Comparative phylogeography and demographic history of the wood lemming (*Myopus schisticolor*): implications for late Quaternary history of the taiga species in Eurasia

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Abstract

The association between demographic history, genealogy and geographical distribution of mitochondrial DNA cytochrome *b* haplotypes was studied in the wood lemming (*Myopus schisticolor*), a species that is closely associated with the boreal forest of the Eurasian taiga zone from Scandinavia to the Pacific coast. Except for a major phylogeographic discontinuity (0.9% nucleotide divergence) in southeastern Siberia, only shallow regional genetic structure was detected across northern Eurasia. Genetic signs of demographic expansions imply that successive range contractions and expansions on different spatial scales represented the primary historical events that shaped geographical patterns of genetic variation. Comparison of phylogeographic structure across a taxonomically diverse array of other species that are ecologically associated with the taiga forest revealed similar patterns and identified two general aspects. First, the major south–north phylogeographic discontinuity observed in five out of six species studied in southeastern Siberia and the Far East implies vicariant separation in two different refugial areas. The limited distribution range of the southeastern lineages provides no evidence of the importance of the putative southeastern refugial area for postglacial colonization of northern Eurasia by boreal forest species. Second, the lack of phylogeographic structure associated with significant reciprocal monophyly and genetic signatures of demographic expansion in all nine boreal forest animal species studied to date across most of northern Eurasia imply contraction of each species to a single refugial area during the late Pleistocene followed by range expansion on a continental scale. Similar phylogeographic patterns observed in this taxonomically diverse set of organisms with different life histories and dispersal potentials reflect the historical dynamics of their shared environment, the taiga forest in northern Eurasia.

Keywords: boreal forest, colonization, cytochrome *b* gene, demographic expansion, mtDNA, refugia

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Introduction

Quaternary climate change had a strong impact on the geographical distribution and demographic history of extant species (Bennett 1997). Palaeoecological evidence suggests that most of northern Eurasia and North America was covered by treeless vegetation during glacial periods (West 2000) and distributions of forest species were contracted to

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refugial areas. Past isolation in separate refugia and routes of postglacial colonization are often reflected in the geographical patterns of intraspecific genetic variation (Hewitt 1996). In Europe and North America, several species of small mammals that are ecologically associated with temperate deciduous forests demonstrate phylogeographic divisions and genetic signs of demographic expansions (Arbogast & Kenagy 2001; Deffontaine *et al.* 2005; Runck & Cook 2005; Kotlik *et al.* 2006; Rowe *et al.* 2006). Consistent with palaeoecological evidence, these patterns of genetic variation imply vicariant separation in different forest

refugia followed by demographic expansion during postglacial colonization. In contrast to the deciduous forest taxa, phylogeographic studies across the Eurasian taiga zone, a continuous belt of coniferous trees from Scandinavia to the Pacific coast, did not reveal substantial phylogeographic structure in several avian species (Kvist *et al.* 2001, 2003; Zink *et al.* 2002a, b), the flying squirrel (Oshida *et al.* 2005) and red wood ants (Goropashnaya *et al.* 2004), all of which are associated with boreal forest. This pattern of genetic differentiation gives no indication for vicariant separation over glacial periods in different boreal forest refugia as expected from palaeoecological evidence (Tarasov *et al.* 2000) in Eurasia. However, most boreal forest species studied to date across Eurasia are highly vagile due to dispersal by flight. Temperate avian species often demonstrate limited phylogeographic structure (Avise 2000). Similarly, dispersal by flight combined with low substitution rate of mitochondrial DNA (mtDNA) in red wood ants (Goropashnaya *et al.* 2004) has likely constrained our ability to infer biotic responses of these species during the Late Quaternary. Genetic signals of past refugial separation and demographic history are expected to be stronger in species with limited dispersal and high substitution rates.

Arvicoline rodents offer a good opportunity to infer biotic history from contemporary patterns of genetic variation for at least three reasons. First, short generation time and fast mtDNA substitution rates increase temporal resolution of phylogeographic analysis allowing for the detection of biotic responses over time spans as shallow as a single glacial period (Fedorov & Stenseth 2002). Second, the relatively limited ability of small mammals to disperse on a large geographical scale preserves the genetic signature of historical events against erosion by substantial gene flow. Third, palaeontological and ecological evidence indicates that a number of arvicoline rodents demonstrate strong associations with particular environments, allowing a more detailed view of environmental factors that affect patterns of genetic variation. The wood lemming, *Myopus schisticolor*, is an arvicoline rodent that is distributed over the majority of the Eurasian taiga zone from Scandinavia to the Pacific coast. This species is tightly associated with the coniferous boreal forest because several species of green mosses that are typical members of taiga communities constitute a considerable part of the wood lemming's diet (Bondrup-Nielsen 1993; Eskelinen 2002). This strong association with taiga communities implies that the refugial and colonization history of this species will largely reflect the Quaternary environmental history of the coniferous boreal forest in Eurasia. We studied the geographical pattern of genetic variation over the Palearctic distribution range of the wood lemming to address the following questions. First, we examined the association between genealogy and geographical distribution of mtDNA haplotypes to assess possible vicariant separation in different glacial forest refugia and routes of postglacial colonization. Second, we examined genetic diversity and demographic history to detect signs of demographic expansion from limited refugial sources. To reveal general trends in the biotic history of the taiga zone, we compare phylogeographic structure and demographic history of the wood lemmings with patterns of genetic variation in other boreal forest species studied across Eurasia. Third, phylogeography of the wood lemming was compared with geographical patterns of mtDNA variation observed in codistributed species of Eurasian rodents that are ecologically associated with open mesic grassland habitats (Brunhoff *et al.* 2003; Fedorov *et al.* 2003). Due to contrasting ecological preferences, differences between phylogeographic patterns of the taiga and grassland rodents may reflect different biotic responses to common historical events. To our knowledge, this study represents the first research effort to elucidate general trends in biotic history of the coniferous boreal forest in Eurasia by combining results from comparative phylogeography across species that are ecologically associated with taiga communities with independent evidence on landscape history that has recently been published on the palaeoecology and palaeogeography of this vast and largely unstudied region.

Materials and methods

Samples collection and DNA extraction

We examined a total of 100 wood lemmings from 30 localities over the majority of this species' distribution in Eurasia (Fig. 1, Table 1). Lemmings were collected from seven localities (4, 5, 20, 21, 26, 27, 28) during the summers of 1988–1995. A subset of tissue samples previously studied from Scandinavia (Fedorov *et al.* 1996) was used in the present study. Specimens from Finland and the northeastern Siberia (localities 2, 3, 29, 30) were obtained through the Beringian Co-evolution Project and archived in the Mammal Collection, University of Alaska Museum. Museum skins from the 18 Siberian localities were provided by the Siberian Zoological Museum, Novosibirsk. Total genomic DNA was isolated from frozen or dry tissue samples by the use of the QIAGEN DNeasy kit.

