecular Ecology*, **18**, 1963–1979.

Lebedev, V.S., Bannikova, A.A., Tesakov, A.S. & Abramson, N.I. (2007) Molecular phylogeny of the genus *Alticola* (Cricetidae, Rodentia) as inferred from the sequence of the cytochrome *b* gene. *Zoologica Scripta*, **36**, 547–563.

Librado, P. & Rozas, J. (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, **25**, 1451–1452.

Linzey, A.V., Henttonen, H., Sheftel, B. & Batsaikhan, N. (2008) *Myodes rutilus. IUCN Red List of Threatened Species. Version 2012.1*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. Available at: http://www.iucnredlist.org/details/4975/0. Downloaded on 16 June 2012.

Markova, A.K., Smirnov, N.G., Kozharivon, A.V., Kazantseva, N.E., Simakova, A.N. & Kitaev, L.M. (1995) Late Pleistocene distribution and diversity of mammals in northern Eurasia. *Paleontologia i Evolucio*, **28–29**, 5–143.

Merow, C., Smith, M.J. & Silander, J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, **36**, 1058–1069.

Miller, G.H., Brigham-Grette, J., Alley, R.B. *et al.* (2010) Temperature and precipitation history of the Arctic. *Quaternary Science Reviews*, **29**, 1679–1715.

Nylander, J. (2004) *MrModeltest v2*. Evolutionary Biology Centre, Uppsala University, Uppsala, Program distributed by the author.

Patterson, B.D., Ceballos, G., Sechrest, W., Tognelli, M.F., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B.E. (2003) *Digital distribution maps of the mammals of the Western Hemisphere*, version 1.0. NatureServe, Arlington, VA.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions*. Princeton University Press, Princeton, NJ.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Pietsch, T.W., Bogatov, V.V., Amaoka, K., Zhuravlev, Y.N., Barkalov, V.Y., Gage, S., Takahashi, H., Lelej, A.S., Storozhenko, S.Y., Minakawa, N., Bennett, D.J., Anderson, T.R., Ôhara, M., Prozorova, L.A., Kuwahara, Y., Kholin, S.K., Yabe, M., Stevenson, D.E. & MacDonald, E.L. (2003) Biodiversity and biogeography of the islands of the Kuril Archipelago. *Journal of Biogeography*, **30**, 1297–1310.

Polezhaeva, M.A., Lascoux, M. & Semerikov, V.L. (2010) Cytoplasmic DNA variation and biogeography of *Larix* Mill. in Northeast Asia. *Molecular Ecology*, **19**, 1239–1252.

Rambaut, A. & Drummond, A.J. (2007) *Tracer v1.4*. University of Edinburgh, Edinburgh, UK. Available at: http://beast.bio.ed.ac.uk/tracer

Ramos-Onsins, S.E. & Rozas, J. (2002) Statistical properties of new neutrality tests against population growth. *Molecular Biology and Evolution*, **19**, 2092–2100.

Rausch, R.L. (1963) A review of the distribution of Holarctic recent mammals. *Pacific Basin biogeography: a symposium* (ed. by J.L. Garrett), pp. 29–44. Bishop Museum Press, Honolulu.

Repenning, C.A., Fejfar, O. & Heinrich, W.D. (1990) Arvicolid rodent biochronology of the Northern Hemisphere. *International Symposium on the Evolution and Phylogenetic Biostratigraphy of Arvicolids (Rodentia, Mammalia)* (ed. by O. Fejfar and W.D. Heinrich), pp. 385–418. Pfeil, Prague, Czechoslovakia.

Rogers, A.R. & Harpending, H.C. (1992) Population growth makes waves in the distribution of pairwise nucleotide differences. *Molecular Biology and Evolution*, **9**, 552–569.

Runck, A.M., Matocq, M.D. & Cook, J.A. (2009) Historic hybridization and persistence of a novel mito-nuclear combination in red-backed voles (genus *Myodes*). *BMC Evolutionary Biology*, **9**, 114.

Sánchez-Gracia, A. & Castresana, J. (2012) Impact of deep coalescence on the reliability of species tree inference from different types of DNA markers in mammals. *PLoS ONE*, **7**, e30239.

Semerikov, V.L., Semerikova, S.A., Polezhaeva, M.A., Kosintsev, P.A. & Lascoux, M. (2013) Southern montane populations did not contribute to the recolonization of West Siberian Plain by Siberian larch (*Larix sibirica*): a range-wide analysis of cytoplasmic markers. *Molecular Ecology*, **22**, 4958–4971.

Semerikova, S.A., Semerikov, V.L. & Lascoux, M. (2011) Post-glacial history and introgression in *Abies* (Pinaceae) species of the Russian Far East inferred from both nuclear and cytoplasmic markers. *Journal of Biogeography*, **38**, 326–340.

Slatkin, M. & Hudson, R.R. (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. *Genetics*, **129**, 555–562.

Stewart, J.R. (2009) The evolutionary consequence of the individualistic response to climate change. *Journal of Evolutionary Biology*, **22**, 2363–2375.

Stewart, J.R., Lister, A.M., Barnes, I. & Dalén, L. (2010) Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 661–671.

Svendsen, J.I., Alexanderson, H., Astakhov, V.I. *et al.* (2004) Late Quaternary ice sheet history of northern Eurasia. *Quaternary Science Reviews*, **23**, 1229–1271.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**, 2731–2739.

Tarasov, P.E., Volkova, V.S., Webb, T., III, Guiot, J., Andreev, A.A., Bezusko, L.G., Bezusko, T.V., Bykova, G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.M. & Panova, N.K. (2000) Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *Journal of Biogeography*, **27**, 609–620.

Tegelström, H. (1987) Transfer of mitochondrial DNA from the northern red-backed vole (*Clethrionomys rutilus*) to the bank vole (*C. glareolus*). *Journal of Molecular Evolution*, **24**, 218–227.

Todisco, V., Gratton, P., Zakharov, E.V., Wheat, C.W., Sbordoni, V. & Sperling, F.A.H. (2012) Mitochondrial phylogeography of the Holarctic *Parnassius phoebus* complex supports a recent refugial model for alpine butterflies. *Journal of Biogeography*, **39**, 1058–1072.

Waltari, E., Hoberg, E.P., Lessa, E.P. & Cook, J.A. (2007) Eastward Ho: phylogeographical perspectives on colonization of hosts and parasites across the Beringian nexus. *Journal of Biogeography*, **34**, 561–574.

Warren, D.L. & Seifert, S.N. (2011) Environmental niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.

Warren, D.L., Glor, R.E. & Turelli, M. (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, **33**, 607–611.

Webb, T., III & Bartlein, P.J. (1992) Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics*, **23**, 141–173.

Wilson, D.E. & Reeder, D.M. (2005) *Mammal species of the world*. Johns Hopkins University Press, Baltimore, MD.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Samples used.
Appendix S2 Supplementary sequencing and species distribution modelling methods.
Appendix S3 Supplementary figures.

BIOSKETCH

This research was part of **Brooks A. Kohli**'s Master's thesis. His general research interests include spatial and temporal variation in evolutionary and ecological processes of vertebrates.

Author contributions: B.A.K. and J.A.C. conceived the ideas; J.A.C. organized the fieldwork; B.A.K. collected the molecular data; B.A.K. and E.W. analysed the data; J.A.C. secured financial support and provided laboratory facilities; V.B.F. contributed to interpretation of results; and B.A.K. led the writing, but all authors contributed.

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