*Molecular genetics in animal ecology. Edited by P. A. Racey,
P. J. Bacon, J. F. Dallas and S. B. Piertney*

Colonization history in Fennoscandian rodents

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Fennoscandia probably constitutes one of the best places on earth to study faunal history. During the height of the most recent glacial period Fennoscandia was completely covered with ice. Thus, the majority of extant species must originate from ancestors who survived the latest glaciation in non-glaciated areas outside Fennoscandia. Moreover, the geography and geological history of Fennoscandia suggests that post-glacial recolonization by land mammals must have been restricted to specific routes in time and space. Phylogeographic surveys of mitochondrial DNA (mtDNA) variation in Fennoscandian rodents have demonstrated that glacial history and patterns of post-glacial colonization have played a major role in shaping present day patterns of genetic differentiation within species. Thus, the genetic imprints of historical demographic conditions and vicariant geographic events have been retained within species and can be used to infer the history of populations. The field vole (*Microtus agrestis*) is used to illustrate these data and processes. Comparisons are made with phylogeographic surveys of the bank vole (*Clethrionomys glareolus*), the eastern house mouse (*Mus musculus*) and the wood lemming (*Myopus schisticolor*) as well as a few other species for which less extensive studies have been performed. The main patterns of post-glacial colonization of Fennoscandia by rodents are described. The effects of timing and patterns of colonization on contemporary population genetic structure and levels of genetic variation are discussed. Specifically, the effects of hybridization and introgression as well as founder events and bottlenecks are explored.

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ADDITIONAL KEYWORDS:—biogeography – phylogeography – mitochondrial DNA – field vole (*Microtus agrestis*) – genetic diversity – bottleneck – Y chromosome – contact zone – glaciation.

CONTENTS

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INTRODUCTION

On the basis of extant subspecies and species distributions as well as subfossil data and geological history, scenarios for the faunal history of Fennoscandia (Finland and Scandinavia) were suggested by Nilsson (1847). He claimed that there were two major routes for the recolonization of Fennoscandia by land mammals after the last glaciation. Thus, some mammals immigrated from the south via land bridges, whereas other species used a north-east colonization route. A third category of species may have used both routes. Ekman (1922) and Siivonen (1972,1982) further extended Nilsson's hypothesis, and recent reviews include Lepiksaar (1986), Liljegren & Lagerås (1993) and Björck (1995b). Evidence for the recolonization scenario is nowadays based upon data from a wide range of scientific fields including, for example, palaeoclimatology and palaeobotany. Yet the data are "too sparse and one-sided to provide a foundation for the reconstruction" of the recent history of Fennoscandia (Lepiksaar, 1986). The recolonization scenarios presented for different organisms remain models which need to be tested (Lepiksaar, 1986).

In this review we will show how new, molecular tools can be used to directly test the old biogeographic hypotheses. Thus, present day genetic methods provide means to describe more detailed patterns of genetic differentiation within species, and make it possible to interpret the evolutionary history of populations. Moreover, the genetic analyses enable us to evaluate to what degree history has shaped the current patterns of intraspecific genetic differentiation. The new field is called 'intraspecific phylogeography' (Avise *et al.*, 1987).

Comparative phylogeography

To date, the majority of phylogeographic analyses in animals have been carried out using mitochondrial DNA (mtDNA). MtDNA is a genetic marker which due to its unique features provides detailed genealogical information and thus enables a phylogenetic and historical perspective on population genetic structure (Avise, 1994). Ideally, a phylogeographic analysis consists of three steps. First, a phylogenetic analysis of genetic variation within a species is performed, and the geographic distribution of significant phylogenetic lineages established. Second, an evaluation or test is made to find out to what degree historical events have shaped the current phylogeographic patterns. Third, an interpretation of the evolutionary history of the phylogeographic units is made.

The second and third steps of the analysis in particular contain many pitfalls. Templeton (Templeton, Routman & Phillips, 1995; Templeton, 1998) has designed a test for distinguishing between historical events (e.g. range expansion and colonization), and evolutionary factors (e.g. restricted gene flow). Unfortunately, the sampling designs of many phylogeographic surveys make them unsuitable for this kind of analysis. Furthermore, although it is now generally recognized that at least large-scale geographic patterns are due to historic factors (Avise, 1994; Barton & Wilson, 1995), the history of genes may not always reflect the history of populations (Avise & Ball, 1990; Barton & Wilson, 1995).