PCR amplification and sequencing

A segment (915 bp) of the cytochrome *b* gene was amplified from frozen tissue DNA template by polymerase chain reaction (PCR) and automatically sequenced using several pairs of primers, as described elsewhere (Fedorov *et al.* 1999). We amplified the same part of the cytochrome *b* gene from the dry museum skins in four overlapping segments using Ampli*Taq* Gold enzyme and specially designed pairs of primers: M1L, TCGCATTTCACTTCATCCTC-3′ and M1H, TTTGTTGGGGATTGATCG-3′ (326 bp); M2L, ATA(CT)
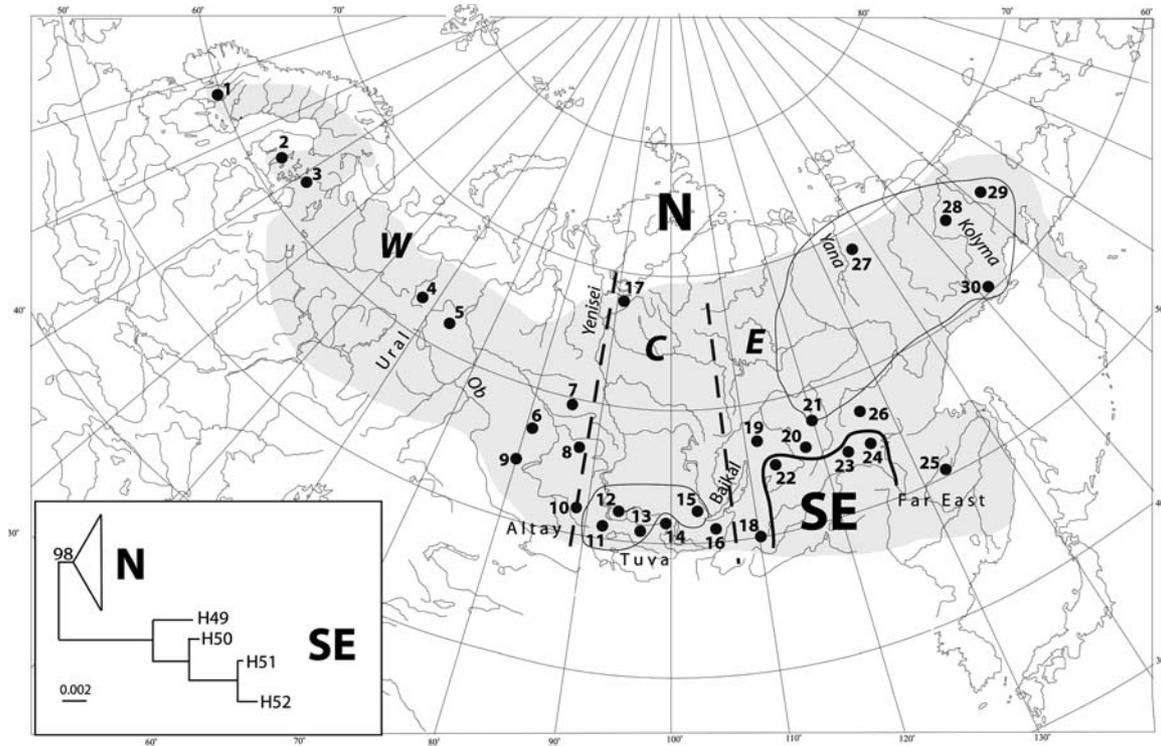
Fig. 1 Map showing sampling localities of the wood lemming, its overall range, the geographical distribution of the main clades revealed by the neighbour-joining tree (insert): N, Northern clade; SE, Southeastern clade; bold line, approximate limit of SE clade range; and geographical distribution of the three haplotype groups within the Northern clade: *W*, Western group; *C*, Central group; *E*, Eastern group; dashed line, approximate limits of the ranges of each group. Thin lines show the star-like haplotype clusters distribution ranges.

TTCCTATTCGCCTACGC-3′ and M2H, AATGATGGCGAA GGGGTATT-3′ 235 bp; M3L, TGAAACCTGAAACGTA GGCA-3′ and M3H, TAGAGCCTGTTTCGTGAAGGA-3′ (287 bp); M4L, CTTCCAACCCCATCAAATATC-3′ and M4H, TGCTGTTGCTATGAGAGTGAG-3′ (321 bp). The same primers were used for sequencing PCR-amplified segments. Excluding missing sites, we scored a total of 886 bp in all individuals (GenBank Accession nos EU165208–165268).

Data analysis

A neighbour-joining tree was constructed using genetic distances among haplotypes based on Kimura 2-parameter substitution model (Nei & Kumar 2000) with the MEGA 3.1 program (Kumar *et al.* 2004). The Kimura 2-parameter model was selected as differences among haplotypes were small (maximum *p* distance of 0.023) and this method is based on the simplest model with correction for uneven number of transitions and transversions (6:1) and a small total variance (Nei & Kumar 2000, p. 112). The average Kimura distance among haplotypes was identical to the Tamura and Nei distance with proportion of invariable sites and gamma correction suggested by MODELTEST. Average nucleotide divergence within phylogeographic groups, net divergence between groups with correction for

intragroup divergence and their standard deviations were estimated according to Nei & Kumar (2000). We compared the log-likelihood scores of trees constructed with and without a molecular clock assumption (Felsenstein 1988) to evaluate constancy in rate of the cytochrome *b* sequence evolution among lineages. To assess approximate timing of historical events, we used the divergence rate of 6.5% per million years as suggested by the net divergence (7.9%; Fedorov *et al.* 2003) in the cytochrome *b* region and the first occurrence of fossil records in North America [1.2 million years ago (Ma)] recently corrected by Repenning (2001) for true lemmings *Lemmus*, the arvicoline genus most closely related to the wood lemming (Conroy & Cook 2000). The timing of the calibration (1.2 Ma) is on the Quaternary timescale; thus, the resulting rate minimizes overestimation of recent divergence times (Ho *et al.* 2005) in the wood lemming. Maximum parsimony median-joining haplotype network was constructed with the NETWORK 3.1.1.1 program weighing characters equally (Bandelt *et al.* 1999). To identify star-like clusters that might be diagnostic of historic demographic expansion, we applied the star contraction algorithm (Forster *et al.* 2001) to the median-joining network. This method distinguishes star-like phylogenetic clusters from nonstar-like branches according to a parameter specifying mutational time depth. Conservatively, we selected

