Regional Landscape Patterns and Distribution of the Siberian Flying Squirrel Pteromys volans in Northern Finland

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Pasi Reunanen, Ari Nikula & Mikko Mönkkönen

Distribution of the Siberian flying squirrel *Pteromys volans* in northern Finland, at the edge of its global range, is fairly distinctive: the species is apparently absent in the western part of the region (Pohjanmaa), occurs regularly in the central part (Koillismaa), and only sporadically further east closer to the Russian border (northern Kainuu). In this study, we examined landscape structure in these three regions using geographic information system (GIS) and multi-source land use and cover data to identify key characteristics in landscape structure that are linked to the observed distribution pattern of the Siberian flying squirrel in northern Finland. We analysed landscape structure by studying habitat type proportions in nature reserves and in large-scale landscape samples within the regions. In addition, landscape configuration and connectivity were analysed within larger landscape sample plots. Our results suggest that the observed distribution pattern is associated with natural patterns in landscape structure at local and regional scales. Open peat lands, bogs and non-forested habitats dominate the landscape in the western part of the region and possibly account for the absence of the Siberian flying squirrel. More subtle differences between the central and eastern parts of the region indicate regional scale landscape responses of the species. The relatively high amount of spruce-dominated mixed forests in the central part was associated with the regular occurrence of the Siberian flying squirrel, whereas the increasing dominance of pine forests towards the east was associated with the low number of sightings. Forest management history is much alike in the different parts of the region, but the effects of forest management on the actual range of the species cannot be estimated owing to a lack of knowledge on accurate population trends in northern Finland. However, human-caused fragmentation and large-scale habitat degradation may have long-term effects on the persistence of the species in northern Finland.

Key words: Finland, GIS, landscape ecology, scale, Siberian flying squirrel

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Species distribution patterns result from different biotic and abiotic factors that operate at different spatial scales. The global range of a species is mainly due to climatic factors (temperature and precipitation) that operate at large spatial scales and evolutionary factors such as the ecological age of a biome, the time period during which species have colonised and adapted to those areas (Ricklefs & Schluter 1993). At the level of a habitat patch, species presence/absence may be determined by species interactions in communities such as intra- and inter-specific competition or predator-prey interactions (Terborgh & Weske 1975). Microhabitat characteristics in vegetation may play a crucial role in habitat selection for specialised species. Species are often not distributed evenly throughout their range. There may even be large gaps where the species is completely absent. This raises the question whether landscape structure could explain species distribution patterns over broad regions where very large-scale factors are not prevailing, and species interactions at habitat-patch scale are not likely to affect distribution boundaries.

Structural characteristics within landscape influence many ecological processes in heterogeneous mosaics of qualitatively different habitat patches (Urban, O'Neill & Shugart 1987, Turner 1989, Forman 1995), for instance, dispersal between populations within a landscape and the colonisation of empty habitat patches and entirely novel areas. Landscape structure consists of landscape composition, configuration and connectivity (Taylor, Fahrig, Henein & Merriam 1993, Merriam 1995). Landscape composition measures the relative proportions of patches of different types and their number in space. Landscape configuration refers to the spatial arrangement of the habitat patches (Dunning, Danielson & Pulliam 1992). Connectivity in landscapes depends not only on landscape structure, but is also, to a large degree, affected by a species' ability to bridge resource patches by dispersal (Merriam 1984, 1991, With & Crist 1995, Bennett 1998).

Populations that live at the border of their global distribution respond to prevailing ecological conditions in their environment in a different way than elsewhere in their range. Geographical distribution, especially in plants, is controlled by the climate and, thus, is a physiological response of individuals to specific weather conditions. Because of the changes along an environmental gradient, populations at the distribution limit tend to become more patchy, which influences population interactions and exchange of individuals in a landscape (Carter & Prince 1981, Prince & Carter 1985, Lennon, Turner & Connell 1997). Andrén (1994) suggested that the effects of habitat fragmentation are non-linearly related to species densities and occurrence. When the amount of preferred habitat falls below a certain threshold level, species numbers and densities start declining more than expected by pure habitat loss due to isolation of habitat patches. Increasing inter-patch distances and/or decreasing quality of matrix composition further reduces the colonisation probabilities of habitat patches particularly at the margins of a species' range where the number of colonising individuals is smaller than in central parts of the species range (Henein & Merriam 1990).

The Siberian flying squirrel *Pteromys volans* is an arboreal rodent that prefers mature mixed forests. Presence of old aspens *Populus tremula* and birches *Betula* spp. for food and cavity supply and large spruces *Abies* spp. for shelter are typical of occupied forest sites in northern Finland (Reunanen, Mönkkönen & Nikula 2002). The core area of the home range of this nocturnal species is 1-5 ha (Hanski 1998). However, the total area visited by radio-tagged individuals, especially adult males, during the course of a year may encompass 130 ha (Hanski, Stevens, Ihalempiä & Selonen 2000, see also Hanski 1998). Dispersing individuals normally remain in the vicinity of the home range of the female but some juveniles disperse several kilometres from their natal home range (Mäkelä 1996, Hanski, Selonen, Stevens & Ihalempiä 1999). As shown by radio-tracking, the Siberian flying squirrel seems to be able to use the landscape matrix when moving between different parts of its home range or when dispersing. Radio-tagged individuals seem only to avoid completely open areas and sapling stands, but dispersing individuals may cross gaps of 100-150 m (Selonen, Hanski, Stevens & Ihalempiä 1999; P. Reunanen, S. Lampila & R. Wistbacka, unpubl. data). Anecdotal observations suggest that individuals can cross wider gaps in winter over the snow cover.