The use of several independent genetic markers represents one way to perform the last steps of a phylogeographic analysis. Here we will mainly present mtDNA data but will refer to other genetic data such as chromosomes and allozymes when

possible. Another widely used method for inferring the history of populations involves comparison of phylogeographic patterns among several species. The underlying idea is that similar patterns among different species are due to common biogeographic events. This comparative approach to phylogeography has been employed with much success in North American studies (Avise, 1992, 1994). Recently, a number of reviews on comparative phylogeography in Europe have been published (Hewitt, 1996; Taberlet *et al.* 1998; Bilton *et al.*, 1998). These papers emphasize the role of glacial refugia and focus on southern and central Europe.

In this review we reconstruct the recent biogeographic history in Fennoscandian land mammals mainly by comparison of phylogeographic surveys of rodent species. The different patterns of post-glacial colonization of Fennoscandia by rodents are described, and the effects of timing and patterns of colonization on contemporary population genetic structure and levels of genetic variation are discussed.

GLACIAL AND BIOGEOGRAPHIC HISTORY OF FENNOSCANDIA

It is now recognized that most extant species in the northern hemisphere have undergone repeated cycles of range contraction and expansion due to habitat shifts induced by glacial periods (e.g. Hewitt, 1996; Riddle, 1996). A detailed knowledge of the geological history thus constitutes a crucial part of a phylogeographic analysis. In this review we focus on the effects of the most recent glacial period with an emphasis on tracking late glacial and post-glacial events. Fennoscandia constitutes an ideal place for the study of the recent faunal history for several reasons. The entire area was covered with glacial ice during the height of the latest glaciation. Consequently, virtually all extant species in Fennoscandia must have survived in populations outside the glacial ice-sheet, and recolonized the area at the end of the glacial period. Moreover, the geography and geological history of Fennoscandia suggest that recolonization by land mammals was restricted to specific routes in time and space. It is also evident that the area constitutes a possible meeting place for three different faunal elements: Arctic, Siberian and European.

The last glaciation (Weichselian) started about 115 000 years ago. The maximum extent of the glacial ice sheet occurred 21 000–17 000 ^{14}C years ago (= BP), when the ice covered most of northern Europe (Andersen & Borns, 1997). The retreat of the ice sheet began soon after, opening up routes from the south and north–east for the recolonization of Fennoscandia by terrestrial animals. The southern immigration route was the first to become accessible with the deglaciation of southernmost Sweden around 14 000 BP (Lagerlund & Houmark-Nielsen, 1993). However, climatic and geological data suggest that colonization from the south by most land mammals, and especially rodents, was not feasible until 11 200 BP when a land bridge connecting southernmost Sweden with the European continent was established (cf. Björck, 1995a). This land bridge lasted for about 400 years, but the latter half of the period was characterized by drastic climate deterioration (Björck & Möller, 1987). Therefore, most founder populations probably went extinct during the cold spell (cf. Jaarola & Tegelström, 1996, Björck, 1995b) as suggested by subfossil records of some mammals (Liljegren & Lagerås, 1993). Instead, it seems likely that most early immigrants used the next land bridge which was established at 10 300 BP and lasted for 1100 years (cf. Björck, 1995a, b; Jaarola & Tegelström, 1996). This wide
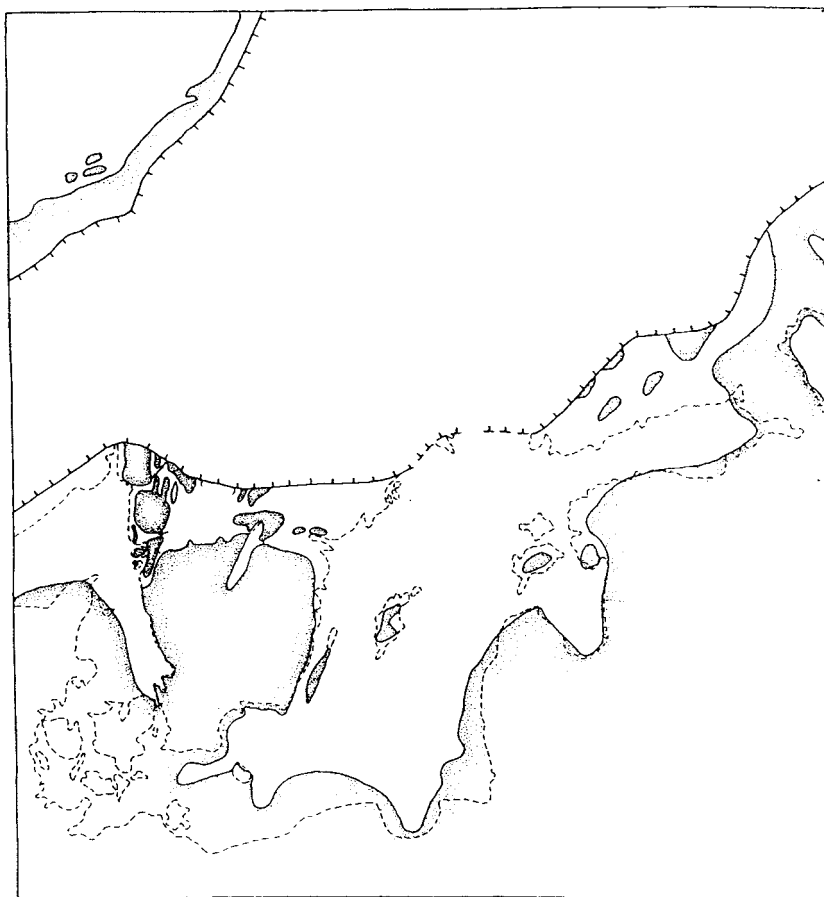
Figure 1. Fennoscandia at 9750 BP (= 11 200 calendar years ago) (after Björck, 1995a, pers. comm.).