Table 1 Haplotype frequencies, haplotype (*h*) and nucleotide (π) diversities with their standard deviations (SD) for the sampling localities of *Myopus schisticolor*. *N* is the number of individuals sequenced. The number of haplotypes that are shared by at least two localities (H5, H15, H26, H44, H48) is shown in separate columns; private haplotypes are listed for each locality (the number of individuals in parentheses if > 1). The haplotype numbers refer to Fig. 2, and the locality numbers to Fig. 1

Population	N	Haplotypes Shared H5	H15	H26	H44	H48	Private	π (SD),%	h (SD)
1. Norway	7	–	–	–	–	–	H19(6), H18	0.06 (0.04)	0.286 (0.196)
2. Heinvesi	6	–	–	–	–	–	H3(4), H4(2)	0.06 (0.02)	0.533 (0.172)
3. Kuhmo	7	3	–	–	–	–	H1(2), H2(2)	0.18 (0.03)	0.762 (0.115)
4. Pechora	7	3	1	–	–	–	H6(3)	0.13 (0.05)	0.714 (0.127)
5. M. Sosva	8	–	3	–	–	–	H16, H17(4)	0.12 (0.04)	0.679 (0.015)
6. Tomsk-1	1	–	–	–	–	–	H8	–	–
7. Tomsk-2	2	–	–	–	–	–	H12, H14	0.56 (0.28)	1.000 (0.500)
8. Kemerovo	1	–	–	–	–	–	H13	–	–
9. Novosibirsk	1	–	–	–	–	–	H7	–	–
10. Altay	6	–	–	–	–	–	H9, H10(2), H11, H22, H23	0.37 (0.10)	0.930 (0.120)
11. W. Sayan	2	–	–	–	–	–	H28(2)	0	0
12. Krasnoyarsk	1	–	–	1	–	–		–	–
13. Tuva-1	4	–	–	1	–	–	H27, H29(2)	0.13 (0.04)	0.833 (0.220)
14. Tuva-2	2	–	–	–	–	–	H24, H25	0.45 (0.23)	1.000 (0.500)
15. Irkutsk	1	–	–	1	–	–		–	–
16. Hamar Daban	3	–	–	–	–	–	H30(3)	0	0
17. Taymyr	2	–	–	–	–	–	H20, H21	0.11 (0.06)	1.000 (0.500)
18. Chita	2	–	–	–	–	–	H38(2)	0	0
19. N. Baikal	1	–	–	–	–	–	H41	–	–
20. Chara	7	–	–	–	–	–	H36(6), H37	0.03 (0.02)	0.290 (0.200)
21. Olekma	2	–	–	–	–	–	H33, H47	0.56 (0.28)	1.000 (0.500)
22. Amalat	3	–	–	–	–	–	H50(3)	0	0
23. Solovievsk	1	–	–	–	–	–	H49	–	–
24. Zeia	4	–	–	–	–	–	H51, H52(3)	0.06 (0.03)	0.500 (0.270)
25. Khabarovsk	2	–	–	–	–	–	H39, H40	0.11 (0.06)	1.000 (0.500)
26. Chulman	5	–	–	–	–	–	H31, H32, H34(2), H35	0.29 (0.08)	0.900 (0.160)
27. Yana	1	–	–	–	–	1		–	–
28. Kolyma	3	–	–	–	1	–	H42, H45	0.38 (0.11)	1.000 (0.270)
29. Omolon	5	–	–	–	2	–	H43(3)	0.07 (0.02)	0.600 (0.180)
30. Magadan	3	–	–	–	–	1	H46(2)	0.08 (0.04)	0.370 (0.314)

only star-like clusters contracted to observed sequences with ancestral state supported by a wide geographical distribution of the central haplotypes (Crandall & Templeton 1993).

We analysed the population data set using the isolation with migration (IM) under changing population size model (Hey & Nielsen 2004; Hey 2005). The model assumes the two populations descended from a panmictic ancestral population at some time in the past with migration possibly continuing between the diverging populations (Nielsen & Wakeley 2001). This model is applicable to intraspecific data as it does not require reciprocal monophyly between samples of sequences from different populations (Won & Hey 2005). To fit the IM model to the data, we used a coalescent simulation that generates all possible genealogies

with a Markov chain Monte Carlo approach and estimates posterior probability densities for seven parameters, each scaled by the mutation rate, including divergence time, two-directional migration rates, the splitting parameter and effective population sizes of the two current and the ancestral populations. We used the IM program (Hey & Nielsen 2004) to run the simulation under the Hasegawa–Kishino–Yano substitution model as four nucleotide sites in the data set had multiple substitutions. The analysis was done using multiple independent runs, starting with a burn-in period of 100 000 steps, and running for 5 million steps. Convergence on a stationary distribution was assessed by monitoring similarity of posterior distributions from independent runs and by assessing the autocorrelation

parameter values over the run (Won & Hey 2004). The peaks of the resulting posterior distributions were taken as maximum-likelihood estimates of parameters (Nielsen & Wakeley 2001). Credibility intervals were recorded for each parameter as the 90% highest posterior density (HPD) interval, which represents the shortest span that includes 90% of the probability density of a parameter (Hey & Nielsen 2004). To convert the divergence time estimates scaled by the mutation rate to calendar years, we used the divergence rate of 6.5% per million years that equates to 2.9×10^{-5} mutations per year for the whole gene region sequenced.

Haplotype (h) and nucleotide (π) diversities and their variances within populations were calculated using the program DNASP version 3 (Rozas & Rozas 1999). As only one individual was available in each of the eight localities 6, 8, 9, 12, 15, 19, 23, 27 (Table 1), these localities were excluded from the population diversity analysis. To assess the distribution of mtDNA variation, we used the analysis of molecular variance (AMOVA, Excoffier *et al.* 1992) incorporating the haplotype frequencies and nucleotide divergence between haplotypes. Significance of genetic differentiation was tested by permuting the haplotypes among the populations and then populations among the regions using the program ARLEQUIN 3.1 (Excoffier *et al.* 2005). We used the frequency distribution of the number of pairwise differences among haplotypes (the mismatch distribution) to detect and estimate timing of population expansion (Rogers 1995). The timing of population expansion was estimated by the mode (τ) of the mismatch distribution expressed in units of mutational time as $t = \tau/2$, where t is the expansion time in number of generations and   is the mutation rate per generation for the whole sequence (Rogers 1995). Parametric bootstrapping was used to test the observed mismatch distribution goodness-of-fit to the sudden expansion model and to obtain confidence intervals around the estimated mode of mismatch distribution (Schneider & Excoffier 1999).