The Siberian flying squirrel is distributed across the Eurasian boreal taiga. Accurate up-to-date estimates of the distribution of the species in western Russia do not exist. In northern Finland, the Siberian flying squirrel is at the northwestern edge of its distribution, and it was assessed almost regionally extinct there in the early 1980s (Hokkanen, Törmälä & Vuorinen 1982). However, intensive old-growth forest inventories carried out during 1993-1995 (Kumpulainen, Itkonen, Jäkäläniemi, Leivo, Meriruoko & Tikkanen 1997) and recent ecological studies (Mönkkönen, Reunanen, Nikula, Inkeröinen & Forsman 1997, Reunanen et al. 2000, Reunanen, Mönkkönen & Nikula 2002) have shown the species to be present in old mixed forests in northern Finland. However, the species is not evenly distributed in

northern Finland: it is absent in the western part of the region (Pohjanmaa), occurs regularly in the central part (Koillismaa), is sporadic further east, and is rare close to the Russian border (northern Kainuu; Rassi, Itkonen, Lindholm & Salminen 1996, Mönkkönen et al. 1997, Reunanen et al. 2002).

In this study, we examined landscape structure at the regional scale to learn if the observed distribution of the Siberian flying squirrel in northern Finland is associated with landscape patterns. We first studied landscape structure in nature reserves in western, central and eastern parts of northern Finland. We assume nature reserves represent the original landscape structure without major human impact. Landscape pattern was also surveyed by analysing landscape structure in a systematic grid superimposed over the entire area. We compared landscape composition, configuration and connectivity measures among the three parts of our study area. Further, we compared landscape patterns within reserves and in surrounding landscapes. We separated natural open areas, i.e. bogs, fens and lakes, from human-caused fragmentation (clear cuts, sapling stands and fields) as independent landscape classes. We address the question whether the regional differences in the distribution of the species in northern Finland are attributable to habitat availability (landscape composition) or whether they also depend on landscape configuration and connectivity.

Material and methods

Study area

The study was conducted in northern Finland (65°N, 28°E; Fig. 1), in an area covering about 40,000 km² in the middle and northern boreal vegetation zones (Ahti, Hämet-Ahti & Jalas 1968). A mosaic of peat lands, forest and lake systems characterise the area. Peat lands form a distinctive landscape element (25% of the total area) and they vary from large bogs and open fens to small wet forest tracts. Forest is mostly pine *Pinus* spp. dominated (70%), spruce being dominant on about 25% of the forest land, which is intensively managed. At present, about 3.0% of the entire study area is protected by law or otherwise preserved from harvest (Anon. 1998). Nature reserves, have been established with a few exceptions on state-owned land, which covers 34% of the study area. Altitude in the region ranges from < 30 to > 400 m a.s.l.

For the present analysis, the western part of the region was delineated from the central part by the clear topographic border along the highest shoreline after the latest glacial period (Koljonen 1992). We defined the eastern part to encompass the areas lying east of the

westernmost large lakes in the region (see Mönkkönen et al. 1997). The eastern and western parts of the region are low lying, whereas higher, hilly areas cross the central parts from south to north. Lakes are most common in the east.

Distribution pattern of the Siberian flying squirrel in northern Finland

In systematic old-growth forest inventories on state-owned land in Finland carried out during 1993-1996 (Rassi et al. 1996, Kumpulainen et al. 1997) the presence of the Siberian flying squirrel was confirmed in the wild from its distinctive faecal pellets on the ground underneath large aspens and tall spruces. In the study area 2,870 km² of forest was surveyed in 220 old-growth forest fragments. The Siberian flying squirrel was recorded in 90 old-growth remnants (Rassi et al. 1996). No observations were made in the western part of the region even though 470 km² were surveyed. In the central part of the region 70 old-growth areas were occupied (820 km² surveyed), and in the eastern part the species was recorded in 20 old-growth remnants (1,580 km² surveyed). Also Mönkkönen et al. (1997) found a much higher occupation level for forest remnants in central part of the region of this study (eight of 12 areas, 75%, occupied) than further east (one of eight areas, 12,5%).

Combining the results from the old-growth forest inventory carried out during 1993-1996 (Rassi et al. 1996) and from our own fieldwork during 1995-1998 (Mönkkönen et al. 1997, Reunanen et al. 2000, 2002) on a map divided into 10×10 km² UTM grid cells
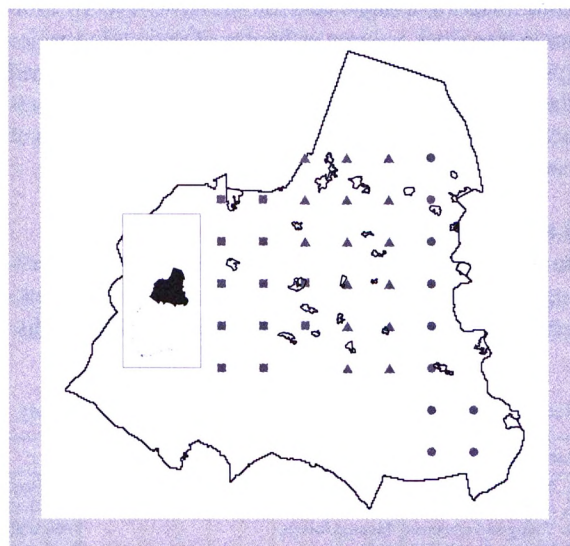

Figure 1. Nature reserves analysed in the study and the systematic landscape-sampling network. Squares denote western, triangles central, and dots eastern parts of the study area.