and long-standing land bridge must have enabled a massive immigration of land mammals (Fig. 1), evidenced by the fact that the oldest subfossil findings of many mammalian species in southern Sweden date back to about 10 000 BP (cf. Lepiksaar, 1986; Liljegren & Lagerås, 1993). A final, rather narrow land bridge between Sweden and the Danish island Zealand lasted for an additional 1000 BP years (Fig. 2), but at 8200 BP southern Sweden was permanently cut off from the continent by the 4–28 km wide Öresund strait.

The north-east colonization route was opened up with the onset of the deglaciation of south-west Finland about 10 000 BP (Ignatius, Korpela & Kujansuu, 1980). A rapid deglaciation of northern Scandinavia began at 9300 BP. By then all of southern and eastern Fennoscandia was ice-free and the climate was as warm as today (Aaris-Sørensen, 1988; Björck, 1995a; Lagerbäck, pers. comm.). An ice-free north–south corridor through northern Sweden was established about 9000 years BP (Björck, 1995a; Lagerbäck, pers. comm.) enabling secondary contact between northern and southern immigration contingents.
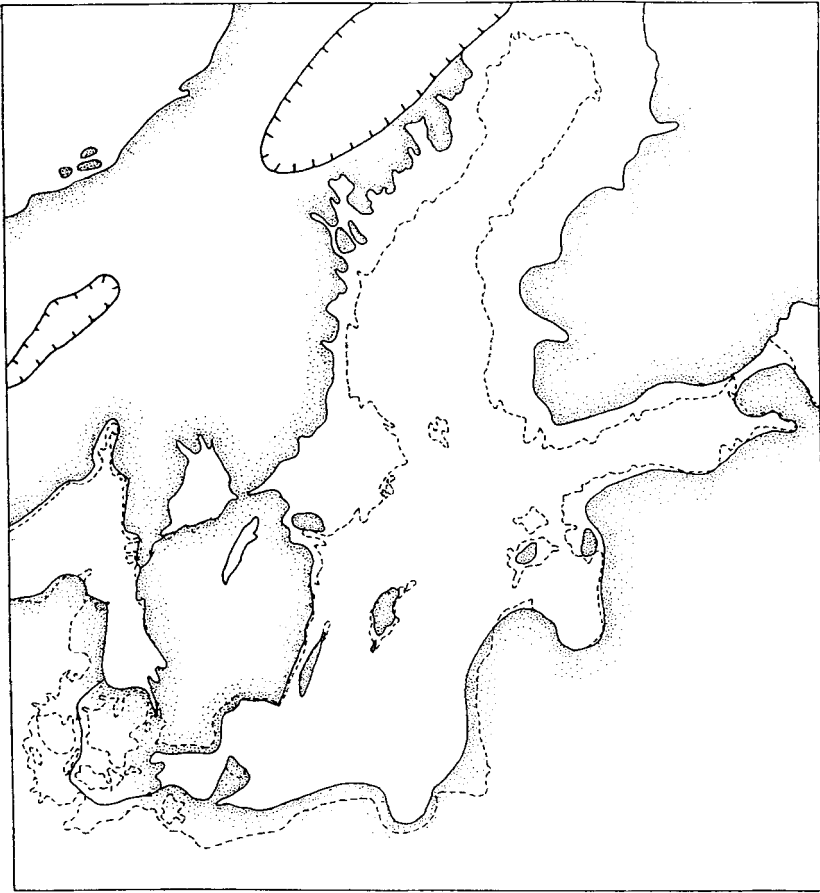
Figure 2. Fennoscandia at 8800 BP (=9900 calendar years ago) (after Björck, 1995a, pers. comm.).