Results

There were 52 different cytochrome *b* haplotypes defined by 67 variable sites among the 100 wood lemmings. Forty-seven nucleotide sites were informative for the maximum parsimony median-joining haplotype network. The comparison of the likelihood scores of trees constructed with and without molecular clock assumption showed that the sequences have evolved at approximately constant rates ($P > 0.05$). Therefore, variation in the cytochrome *b* gene is suitable for approximate dating of historical events.

Phylogeographic structure

The neighbour-joining tree (Fig. 1) shows that the wood lemming haplotypes are divided into two reciprocally monophyletic clades with significant bootstrap support. The maximum-likelihood trees in the molecular clock test recover the same monophyletic clades. All haplotypes from the Amalat River (H50; location 22) and the Zeya River basin (H49, H51, H52; locations 23, 24) formed a Southeastern clade (Figs 1 and 2) and a Northern clade included 48 haplotypes distributed over a vast area from Scandinavia to the Pacific Coast. The net nucleotide divergence (0.9 ± 0.3%) between the two clades with correction for intraclade divergence indicates that this division resulted from separation about 138 000 years ago (95% CI, 49 000–229 000 years).

There were no significant phylogenetic divisions within the Northern clade. Only four external nodes, that defined clusters with no more than two haplotypes from the same populations, received higher than 90% support from the bootstrap test on the neighbour-joining tree (Fig. 2). However, shallow phylogeographic structure without significant monophyly was detected as haplotypes from the same geographical regions formed separate clusters. To further investigate the shallow phylogeny of the Northern clade and identify ancestral haplotypes, we used the median-joining network, an approach developed specifically for intraspecific data. The network (Fig. 3) shows the three basal nodes that putatively represent ancestral roots for respective groups of haplotypes within the Northern clade. The Western group of haplotypes is distributed from Scandinavia (location 1) through Finland (2, 3), Northern Ural (4), the Ob River (5, 6, 7, 8, 9) to the Altay Mountains (10) in the south (Figs 1 and 3; Table 1). This is the only group for which the most basal haplotype (H5) was observed and its ancestral state in the Western group is further supported by wide geographical distribution (Crandall & Templeton 1993) from Ural (4) to Eastern Finland (3; Table 1). The Central group includes haplotypes distributed in the Yenisey River basin (11, 12, 17), Tuva Mountains (13, 14) in the south, and to the west end of Baikal Lake (15, 16). The Eastern group is distributed over a wide sector of Northern Asia to the east of Baikal Lake. These three groups of haplotypes are allopatrically distributed and, thus, represent phylogeographic groups within the Northern clade. The only exception is that the haplotypes H22 and H23 from the Central group were found in the Altay Mountains (10) in secondary contact with haplotypes belonging to the Western group.

Population differentiation, mtDNA diversity and demographic history

To assess the distribution of mtDNA variation within the geographical range of the Northern clade, we used AMOVA incorporating the haplotype frequencies and nucleotide divergence between the haplotypes (Φ_{ST}) among 13 populations with sample size of three or more individuals (Table 1). We
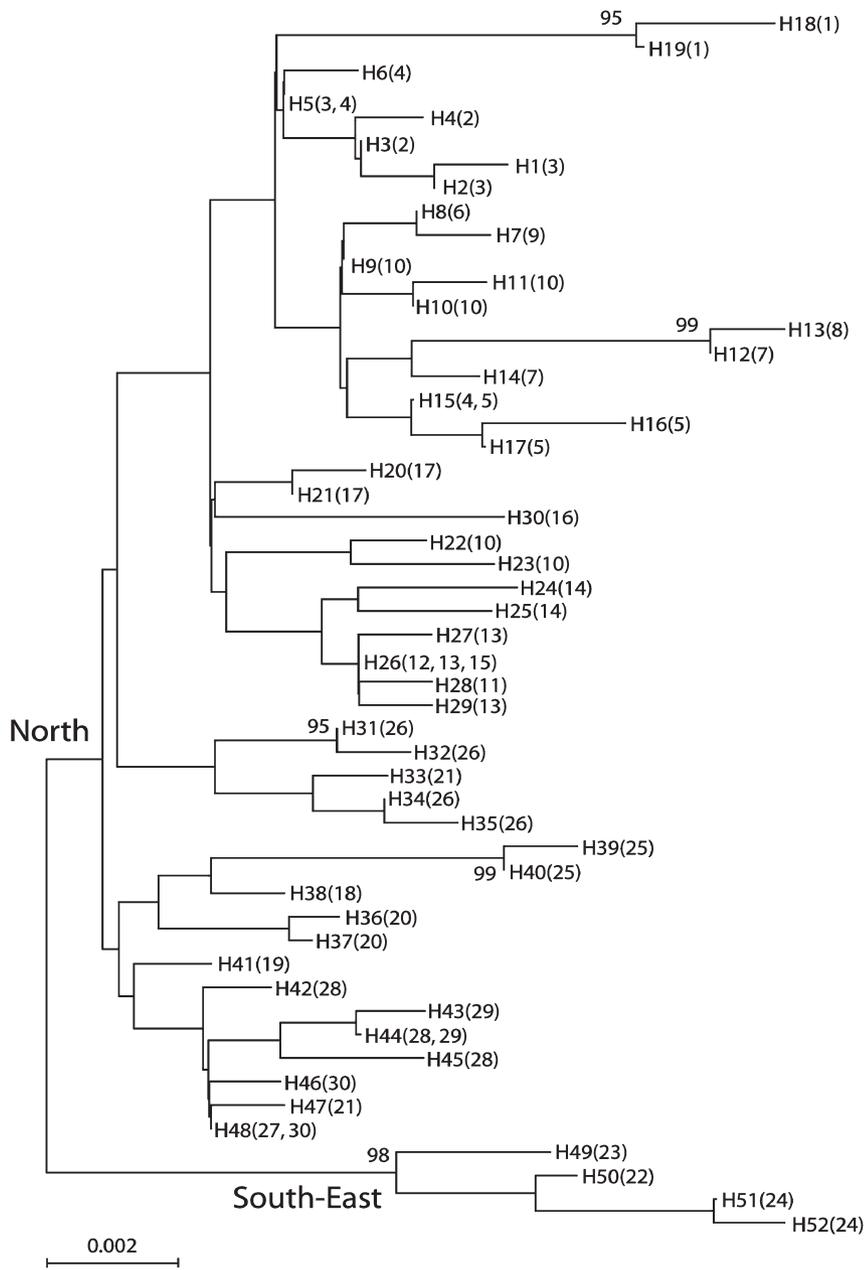
Fig. 2 Neighbour-joining tree showing phylogenetic relationships among haplotypes in the wood lemmings. Clades are designated as in Figs 1 and 3. Haplotype numbers and location numbers in brackets refer to Table 1. Bootstrap percentages with values over 90 are shown for nodes.