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showed that the three regions differed statistically significantly from each other in terms of occupancy level ($\chi^2 = 67.7$, df = 2, P < 0.001). In the west none of the 114 10×10 km^2 UTM grid squares were occupied, but 46 and nine of the 129 and 119 squares were occupied in the central and eastern parts, respectively. This indicates that the division of the region into three parts based on topographic features matches well with the distribution pattern of the flying squirrel in northern Finland.

Landscape data and GIS analysis

To see if this distribution pattern can be traced back to landscape structure, we derived information on land use and forest data from classified Landsat TM5 images from 1992 prepared by the national forest inventory (NFI) of Finland (Tomppo 1991, 1993, 1996). In the NFI, several variables describing forest structure are measured in permanent field plots (for further information on the method see Tomppo, Katila, Mäkelä & Peräsaari 1998). In order to yield current estimates of forest resources, NFI field plot data are utilised in classification procedures as well as digital maps of roads, agricultural land, inhabited areas and other non-forest areas. Output of the procedure is a multi-channel image where each channel gives estimates for certain forest characteristics, such as tree stock volume separately for pine, spruce and deciduous trees, age and growth for each 25 m × 25 m pixel. Non-forest classes are included in the output. This multi-channel output can be imported into GIS for further classification and analysis (Tomppo 1991, 1993, 1996). In GIS (Arc-Info) we classified satellite images to a single land use and cover layer by summing tree stock volume estimates of main tree species (pine, spruce, birch and other) for each pixel. We defined the dominant tree species (or mixed species) and age class according to total tree stock volume and proportions of each tree species (Table 1).

Landscape classification

In our classification, we distinguished habitats according to preferences of the Siberian flying squirrel (Mönkkönen et al. 1997, Reunanen et al. 2000, 2002). We distinguished naturally unsuitable areas from areas unsuitable because of human land use practices. We classified the satellite image into seven habitat types: 1) natural fragmentation (naturally open areas, bogs and lake systems), 2) anthropogenic fragmentation (clear cuts and sapling stands, fields, roads and inhabited area), 3) young forests, 4) mature pine-dominated forests, 5) mature pine/spruce forests, 6) mature spruce-dominated forests, and 7) mature mixed forests (preferred habitat for the Siberian flying squirrel; for habitat preferences see Mönkkönen et al. 1997, Hanski 1998, Reunanen et al. 2000, 2002; see Table 1). In this classification, anthropogenic fragmentation represents the effect of forest management since the 1990s. Young forests describe modern forest history from 1950 to 1990. In nature reserves, forests with timber volumes of less than 35 m^3/ha on mineral soil ('anthropogenic fragmentation') are in fact transition zones between peat land and forest land and other sites with low volumes of timber, for example, rocky soils. Mature old forests have not yet been modified by the modern forest management practices. Because of efficient fire suppression, burnt areas are rare and small.

Landscape analysis

Landscape structure of each nature reserve and grid cell (see later) was analysed with Fragstats (McGarigal & Marks 1995). For the landscape composition and configuration analysis we examined the cover and proportion of different landscape classes in existing nature reserves and in overall landscape in the three regions. Present day nature reserve network represents landscape structure without major human interference. In order to have an appropriate landscape sample of natural variation in habitat types and spatially well distributed samples from each region we chose the largest protected areas. They were mainly newly established old-growth forest reserves, but also peat land reserves were included (Table 2). We recognise that peat land reserves are not necessarily the best samples for an arboreal species, but peat land reserves are the most common reserve type in the western region. They are without exception large in size and necessarily include a good selection of local habitat types, such as old spruce

Table 1. Habitat types and classification criteria used in the study.

Land cover class	Classification criteria
1. Natural fragmentation	Water systems, peat land with a total timber volume of 0-35 m^3/ha
2. Anthropogenic fragmentation	Total timber volume of 0-35 m^3/ha on forest land, field, road, inhabited area
3. Young and advanced thinning forests	Total timber volume of 36-100 m^3/ha
4. Mature pine-dominated forests	Total timber volume of >100 m^3/ha, pine >50% of volume
5. Mature pine-spruce forests	Total timber volume of >100 m^3/ha, pine+spruce or pine+deciduous > spruce+deciduous
6. Mature spruce-dominated forests	Total timber of volume > 100 m^3/ha, spruce >50% of volume
7. Mature mixed forests	Total timber volume of >100 m^3/ha, spruce+deciduous > pine+spruce or pine+deciduous

Table 2. Nature reserves in the three regions used in the landscape analysis in the study. In the column 'Nature reserve' numbers in brackets indicate the number of reserves from which the total areas were calculated. Data from Rassi et al. 1996 and Aapala & Lindholm 1995.