COLONIZATION PATTERNS IN FENNOSCANDIA AS REVEALED BY GENETIC ANALYSES

Phylogeographic surveys of rodents have shown that there are three main patterns for late glacial and post-glacial colonization of Fennoscandia by land mammals—from the north-east, from the south, and from both directions.

Colonization from one direction only is exemplified by the wood lemming (*Myopus schisticolor*) (from the north) and the eastern house mouse (*Mus musculus*) (from the south), whereas the bidirectional pattern is illustrated by the field vole (*Microtus agrestis*) and the bank vole (*Clethrionomys glareolus*) as well as a few other terrestrial mammals.

Colonization from the north-east

The wood lemming belongs to the taiga fauna and mainly occurs in old spruce forests rich in mosses. There are no subfossil findings of wood lemmings in Scandinavia, and the hypothetical colonization scenario of the species is therefore
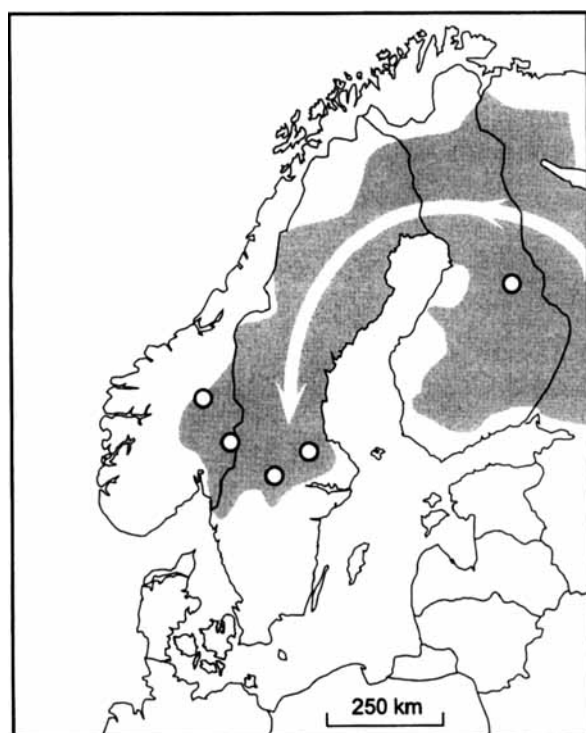
Figure 3. Post-glacial recolonization of Fennoscandia from the north-east as exemplified by the wood lemming. The geographic distribution of the Fennoscandian mtDNA lineage in the wood lemming is indicated in white (after Fedorov *et al.*, 1996). The shaded area shows the current distribution range of the woodlemming.

based upon the expansion of spruce forest into the Scandinavian peninsula (Lepiksaar, 1986). Consequently, the wood lemming is postulated to have immigrated to northern Scandinavia from the north-east through Finland during the subboreal climatic period between 5000 and 2500 BP (Lepiksaar, 1986).

Genetic surveys based on RFLP analyses of mtDNA (Fedorov, Jaarola & Fredga, 1996) and allozymes (Fedorov, Fredriksson & Fredga, 1995) demonstrate that Lepiksaar's colonization model for the wood lemming is correct. Thus, the mtDNA haplotypes observed in wood lemmings from Sweden and Norway are closely related to the haplotypes found in specimens from Finland, indicating colonization from the north-east (Fig. 3). Furthermore, the occurrence of a star-like mtDNA phylogeny with a central, common haplotype and low nucleotide diversity ($\pi = 0.02\%$, $n = 30$) in Scandinavia, suggests recent post-glacial colonization by a limited number of founders (Fedorov *et al.*, 1996). The allozyme data (Fedorov *et al.*, 1995) are in accordance with this scenario, and it is thus likely that the mtDNA data do reflect the recent population history of Scandinavian wood lemmings.