divided populations into three regional groups according to geographical distribution of the Western, Central and Eastern groups defined by the haplotype network. The analysis revealed significant differentiation among geographical regions (Φ_{CT} = 0.33; P < 0.001; 32.6% of total variance) corresponding to the ranges of the phylogeographic groups and among populations within regions (Φ_{SC} = 0.76; P < 0.0001; 50.9% of total variance). Most haplotypes were restricted to a single population (Table 1); only five haplotypes (H5, H15, H26, H44, H48) were shared among two or three populations. Significant genetic differentiation reflects smaller genetic distances among individuals from

the same region or population compared to the distances between haplotypes from different regions or populations.

To infer the divergence time and migration parameters between the regional groups of haplotypes, we used the IM model for two comparisons: the Western (n = 44) and Central (n = 17) groups and then the Central (n = 17) and Eastern (n = 31) groups. The marginal posterior probability distribution of the divergence time parameter t was clearly resolved for both comparisons with sharp peaks at 3.1 (90% HPD interval: 2.0–5.0) for Western and Central (Fig. 4a); 3.7 (90% HPD: 2.4–6.2) for Central and Eastern (Fig. 4b). When converted to a scale of years, the divergence time between
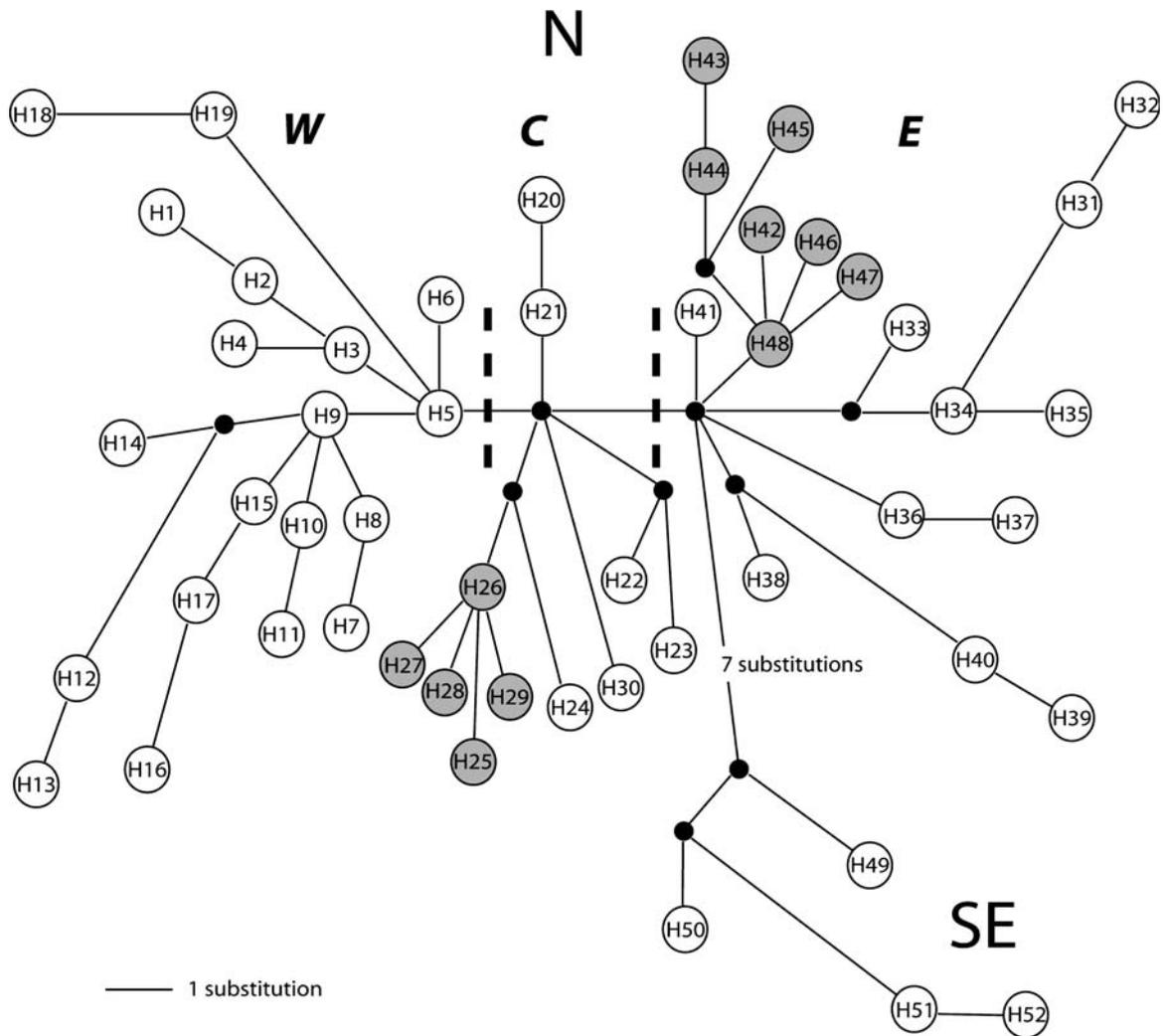
Fig. 3 Median-joining network showing phylogenetics relationships among haplotypes in the wood lemming. Clades and haplotypes groups are designated as in Figs 1 and 2. Haplotype numbers refer to Table 1, and haplotypes belonging to the two star-like clusters are shaded.

the Western and Central groups was estimated to be 106 000 years ago (90% HPD: 69 000–172 000 years), and 127 000 years ago (90% HPD: 83 000–214 000 years) between the Central and Eastern groups. These similar divergence time estimates suggest that divergence of the three regional groups was initiated no later than the early stages of the last glacial period (Weichselian; 10 000–115 000 years ago; Svendsen *et al.* 2004). The migration parameters for both directions in the two comparisons revealed peaks at 0.005 (Fig. 4c, d), the lower limit of 90% HPD intervals. Following Won & Hey (2005), the locations of the maximum-likelihood estimates of all migration parameters were interpreted as being at zero. From the IM analysis, the three regional groups of haplotypes appear to have been isolated without gene flow since they began to diverge.