Region	Nature reserve	Status	Total area (ha)	[a]Forested land (ha)	Relative proportion of forest land (%)
West	Litokaira	Peat land and old-growth forest reserve	17427	2478	14.2
	Ohtosensuo	Old-growth forest reserve	2068	413	19.9
	Hirvisuo	Peat land reserve	4136	208	5.0
	Olvassuo	Peat land reserve	5376	990	18.4
	Ison Tilansuo-Housusuo	Peat land reserve	2944	687	23.3
	Saarijärvi	Old-growth forest reserve	1358	773	56.9
	Sarvisuo-Jerusaleminsuo	Peat land reserve	3633	708	19.4
		Total	36942	6257	16.9
Central	Syöte (4)	Old-growth forest reserve	11384	7308	64.1
	Salmitunturi	Old-growth forest reserve	5335	3302	61.8
	Pajupuro	Old-growth forest reserve	3200	1497	46.7
	Tervajärvi	Old-growth forest reserve	1183	556	46.9
	Metsäkylä (2)	Old-growth forest reserve	2608	2001	76.7
	Kuirivaara	Old-growth forest reserve	1755	1495	85.1
	Siikavaara	Old-growth forest reserve	2092	1969	94.1
	Ilosenkangas	Old-growth forest reserve	724	408	56.3
	Saarijärvi	Old-growth forest reserve	1306	867	66.3
	Paljakka (2)	Old-growth forest reserve	3117	2571	82.4
		Total	32704	21974	67.1
East	Iivaara	Old-growth forest reserve	2329	1488	63.8
	Närängänvaara	Old-growth forest reserve	4210	2595	61.6
	Romevaara	Old-growth forest reserve	3304	2140	64.7
	Pahamaailma	Old-growth forest reserve	1898	1192	62.8
	Martinselkonen	Special protected area	5852	2710	46.3
	Murhisalo	Old-growth forest reserve	4646	2767	59.5
	Tulisuo-Varpusuo (4)	Peat land and old-growth forest reserve	3902	1809	46.3
	Elimyssalo	Special protected area and old-growth forest reserve	8124	4186	51.5
		Total	34265	18887	55.1

[a] Forest land is defined according to the productivity of the soil at the site where the potential increase of timber volume is at least 1 m³/ha annually.

forests, hence, representing their natural variability in that particular landscape. It is important to note, however, that in Fennoscandia nature reserves have often been established on waste and less productive land, and very seldom on productive forest land (Nilsson & Götmark 1992), and this may bias our reserve sample. In all, we examined 33 separate protected areas covering 370 km² in the western (N = 7), 330 km² in the central (N = 15), and 340 km² in the eastern part (N = 11) of the region. Some inventoried nature reserves, especially in the central part, are compiled from two or more old-growth areas that together form a uniform continuous area (see Fig. 1). We also analysed landscape structure in a grid of 30 × 30 km² squares superimposed systematically on each of the three parts of the region (see Fig. 1). There were 12 squares in the western, 15 in the central, and 10 in the eastern part, respectively. This landscape sampling included all nature reserves in each region. Nature reserves represent < 3.7% of the total area in the regions.

For both landscape samples we analysed landscape composition and configuration of all the landscape classes. We describe landscape composition by proportion of each habitat type, %Land, which directly measures the amount of habitat types available to the flying squirrel. Configuration was measured by patch density (PD), mean patch size (MPS), and interspersion and juxtaposition index, IJI, which describes the interspersion of focal habitat patches in relation to all other habitat types in a landscape mosaic. The IJI measures the relative dispersion and juxtaposition of the habitat class, 100% being perfectly even dispersion and 0% representing maximum aggregation (McGarigal & Marks 1995). The degree of fragmentation increases when mean patch size decreases, and when patch density and IJI increases.

Landscape connectivity was studied in the same grid as the systematic landscape analysis. For connectivity analysis, we used total timber volume of 50 m³/ha as a classification criterion. Forests of > 50 m³/ha represent advanced thinning forests (40-60 years old) or older forests (Tomppo et al. 1998). All closed canopy forests on mineral soil can be considered as potential dispersal habitat for the species (Reunanen et al. 2000). Therefore, we examined only this habitat class for landscape connectivity. As measures of structural landscape connectivity we use the maximum patch diameter (MAXDIA), the longest straight line that can be fitted in a dispersal habitat patch, and the mean nearest neighbour distance (MNN) between dispersal habitat patches. We used 15 × 15 km² squares to yield the connectivity measures for each landscape grid square.

Data analysis

In order to determine the large-scale landscape patterns in northern Finland, we compared landscape variables between the three parts of the region. Because landscape variables derived from the natural landscape pattern did not fulfill the assumption of equal variances even after transformations we used the non-parametric Kruskal-Wallis test. For *a posteriori* pair-wise testing we applied the Nemenyi test (Day & Quinn 1989, Zar 1996). Our systematic landscape analysis covered the three regions completely. Because the analysis was not based on sampling no statistical testing was needed.

We used principal component analysis (PCA) to extract independent landscape axes summarising information on multiple landscape measures. PCA was performed on a correlation matrix of all original untransformed variables. Most multivariate tests are rather robust to equal-variance and multinormality assumptions. PCA was run without any rotation both for nature reserves and systematic landscape squares. For each nature reserve and landscape square, we saved the PC-scores on the three first principal components and tested if scores differed among regions using ANOVA. All statistical analyses were performed using SPSS for Windows (version 7.0).