Colonization from the south

In contrast to all the other rodent species reviewed here, the house mouse is not a natural colonizer but a commensal species introduced via human assistance. The
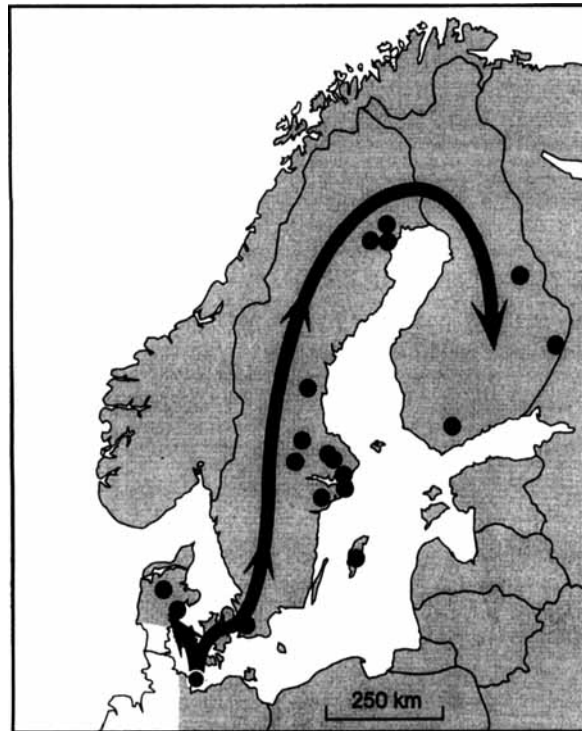
Figure 4. Post-glacial recolonization of Fennoscandia from the south as exemplified by the eastern house mouse (*M. musculus*). The sampling localities with *M. musculus* carrying *M. domesticus* mtDNA haplotypes are indicated in black (after Gyllensten & Wilson, 1987; Prager *et al.*, 1993). The southernmost locality represents a number of sampling localities in East Holstein, Germany. The shaded area shows the current distribution range of *M. musculus*.

establishment of Fennoscandian house mouse populations is believed to have occurred about 4000–5000 calendar years ago with the introduction of agriculture (Prager *et al.* 1993). As the last land connection between southern Sweden and the European continent was cut off already at 8200 BP (see above), it is clear that house mice must have been introduced to Fennoscandia through human mediated transport on boats.

House mice from Sweden, Norway and Finland belong to the eastern species *Mus musculus*, but carry the mtDNA of the western house mouse *M. domesticus* (Gyllensten & Wilson, 1987; Prager *et al.*, 1993). Thus, Fennoscandian house mice represent a clear example of inconsistency between gene phylogeny (mtDNA) and population history.

Using D-loop sequencing data, Prager *et al.* (1993) showed that the Swedish and Finnish house mice immigrated from the East Holstein peninsula in northern Germany (Fig. 4), a process that probably involved island-hopping via Danish islands to southernmost Sweden as originally suggested by Gyllensten & Wilson (1987). Allozyme data support this scenario (Gyllensten & Wilson, 1987). Thus, the Finnish mice are supposed to derive from the population that first colonized southern Sweden and then expanded north and north-east. The occurrence of one locality
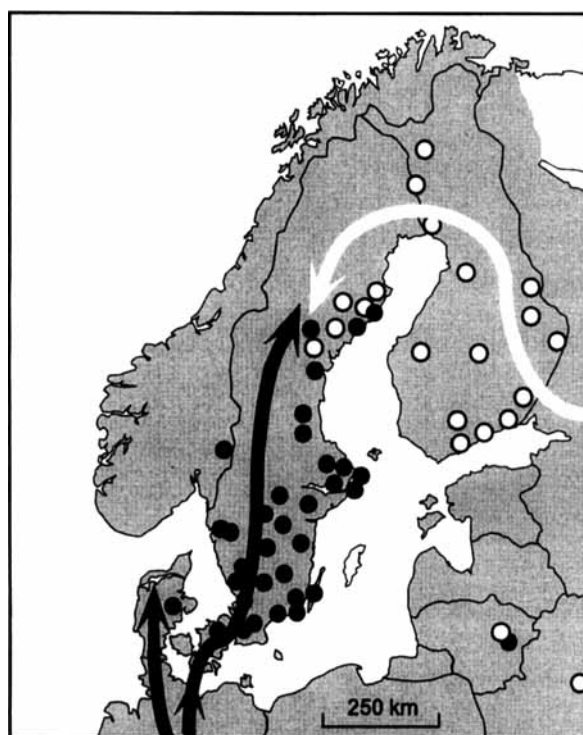
Figure 5. Post-glacial recolonization of Fennoscandia from the south and north-east as exemplified by the field vole. The geographic distribution of the two major mtDNA lineages, north-east (white) and south (black), is also depicted (after Jaarola & Tegelström, 1995, 1996; Jaarola & Searle, 1998). The shaded area shows the current range of the field vole.

in Norway showing mtDNA haplotypes only distantly related to the other Fennoscandian haplotypes suggests the possibility of additional colonization paths to Scandinavia (Prager *et al.*, 1993).

Colonization from the south and north-east

The clearest example of bidirectional colonization is observed in the field vole. The species exhibits two major mtDNA lineages in Fennoscandia, and the geographic distribution of these lineages shows a strict south–north-east partitioning (Fig. 5).