Populations showed a wide span of mtDNA haplotype diversity, ranging from zero to one (Table 1). Nucleotide

diversity varied from zero to 0.56%. Among the populations with three or more individuals sampled, the highest nucleotide diversity estimates (0.37%; 0.38%) were found in the southernmost (about 50°N) location (10) in Altay and in the northern (about 67°N) population (28) from the Kolyma River (Table 1). No significant correlation was detected between nucleotide diversity and geographical latitude (Spearman's rank correlation $r = 0.19$, $P = 0.3901$).

Mismatch distribution analysis showed that the observed distribution of the pairwise mutation differences among haplotypes from the Northern clade was unimodal and fit ($P = 0.22$) the expected distribution under a model of sudden expansion (Fig. 5). The timing of demographic expansion was estimated at 125 000 years ago (95% CI, 85 000–151 000 years) by the mode of mismatch distribution ($\tau = 7.2$, 95% CI, 4.9–8.7) and the mutation rate per generation for the whole sequence (Rogers 1995) obtained from the cytochrome
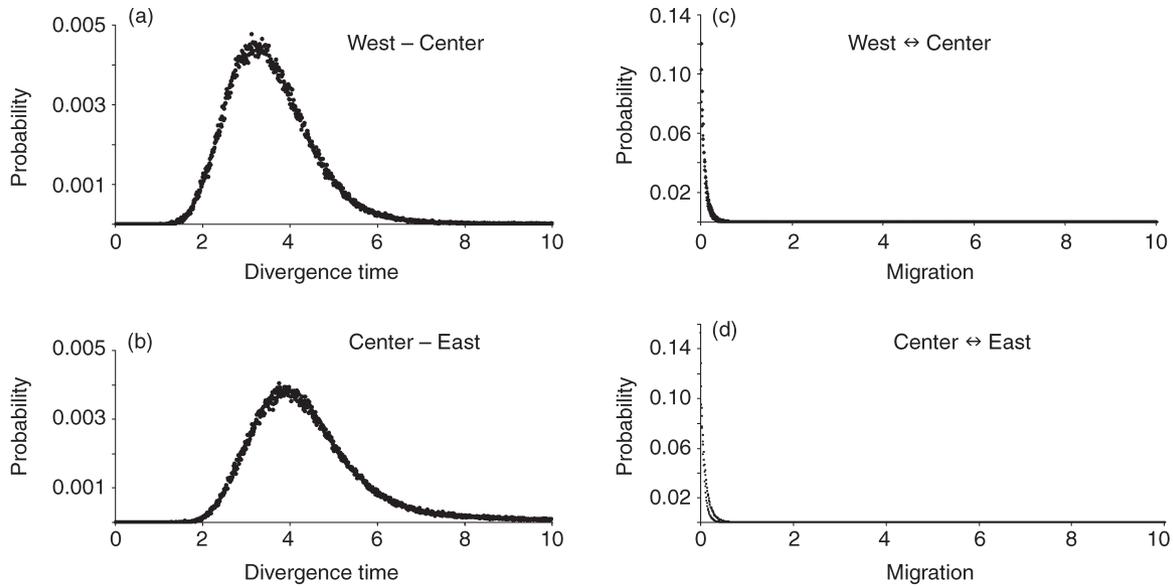
Fig. 4 The marginal posterior probability distribution (scaled by the mutation time) estimated for divergence times (*a, b*) and two-directional migration rates (c, d) between the Western and Central; and the Central and Eastern groups of haplotypes.
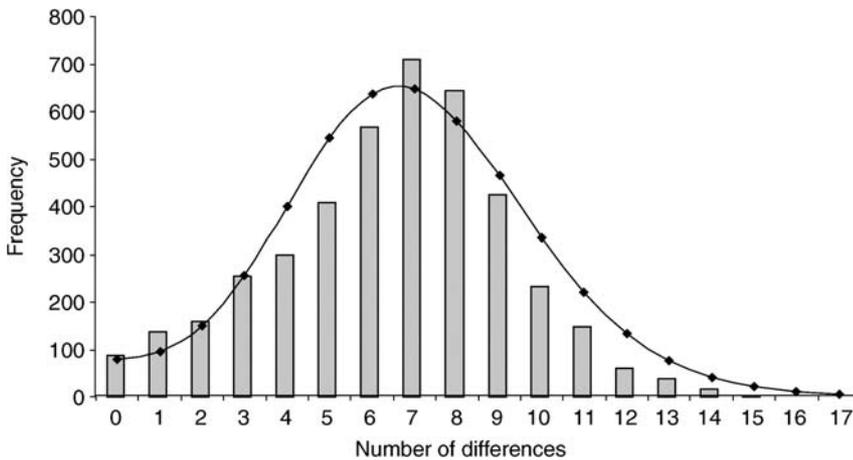
Fig. 5 Distribution of the number of pairwise differences among 92 haplotypes from the Northern clade of the wood lemming. Bars represent the observed distribution and the line represents the expected distribution under the model of sudden expansion fitted to the data.

b divergence rate (6.5% per million years). Similar to the pooled sample from the range of the Northern clade, the mismatch distributions in the Western, Central and Eastern groups did not differ from the distributions expected under the sudden expansion model (P = 0.53; 0.22; and 0.38). The timing of demographic expansion is similar for the Central group 112 000 years ago (95% CI, 80 000–149 000 years; τ = 6.5; 95% CI, 3.5–8.6) and 104 000 years ago (95% CI 59 000–137 000 years; τ = 6.0; 95% CI 3.4–7.9 years) for the Eastern group. A more recent time estimate of 44 000 years ago (95% CI, 15 000–159 000 years; τ = 2.4; 95% CI, 0.9–9.2) was obtained in the Western group. These estimates are approximate but suggest that demographic expansions predated forest advances (after 13 000 years; Demske *et al.* 2005) following the last glacial maximum at 15 000–25 000 years ago (Svendsen *et al.* 2004).