Results

Landscape structure within nature reserves

Compositional characteristics of landscape in nature reserves varied among the three regions in northern Finland. Except for anthropogenic fragmentation and young forests, there were significant differences among regions in the amount of different habitat types (Fig. 2). Natural fragmentation prevailed in the west, and a high proportion of pine-spruce and spruce forests characterised nature reserves in the central and eastern parts. The eastern part differed from the other two areas by the dominance of pine in mature forests. The central part had more mixed spruce-deciduous forests than the other two regions (see Fig. 2). Spruce dominated more in the central part (spruce and mixed spruce-deciduous forests together comprise 27% of the area) than in the eastern (15.5%) and the western parts (3.2%).

There were significantly fewer patches in anthropogenic fragmentation, young forests and most mature forest classes in the western part of the study area than in the other areas. However, patch density of mixed forest was significantly higher in the central part than in both the east and the west (Fig. 3). Differences in mean patch sizes among areas were small although significant
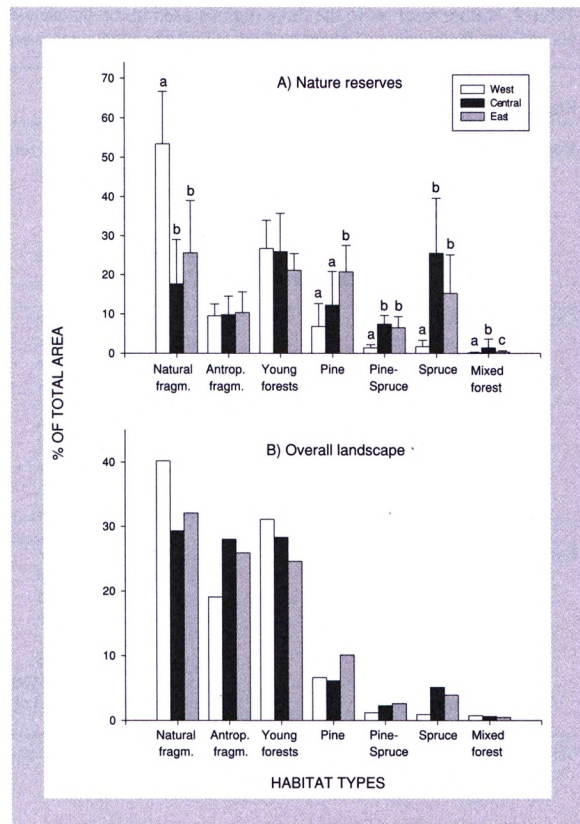

Figure 2. Composition of the habitat type (in % of total area; mean and SD) in nature reserves (A) and overall landscapes (B) in the three regions. For each habitat type lettering above the bars denote significance of the pairwise differences in *a posteriori* tests (Nemenyi test) so that regions with different letters differ statistically. For overall landscapes no statistical tests were needed because our analysis was not based on sampling, but entire regions were analysed. The significance level for pairwise tests was P < 0.05.

in many cases (Fig. 4). The average size of naturally fragmented patches was highest in the west, and large pine-forest patches characterise the east. Large patches of spruce forest were typical of the central area.

Overall landscape structure

Results from overall landscape structure repeat the same pattern as in the nature reserves. However, although overall landscape in the western region was dominated by peat lands (natural fragmentation), the eastern part by pine and the central part by spruce, differences were smaller than they were within the nature reserves (see Fig. 2).