This phylogeographic pattern is shown both by restriction site data (Jaarola & Tegelström, 1995) and sequencing of the cytochrome *b* gene (Jaarola & Searle, 1998). Actually, the two major field vole mtDNA lineages observed in Fennoscandia are part of widespread lineages which, except for a Mediterranean lineage, split the whole species into a western and an eastern unit (Jaarola & Searle, 1998). The two Fennoscandian mtDNA lineages represent ancient evolutionary units that have remained separated for at least one glacial period (Jaarola & Tegelström, 1995). The southern mtDNA lineage in Fennoscandia most likely derives from a Balkan refugium (Jaarola & Searle, 1998). This population expanded into Fennoscandia

from the south via the late glacial and post-glacial landbridge(s) connecting southern Sweden with the Danish islands and Germany (Jaarola & Tegelström, 1995, 1996). Subfossil data show that the field vole was already present in Denmark 12 000 BP (Aaris-Sørensen, 1988). Thus it is possible that some colonization of southern Sweden may have occurred around 11 000 BP, but that the majority of the ancestors of the present day field voles most likely immigrated after 10 200 BP (Jaarola & Tegelström, 1996). The north-east lineage derives from a Russian refugium (Jaarola & Searle, 1998). The ancestors of this lineage first colonized Finland, probably soon after the deglaciation which started 10 000 BP, and then expanded their range into northern Sweden (Jaarola & Tegelström, 1995).

Strong support for this biogeographic scenario comes from comparison with other mammals. Thus, similar phylogeographic patterns are also observed in the bank vole (Tegelström, 1987), the common shrew (*Sorex araneus*) (Fredga & Nawrin, 1977; Searle, 1984; Fredga, 1996) and the brown bear (*Ursus arctos*) (Taberlet & Bouvet, 1994.

The bank vole shows a macrogeographic pattern of mtDNA lineage distribution that is very similar to that of the field vole. However, the phylogeographic pattern is somewhat more complicated with the Danish population belonging to the north-east lineage (Tegelström, unpublished; Mascheretti & Searle, manuscript). Furthermore, the bank voles in northern Sweden and Finland carry mtDNA derived from the red-backed vole (*C. rutilus*) (see below) (Tegelström, 1987; Tegelström *et al.*, 1988). All in all, however, it is clear that the bank vole represents an early immigrant that has used both the southern and north-eastern colonization routes (cf. Jaarola & Tegelström, 1995).

The brown bear in Fennoscandia currently has a fragmented distribution, but it is obvious that the mtDNA phylogeographic pattern in this species represents yet another case of south–north-east division (cf. Taberlet & Bouvet, 1994). In the common shrew the phylogeographic pattern is represented by chromosome races (Fredga & Nawrin, 1977; Searle, 1984; Fredga, 1996). Hence, the chromosome races in southern and central Sweden belong to the West European karyotypic group, whereas the races in northern Fennoscandia belong to the North European group (references in Searle & Wojcik, 1998).

In summary, the similar phylogeographic patterns among several species of small mammals, as well as the brown bear, clearly demonstrate that an explanation for the congruent intraspecific patterns can be found in common historic events (Jaarola & Tegelström, 1995). Further support for the recolonization model comes from an example of co-evolution of virus and host animal. Hörling *et al.*, (1996) showed that the Puumala hantavirus in the bank vole exhibits two distinct lineages in Sweden, and that the geographic distribution of these RNA virus lineages coincides with the distribution of the two major bank vole mtDNA lineages. Consequently, the two genetic variants of the Swedish Puumala virus mirror the recent evolutionary history of the bank vole.

CONTACT AND SUTURE ZONES

Intraspecific contact zones for all the small mammal species above, i.e. the field vole (Jaarola & Tegelström, 1995), the bank vole (Tegelström & Jaarola, 1998), and
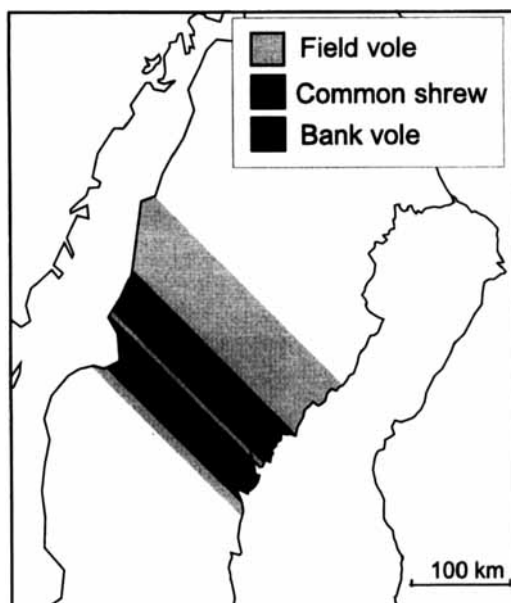
Figure 6. Schematic illustration of the geographic location and width of the small mammal contact zones in northern Sweden. The vole zones constitute contact between major mtDNA phylogeographic groups, and the contact zone for the common shrew reflects contact between two karyotypic groups. (After Jaarola & Tegelström 1995; Fredga 1996, Tegelström & Jaarola, 1998; Fredga & Narain, in press.)