The star contraction algorithm (Forster *et al.* 2001) identified two star-like clusters in the median-joining network. One star-like cluster was detected within the Central groups (Fig. 3) and contained the haplotypes (H25–H29) from Tuva Mountains (13, 14) and the adjacent part of the Yenisey River basin (11, 12, 15; Table 1; Fig. 1). Another star-like cluster was identified in the northern part of the Eastern group and included all haplotypes (H42 – H48) found from the Yana River (27) through the Kolyma River Basin (28; 29) to the north Pacific Coast (30). The star-like phylogeny indicates a reduction in historical effective size followed by a demographic expansion (Slatkin & Hudson 1991). The time to common ancestry, specifically post-bottleneck time, can be estimated from nucleotide diversity divided by the divergence rate (Rogers & Jorde 1995). From the nucleotide diversity estimates of 0.16 ± 0.05% and 0.27 ± 0.04%, the

Table 2 Eurasian taiga species included in phylogeographic comparisons. Details are in the text and references

Species	mtDNA marker	Phylogenetic discontinuity in SE Siberia	Signs of demographic expansion	Reference
Wood lemming *Myopus schisticolor*	Cyt *b* (886 bp)	0.9%	+	This study
Flying squirrel *Pteromys volans*	Cyt *b* (1140 bp)	0.7%	+	Oshida *et al.* (2005)
Great tit *Parus major*	Control region (578 bp)	5.6%	+	Kvist *et al.* (2003)
Great spotted woodpecker *Dendrocopos major*	ND2, 3; cyt *b* (1365 bp)	3.0%	+	Zink *et al.* (2002a)
Siberian newt *Salamandrella keyserlingii*	Cyt *b* (825 bp)	10.5%	+	Berman *et al.* 2005
Willow tit *Parus montanus*	Control region (592 bp)	Not detected	+	Kvist *et al.* (2001)
Three-toed woodpecker *Picoides tridactylus*	ND2, 3; cyt *b* (1234 bp)	Not sampled	+	Zink *et al.* (2002b)
Hairy wood ant *Formica lugubris*	ND6, cyt *b* (1442 bp)	Not sampled	+	Goropashnaya *et al.* (2004)
Black-backed meadow ant *Formica pratensis*	ND6, cyt *b* (1442 bp)	Not sampled	+	Goropashnaya *et al.* (2004)

expansion time could be estimated as 25 000 years ago (95% CI, 9500–39 700 years) for the Tuva–Yenisey group and 41 500 years ago (95% CI 29 500–53 500 years) for the Yana–Kolyma group of haplotypes.

Discussion

Phylogeographic discontinuity in Southeastern Siberia

The only major phylogeographic discontinuity found in the wood lemming across Eurasia is between the Northern and Southeastern clades of haplotypes. Amount of divergence between the clades suggests that separation was initiated around 140 000 years ago, long before the last glacial maximum (15 000–25 000 years ago), and the confidence interval includes the period of the extensive penultimate glaciation (Saalian, 130 000–190 000 years ago, Svendsen *et al.* 2004). While palaeoenvironments of eastern Eurasia during the Saalian glaciation are not well documented, this phylogeographic division implies that two main lineages of the wood lemming were separated in different refugial areas over the two glacial periods. Their genetic distinctiveness may have been reinforced by secondary contact during the interglacial as suggested for a diverse array of species (Hewitt 2004). The haplotypes of the Southeastern clade were found only in the three locations on the southern limit of the sampling range. Additional sampling farther south, specifically in the taiga regions of northern China (Dongbei region; Xiang *et al.* 2004) is needed to identify the distribution of the Southeastern clade. Although there are limited differences with regard to geographical sampling design, a major south–north phylogeographic break in the Far East also was reported in all other boreal forest species studied from this region (Table 2). The single exception reported to date is the willow tit, *Parus montanus* (Kvist *et al.* 2001). However, additional sampling is needed for the willow tit, as that study included only five individuals from a single location in the south of the Far East. Similar

to the wood lemming, the time of separation between the northern and southern mtDNA lineages was estimated as 140 000 years ago in the flying squirrel (Oshida *et al.* 2005). This similarity indicates temporal congruence in vicariant history (Cunningham & Collins 1994) of the two boreal forest mammals, likely as a result of shared response to the same historical events. In the absence of present geographical barriers, the south–north discontinuity observed in a diverse array of taiga species in the eastern Siberia and the Asian Far East seems to represent a general pattern that reflects isolation followed by colonization from two different refugial sources.

Phylogeography and demographic history in northern Eurasia

In contrast to southeastern Siberia, no phylogeographic discontinuities associated with significant reciprocal monophyly were detected within the Northern clade across the majority of Eurasia. This pattern provides no evidence for refugial separation over several glacial periods. Analysis of demographic history indicated significant demographic expansion in the Northern clade about 125 000 years ago with a confidence interval for the demographic expansion that includes the last interglacial (Eemian, 115 000–130 000 years ago; Anderson & Borns Jr 1997; Svendsen *et al.* 2004). Thus, it is reasonable to assume that the climatic conditions during one of the most extensive penultimate Saalian glaciation (Svendsen *et al.* 2004) would have contracted the wood lemming distribution range across northern Eurasia to a single refugial area. There is no palaeoecological data available to detect geographical location of a boreal forest refugium during the Saalian glaciation. As haplotypes (H41 and H48) most closely related to the basal node (Fig. 2) of the Northern clade were observed east of Lake Baikal, it is possible that current populations of the wood lemming originated in eastern Siberia, underwent demographic expansion and colonized most of Eurasia during forest

advances in the last interglacial (Sher 1991; Tarasov *et al.* 2005). Similar to the wood lemming, no substantial phylogeographic divisions (but clear signs of demographic expansion) were reported in all boreal forest species studied to date across northern Eurasia (Table 2). This taxonomically diverse set includes four avian species, two species of red wood ants and the Siberian newt. While the mismatch distribution was not analysed in the flying squirrel (Oshida *et al.* 2005), the estimate of nucleotide divergence of 0.62% within its north Eurasian lineage suggests a time to common ancestry of 124 000 years ago in the last interglacial. In line with the taiga mammals, the mismatch distribution analysis showed that the last interglacial was probably a period of demographic expansion in the two species of red wood ants (Goropashnaya *et al.* 2004). Contraction of the range of each species to a single refugial area during the Late Pleistocene followed by demographic expansion seems to be a general cause for the limited phylogeographic structure observed across most species of northern Eurasia that are ecologically associated with taiga forest.