Anthropogenic fragmentation comprised two to three times more of the overall landscapes than they did within the reserves, and this habitat type was proportionally more common in the central area (28%) than in the west (19%) and east (25%), respectively. Patch
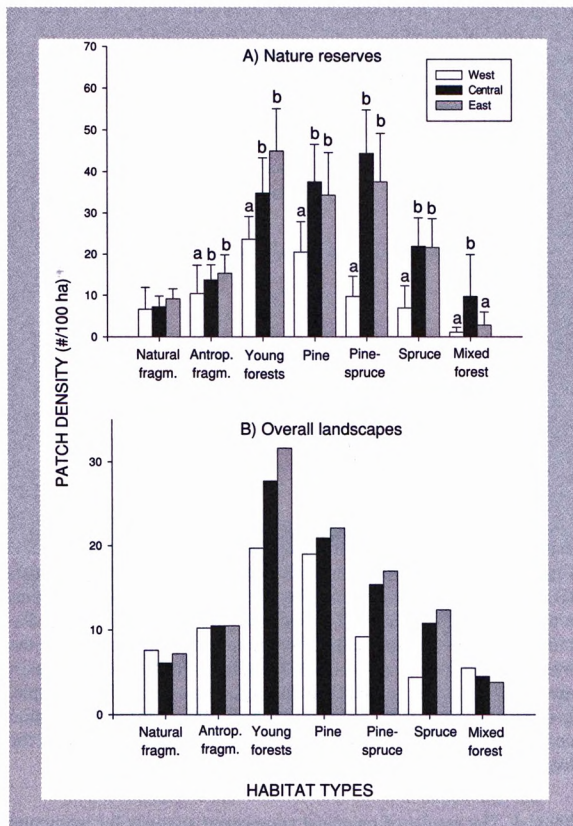
Figure 3. Patch density of the habitat types (per 100 ha; mean and SD) in nature reserves (A) and in overall landscapes (B) in the three regions. For each habitat type lettering above the bars denote significance of the pairwise differences in *a posteriori* tests (Nemenyi test) so that regions with different letters differ statistically. For overall landscapes no statistical tests were needed because our analysis was not based on sampling, but entire regions were analysed. The significance level for pairwise tests was P < 0.05.
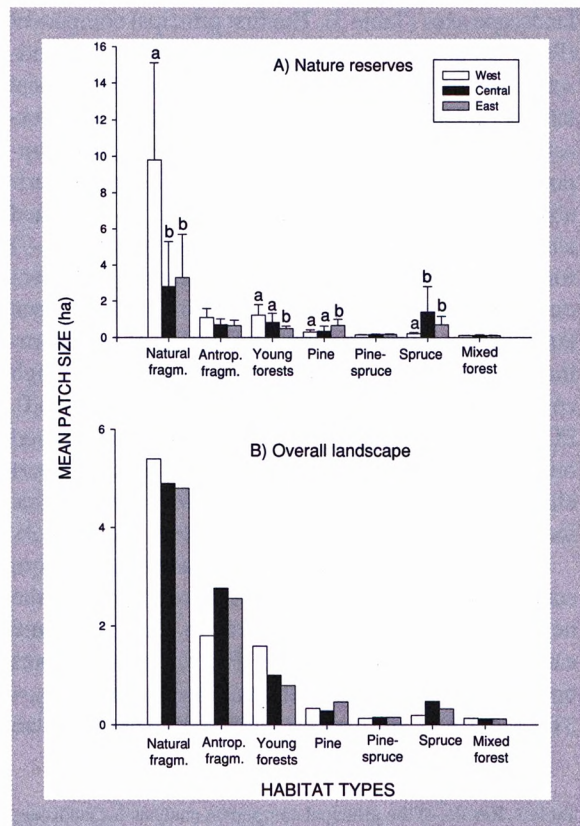

Figure 4. Mean patch size of the habitat types (in ha; mean and SD) in the study areas. For each habitat type lettering above the bars denote significance of the pairwise differences in *a posteriori* tests (Nemenyi test) so that regions with different letters differ statistically. For overall landscapes no statistical tests were needed because our analysis was not based on sampling, but entire regions were analysed. The significance level for pairwise tests was P < 0.05.

density of anthropogenic patches was the same in all three areas (see Fig. 3). The cover of young forests decreased towards the east (see Fig. 2), and the opposite trend was observed in patch density (see Fig. 3).

In the east, old-growth or mature forests comprised a larger proportion of area (17%) than in the central (14%) and western (10%) parts of the region. Pine and pine-spruce forests characterised old mature forests in the west and the east, whereas spruce domination was distinctive in the central part (see Fig. 2).

Landscape connectivity

Maximum diameters of most closed canopy patches were small (< 100 m), providing on average only 126 m of suitable habitat for dispersal in the west (N = 10,447), 109 m in the central (N = 15,847), and 122 m in the east (N = 11,457; $\chi^2 = 12.69$, df = 2, P = 0.002). The figure for the central area was significantly small-

er than those for the east (Nemenyi test: Q = 2.47, P < 0.05) and west (Q = 3.04, P < 0.01). If small patches (< 1 ha) were omitted from the analysis because of their unimportance for landscape connectivity, the trend remained the same ($\chi^2 = 5.59$, df = 2, P = 0.061). Interestingly, maximum patch diameters were consistently shorter in the central part than in the other two areas. The regional averages of mean nearest neighbour distances between closed canopy patches for dispersal ranged within 38-43 m and did not differ among regions ($\chi^2 = 0.54$, df = 2, P = 0.76). If patches less than 1 ha in size were removed, the result remained the same (mean values varying between 68 and 87 m; $\chi^2 = 0.13$, P = 0.94).

Multivariate analysis

The principal component analysis of the landscapes within the nature reserves extracted three independent

landscape axes (Table 3). The first principal component (PC1) explained one third of all variation in the landscape data and can be interpreted as a gradient from peat land dominated (naturally fragmented) to mature forest dominated landscapes. This interpretation is supported by both compositional and configuration variables, e.g. reserves at the positive end of PC1 contained a high proportion of mature forest classes (LAND4-7) forming numerous large patches (see Table 3). The second principal component (PC2) discriminated between landscapes containing a high proportion of pine-dominated forests (negative end) and landscapes with high cover of spruce-deciduous mixed forests (positive end). PC3 separated differently configured landscapes based on interspersion and juxtaposition of mature forest classes as well as mean patch size of mature spruce forests and patch density of young forests (see Table 3).