the common shrew (Fredga, 1996; Fredga & Narain, in press) (Fig. 6) as well as the brown bear (Taberlet *et al.*, 1995), are found in the same area in northern Sweden. The contact zone for the Puumala virus lineages has not been located yet, but it seems likely that this zone occurs in the vicinity of the others (cf. Hörling *et al.* 1996). Within each of the mammal species, the contact zone reflects post-glacial secondary contact between southern and northern recolonization contingents having expanded from different glacial refugia. Together these four contact zones thus form a suture zone (Jaarola & Tegelström, 1995) as defined by Remington (1968). The suture zone in northern Sweden constitutes one of four main suture zones described in Europe (Taberlet *et al.*, 1998).

The occurrence of suture zones is often explained as a consequence of some past or present geographic barrier for dispersal. However, the suture zone in northern Sweden is presently not associated with any climatical or zoogeographic boundary, and no major geographic barriers can be found in the area (Jaarola & Tegelström, 1995). For example, *Limes Norrlandicus*, which represents a major floral and faunal border in central Sweden, is located about 300 km south of the centre of the suture zone.

Instead, it seems that the coincidence of the small mammal contact zones is best explained by the species' post-glacial recolonization patterns. All the available data suggest that both the two vole species as well as the common shrew represent early colonizers: the subfossil data (Lepiksaar, 1986), the bidirectional recolonization pattern, and the occurrence of intraspecific contact zones in the same area.

Specifically, the high levels of mtDNA variation observed in all of the three small

mammals in southern and central Sweden (Tegelström, 1987; Jaarola & Tegelström 1995, 1996; Tegelström & Jaarola, unpublished) suggests massive colonization waves via land bridges in the south. By the time the deglaciation of northern Sweden began about 9300 BP, these species were most probably already present north and south of the receding ice-sheet, following it closely. Hence, the last remains of the glacial ice may have acted as a temporary geographic barrier for dispersal south and north, respectively, until an ice-free corridor through northern Sweden was established after 9000 BP (Jaarola & Tegelström, 1995). Thus, the coincidence of the contact zones for the three small mammals in northern Sweden is best explained by synchronous timing of secondary contact due to early range expansion and a past, temporary geographic barrier (Jaarola & Tegelström, 1995).

REGIONAL PATTERNS OF GENETIC VARIATION AND *IN SITU* EVENTS

The southern field vole mtDNA lineage in Sweden can be divided into seven mtDNA sublineages that show a strict but complex phylogeographic pattern (Jaarola & Tegelström, 1996). Substructuring within the southern mtDNA lineage is also observed in the bank vole (Tegelström, 1987; unpublished). Stochastic lineage sorting and limited contemporary gene flow has probably played some role in shaping these patterns. However, both mtDNA and Y chromosome data in the field vole imply that historic events have strongly affected the phylogeographic patterns also at this shallow level. Thus, the pattern of postglacial recolonization of Sweden seems to have largely determined the current population genetic structure of field voles also at this regional level (Jaarola & Tegelström, 1996; Fredga & Jaarola, 1997). Of special interest are indications of *in situ* events.

Within the southern field vole mtDNA lineage there are at least two sublineages that show the imprints of recent bottlenecks (Jaarola & Tegelström, 1996). The strongest evidence for an *in situ* event comes from the southwestern mtDNA sublineage. The geographic distribution of this sublineage is highly coincident with the range of a rearranged Y chromosome not found elsewhere in the species distribution area. Together, these two genetic markers delimit a unique evolutionary unit called the 'Lund' population (Fig. 7) (Jaarola & Tegelström, 1996; Fredga & Jaarola, 1997). The low nucleotide diversity ($\pi = 0.08\%$, $n = 72$) and a star-like phylogeny of mtDNA haplotypes with one or two central haplotypes that are common and widespread, suggest that the Lund population underwent a recent bottleneck in population size, most likely during the initial stages of recolonization of southern Sweden. It also likely that the bottleneck lead to fixation of both the mtDNA and Y chromosome variants. Thus, the Lund population provides one of the few examples in mammals on the fixation of a chromosomal variant directly associated with a drastic reduction of population size. Analysis of the contact zone between the Lu-population and a standard population suggests selection against one type of male hybrids (Jaarola, Tegelström & Fredga, 1997).