In contrast to other boreal forest species, this study revealed shallow but significant regional genetic structure in the wood lemming across northern Eurasia. There are three allopatric and genetically distinct groups of haplotypes within the distribution of the Northern clade. The IM analysis suggests that divergence of these geographical groups occurred in isolation that was initiated during early stages of the last glacial period after a continental scale expansion across northern Eurasia from a single refugial source. Thus, the divergence time in mutational units was too short to generate significant reciprocal monophyly for these geographical groups of haplotypes. All three geographical groups demonstrate signs of demographic expansion dated to the last glacial period (Weichselian; 10 000–115 000 years ago; Svendsen *et al.* 2004) and prior to the last postglacial forest advances (after 13 000 years; Anderson *et al.* 2002; Demske *et al.* 2005). Taken together, these results suggest that shallow regional genetic structure in northern Eurasia probably reflects taiga forest dynamics during the last glacial period. Palaeogeographical reconstruction detected three major glacial advances (80 000–90 000 years ago; 50 000–60 000 years ago and 15 000–25 000 years ago) associated with severe climatic conditions during the last glacial period (Svendsen *et al.* 2004). Genetic signs and timing of regional expansions are compatible with range contraction to refugial areas during the most extensive early (80 000–90 000 years ago) or middle (50 000–60 000 years ago) glacial advances followed by expansion within geographical regions in relatively warm interstadials. Although fragmentary, palaeoecological data (Tarasov *et al.* 2000; Anderson *et al.* 2002; Brubaker *et al.* 2005) and fossil records of red-backed voles of the genus *Clethrionomys* (*Myodes*) that are associated with forest environment (Markova *et al.* 1995) show that during glacial advances boreal forest refugia could be located in the Ural and adjacent areas of western Siberia (Western group), northern Mongolia (Central group) and sheltered mountain valleys in eastern Siberia (Eastern group). The high frequency of the most basal haplotype of the Western group and the geographically widespread haplotype (H5) in the Urals further supports a putative forest refugium in this area. While contraction and isolation in regional forest refugia might be important for initiating common ancestry among haplotypes and generating signs of demographic expansion within geographical regions, a higher level differentiation among the populations within the regions (50.9% of total variance) than among the regional groups (32.6%) implies a relatively short time of refugial contraction followed by continuous period of accumulation of mutational differences among populations after expansion from refugial sources. This scenario is indirectly supported by a wide geographical range in the fossil record of forest voles (*Clethrionomys*), indicative of local patches of taiga forest over most of the last glacial period in northern Eurasia (Markova *et al.* 1995).

The two star–like clusters of haplotypes detected within the Central and Eastern groups indicate bottleneck events followed by population expansion on a smaller geographical scale. The estimate of post-bottleneck time (25 000 years ago) and the confidence interval for the Tuva–Yenisey cluster includes a period of forest advance after the last glacial maximum (after 13 000 years; Demske *et al.* 2005). This pattern suggests survival during the last glacial advance in a forest refugium possibly located in northern Mongolia (Tarasov *et al.* 2000) followed by recent colonization of the upper Yenisey River basin. Notably for the present study, this is the only example of a demographic event clearly associated with the last glacial maximum (15 000–25 000 years ago). The haplotypes forming the second star–like cluster are distributed over a wide area from the Yana River through the Kolyma basin to the Pacific coast in northeastern Siberia. The time of common ancestry, specifically post-bottleneck time estimated at 42 000 years ago, precedes the last glacial maximum and implies expansion from a local refugial source of limited size during the warm interstadial following the glacial advance at 50 000–60 000 years ago (Svendsen *et al.* 2004). Recent palaeoecological evidence supports the existence of glacial forest refugia in northeastern Siberia (Brubaker *et al.* 2005). In line with palaeoecological data, our results suggest colonization of northeastern Siberia by the wood lemming from a local forest refugium.

Comparison of phylogeographic structure across a taxonomically diverse array of species that are ecologically associated with the taiga forest (Table 2) revealed a similar pattern with two general aspects. First, the major south–north phylogeographic discontinuity observed in five out of six species studied in the southeastern Siberia implies vicariant separation in two different refugial areas. Similar divergence estimates across the major split suggest that separation was

initiated during the penultimate glacial period and indicate temporal congruence of vicariant history in the two mammalian species. Limited distribution of the Southeastern lineages provides no evidence for the importance of the putative Southeastern refugial area for postglacial colonization of northern Eurasia by boreal forest species. Second, the lack of phylogeographic divisions associated with significant reciprocal monophyly and genetic signs of demographic expansion in all nine boreal forest animal species studied to date across northern Eurasia imply contraction of each species to a single refugial area during the Late Pleistocene followed by range expansion on a continental scale. Estimates of demographic expansion time in four species of insects and mammals are compatible with the period of forest advance during the last interglacial. Similar phylogeographic patterns observed in this taxonomically diverse set of organisms with different life histories and dispersal potentials likely reflects the historical dynamics of their common environment, the taiga forest in northern Eurasia.

To further elucidate the importance of historical landscape dynamics, we compared phylogeographic patterns across codistributed, taxonomically closely related species with similar life histories but contrasting habitat and landscape associations. Phylogeography of the wood lemming was compared with geographical patterns of cytochrome *b* variation observed in codistributed species of north Eurasian arvicoline rodents, like true lemmings *Lemmus* and the root vole *Microtus oeconomus*, both ecologically associated with mesic tundra and grassland habitats (Brunhoff *et al.* 2003; Fedorov *et al.* 2003). Although the majority of the distribution of true lemmings covers the Arctic tundra, *Lemmus* occurs in mountain tundra and open bog habitats within the boreal forest zone in Fennoscandia and the eastern Siberia. The root vole is largely codistributed with the wood lemming and associated with open mesic grassland habitats across the taiga zone, but also occurs in the tundra and steppe zones. In contrast to the wood lemming, both species demonstrate strong phylogeographic structure across northern Eurasia with three significant longitudinal divisions. The average intergroup divergence estimates of 4.5% (range 1.8–7.9%; minimum 280 000 years of separation) for true lemmings and 2.3% (2.0–2.9%; minimum 300 000 years) for the root vole are an order of magnitude greater than the average estimate of 0.25% among the regional groups of the wood lemming. While the limited phylogeographic structure in the Northern clade of the wood lemming reflects isolation during the last glaciation after a continental scale expansion across northern Eurasia from a single refugial source during the last interglacial, the depth of phylogeographic splits in the arvicoline species associated with treeless habitats and landscapes suggests continuous vicariant separation over several glacial–interglacial periods. Results of intraspecific comparisons show that this history

of a dynamic landscape was important in determining continental-scale phylogeographic structure in northern Eurasia.

In conclusion, continental wide phylogeography and demographic history of the wood lemming reflect the dynamic history of the taiga forest during the Late Neogene. Successive range contractions and expansions on different spatial scales represented the primary historical events that shaped geographical patterns of genetic variation. Approximate time estimates, even under a relatively fast substitution rate, suggest that the majority of contraction–expansion events predated the last glacial maximum and subsequent period of the forest expansion in northern Eurasia. More broadly, our study is consistent with recent evidence suggesting that rather then shifting south to track warmer environments, some forest species survived the last glaciation in northern refugia with a locally favourable climate permitting development of tree cover (Goropashnaya *et al.* 2004; Kotlik *et al.* 2006). Our comparative phylogeographic study also identifies a contact zone between two evolutionarily isolated areas (in southeastern Siberia and the Far East) and generates an impetus for similar analyses in other species from this region with implications for conservation strategies.

Acknowledgements

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