All three PC-axes separated the three regions from each other. PC1 placed western nature reserves at the negative end and nature reserves in the central and eastern areas at the positive end (Fig. 5). Average scores on PC1 were significantly different among areas ($F_{2, 30} = 31.8$, $P < 0.001$), and the west differed from the other two
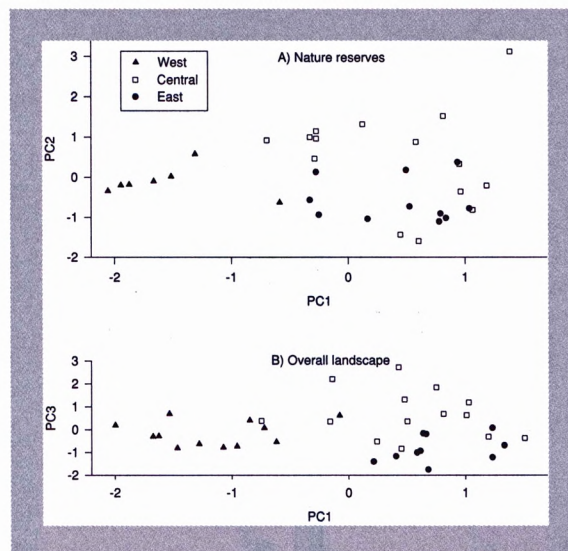

Figure 5. Location of the nature reserves (A) and overall landscapes (B) in the principal component space. Locations of the nature reserves are shown on PC1 and PC2 because these axes most strongly discriminated between the regions. For the same reason, locations of the overall landscapes are given on PC1 and PC3. For both analyses axes are scaled according to their relative explanatory power. For example, in overall landscapes PC1 explained about 40% of the total variation and PC3 only 10%, and consequently the PC1 axis is four times the length of PC3 axis.

Table 3. Results of the principal component analysis for landscape variables in the nature reserves studied. The variables LAND1-7 refer to the proportion of habitat types 1-7 (see Table 1) in the reserves. IJI denotes interspersion and juxtaposition index, MPS means patch size and PD patch density of habitat types. Principal component loadings >|0.5| are shown in italics.

Variable	PC1	PC2	PC3
LAND1 (natural fragmentation)	*-0.883*	-0.087	0.321
LAND2 (antropogenic fragmentation)	-0.044	0.167	*0.520*
LAND3 (young forests)	-0.339	0.483	-0.158
LAND4 (pine forests)	*0.569*	*-0.673*	0.031
LAND5 (pine-spruce forests)	*0.903*	0.198	-0.097
LAND6 (spruce forests)	*0.743*	0.090	-0.480
LAND7 (mixed forests)	0.323	*0.746*	-0.079
IJI1	*0.847*	-0.156	0.063
IJI2	0.079	-0.258	0.283
IJI3	*0.620*	*0.559*	-0.157
IJI4	*0.718*	0.146	*0.589*
IJI5	-0.132	0.444	*0.714*
IJI6	-0.140	*0.634*	0.446
IJI7	0.166	-0.023	0.401
MPS1	*-0.824*	0.001	0.245
MPS2	*-0.537*	0.159	0.312
MPS3	*-0.544*	0.342	-0.461
MPS4	0.276	*-0.671*	0.099
MPS5	0.475	0.180	0.137
MPS6	0.481	-0.083	*-0.552*
MPS7	0.061	*0.699*	0.058
PD1	0.341	-0.463	0.220
PD2	0.305	-0.038	0.369
PD3	*0.536*	-0.150	*0.710*
PD4	*0.759*	0.107	-0.075
PD5	*0.934*	0.164	-0.205
PD6	*0.719*	0.169	0.264
PD7	0.353	*0.824*	-0.079
Eigenvalue	9.390	4.453	3.489
% of variance explained	33.5	15.9	12.5
Cumulative % explained	33.5	49.4	61.9

Table 4. The results of principal component analysis for landscape variables in the overall landscapes. See Table 3 for explanation of abbreviations. Principal component loadings >|0.5| are shown in italics.

Variable	PC1	PC2	PC3
LAND1 (natural fragmentation)	*-0.723*	-0.366	-0.430
LAND2 (antropogenic fragmentation)	*0.801*	-0.135	0.119
LAND3 (young forests)	*-0.698*	0.301	*0.562*
LAND4 (pine forests)	0.479	*0.702*	-0.398
LAND5 (pine-spruce forests)	*0.895*	0.139	0.185
LAND6 (spruce forests)	*0.812*	-0.133	0.484
LAND7 (mixed forests)	-0.004	*0.706*	0.294
IJI1	*0.877*	0.092	-0.207
IJI2	*0.609*	0.421	*-0.560*
IJI3	*0.677*	0.306	0.401
IJI4	*0.945*	-0.020	-0.050
IJI5	*0.821*	-0.042	-0.263
IJI6	0.412	-0.431	-0.237
IJI7	*0.723*	-0.422	-0.080
MPS1	-0.243	*-0.768*	-0.239
MPS2	*0.699*	-0.236	-0.034
MPS3	*-0.881*	0.179	0.323
MPS4	0.332	*0.597*	*-0.573*
MPS5	*0.652*	-0.211	0.124
MPS6	*0.631*	-0.168	*0.603*
MPS7	-0.027	*0.546*	-0.023
PD1	-0.293	*0.751*	-0.108
PD2	-0.200	0.262	0.192
PD3	*0.873*	-0.107	-0.261
PD4	*0.617*	*0.605*	0.139
PD5	*0.891*	0.213	0.218
PD6	*0.876*	-0.054	0.053
PD7	-0.017	*0.639*	0.330
Connectivity1	-0.364	*0.553*	-0.365
Connectivity2	-0.092	0.499	-0.233
Connectivity3	0.099	-0.003	0.290
Eigenvalue	12.44	5.34	3.12
% of variance explained	40.1	17.2	10.1
Cumulative % explained	40.1	57.4	67.4

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areas (Tukey-HSD: $P < 0.05$). PC2 differentiated the east (more pine) and the central area (more spruce) from each other ($F_{2, 30} = 4.45$, $P = 0.020$; *a posteriori* test being significant only for east vs central parts, $P < 0.05$; see Fig. 5). The position of nature reserves on PC3 suggests that landscape configuration differed between the eastern and central areas ($F_{2, 30} = 4.06$, $P = 0.028$; *a posteriori* test being significant only for the eastern vs central comparison with $P < 0.05$) the east being characterised by higher scores on PC3.