The wood lemming (Fedorov *et al.*, 1996) and the house mouse (Gyllensten & Wilson, 1987; Prager *et al.*, 1993) represent two other well characterised cases of mtDNA lineages that show the genetic imprints of either recent population bottlenecks or founding from a few individuals.
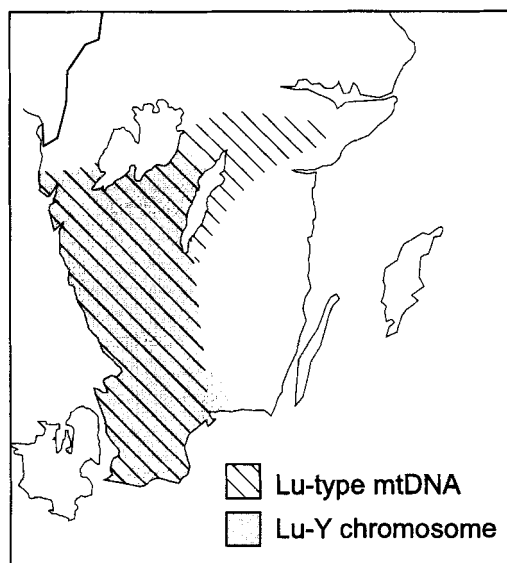
Figure 7. Distribution of the Lund (Lu-) population in the field vole as demonstrated by female (mtDNA) and male (Y chromosome) genetic markers (after Jaarola & Tegelström, 1996; Fredga & Jaarola, 1997; Jaarola *et al.*, 1997).

LEVELS OF GENETIC DIVERSITY ON RECENTLY GLACIATED LAND

As described above there are a number of rodent species that are characterized by low levels of variation either throughout their Fennoscandian range, or in certain populations. Specifically, the fine mapping studies of the field vole demonstrate that striking geographic heterogeneity in the amount of genetic variation can occur locally within a species that shows high overall levels of diversity (Jaarola & Tegelström, 1995, 1996). Furthermore, a few species seem to exhibit south–north clines of genetic diversity within Fennoscandia (Jaarola & Tegelström, 1995; Fedorov *et al.*, 1996). There is a tendency for late immigrants like the house mouse (Gyllensten & Wilson, 1987; Prager *et al.*, 1993), the wood lemming (Fedorov *et al.*, 1996), the harvest mouse (*Micromys minutus*) (Jaarola *et al.*, 1995) and the sibling vole (*Microtus rossiaemeridionalis*) (Jaarola *et al.*, in prep.) to exhibit low levels of genetic variation.

These data are in agreement with an often proposed hypothesis according to which northern populations of mammals carry relatively low levels of genetic diversity (Sage & Wolff, 1986; Hayes & Harrison, 1992; Hewitt, 1996). According to this hypothesis, the processes associated with cyclical range shifts and post-glacial recolonization have lead to a loss of genetic variation. Although the generality of this model remains to be tested through surveys of additional species, the mtDNA studies of north European rodents show that there are a number of northern species that do not fit this model. Thus, many species exhibit very high overall levels of genetic diversity despite living on recently deglaciated land. For example, among 242 field voles from 98 localities, 105 mtDNA haplotypes were observed (Jaarola, 1995). Small mammal species with high levels of genetic variation in Fennoscandia include the field vole, the bank vole, the common shrew and the yellow-necked mouse (*Apodemus flavicollis*) (Tegelström, 1987; Tegelström & Jaarola, 1989; Jaarola

& Tegelström, 1995, 1996; Tegelström & Jaarola, unpublished). Interestingly, a study of lemmings (*Lemmus*) in the Eurasian arctic by Fedorov *et al.* (1999) demonstrates *higher* levels of genetic variation on glaciated land than on non-glaciated land.

The degree of genetic variation that we observe today will be dependent on the weight of creative and protective processes on one hand, and processes that lead to loss of genetic variation on the other hand. To date, there has been much focus on the latter processes, but the Fennoscandian mtDNA analyses clearly demonstrates a number of factors that have promoted the creation and preservation of genetic variation within species in northern Europe:

(1) many large, and probably, substructured, glacial refugia;
(2) recolonization of the same area by animals derived from several refugia, i.e. late glacial and postglacial mixing of formerly isolated populations;
(3) early colonization by many individuals – involving the use of land bridges;
(4) rapid late glacial and postglacial population expansions;
(5) large historical and present day populations.

Thus, the timing and pattern of recolonization after the last glaciation have played a major role not only in shaping the present day population genetic structure, but also in determining the level of genetic variation within populations and species. As opposed to traditional models, the data from Fennoscandia shows that the processes associated with recolonization may sometimes preserve and promote high levels of genetic variation within species.

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