The principal component analysis for overall landscapes suggested a relatively similar interpretation for the three regions as the PCA from nature reserves proposed. First, PC1 was a gradient from peat land and young forest dominated landscapes to mature forest dominated areas. PC2 referred to the spatial arrangement of habitat types and PC3 scaled from landscapes with a high proportion (and large patches) of pine to landscapes with more spruce and young forests occurring in large patches in the landscapes (Table 4).

Only PC1 and PC3 discriminated between the three regions. As with nature reserves, PC1 separated the western area with a high proportion of natural fragmentation and young forests from the other two areas (see Fig. 5 lower panel; $F_{2, 30} = 35.8$, $P < 0.001$; *a posteriori* tests being significant for west vs central and for west vs east). PC3 discriminated between the central and the other two areas, the central area being more spruce and young forest dominated than the other two areas ($F_{2, 30} = 11.9$, $P < 0.001$; *a posteriori* tests being significant for west vs central and for central vs east).

Discussion

The results of our study suggest that landscape patterns at the regional scale in northern Finland are associated with the occupancy and persistence of the Siberian flying squirrel in habitat mosaics of different structural quality. In the central part of the region, where the species still is rather common, spruce forests and mixed spruce-deciduous forests (preferred habitat) are relatively widespread whereas in other regions, especially in the west, this habitat type is less common. Unsuitable peat land is concentrated in the western parts of the region. The spatial dispersion of anthropogenic fragmentation and young forests from systematic harvesting in the last 50 years is more or less evenly distributed across all of northern Finland. There were very little or no differences in landscape connectivity among the three areas.

We have earlier shown in a landscape level study in the central region that forest areas occupied by the Siberian flying squirrel were characterised by a larger amount of mixed forest and a higher degree of landscape connectivity at the local scale than the landscape in general (Reunanen et al. 2000). Radio-tracking studies have shown that individuals can use several habitat types within their home range, but their distribution is concentrated on spruce-dominated forest patches (Selonen et al. 1999, Reunanen et al. 2002). Our present results suggest that at the regional scale, landscape connectivity seems to be less important for the occurrence of the species than the availability of mixed and spruce-dominated forest habitat. Spatial spacing and the amount of these habitat types obviously have an influence on the regional distribution of the Siberian flying squirrel.

Regional scale patterns in landscape structure, especially the lack of mixed forest and spatial arrangement of unsuitable habitat patches are contributing to the absence of the species in the western part of the region. This area is dominated and naturally fragmented by large peat land areas and includes relatively few spruce forests. In addition, preferred landscape types for the Siberian flying squirrel are small and sparsely scattered in these landscapes. Large tracks of unsuitable habitats such as open wetlands and bogs dominated by stunted pines effectively prevent the movement and dispersal of an arboreal rodent. On the other hand, intensive drainage of bogs, however, has improved landscape connectivity to some extent by increasing the amount of forested patches in an otherwise unsuitable landscape.

There were more subtle differences between the eastern and central parts of the region in landscape structure in terms of relative proportion of forested habitat types. At large scale, subtle but repeated changes in landscape structure, which are unfavourable, may reduce the relative quality of landscapes in the east and make them less suitable for the Siberian flying squirrel. Landscape structure eventually becomes unsuitable for the species when the preferred habitat becomes too scattered and isolated amongst suboptimal habitats for successful colonisation. Recent inventories on mammal fauna and biodiversity values in Russian Karelia, just east of our study areas, indicate the species to be absent or rare in westernmost Russian Karelia (Pyykkö 1996, Pozdnyakov 1997).

In model landscapes, the abundance of preferred habitat has been found to greatly influence regional distribution of species and the success of individuals to find suitable patches when moving through the landscape matrix (Venier & Fahrig 1996). However, before any-

thing explicit about interactions between landscape structure and population persistence can be stated some detailed demographic data on population fecundity, emigration/immigration patterns, and growth rate in structurally different landscapes should be available (Dooley & Bowers 1998, With & King 1999). Such data do not exist for the Siberian flying squirrel, not even at habitat patch scale.

Landscape patterns within nature reserves illustrate landscape structure without major human impact in our study area. Drastic changes have taken place in northern Finland during the past 50 years. For example, the number and size of young forests has greatly increased as a result of intensive logging operations in all regions, and more than 50% of mires have been drained in the western region (Anon. 1998). The amount of old-growth forest has declined during the last 50 years from ca 30% to less than 20%. At the same time, the area of spruce-dominated forests has diminished by 30% owing to harvesting and planting of pine (Anon. 1998). Hence, the overall composition in the landscape has become less favourable for the Siberian flying squirrel during the past 50 years.

A comparison between nature reserves and overall landscapes indicate that due to their common history of intensive forest management the three parts of the region have become more similar than they were in the past (see Fig. 2). Modern forest management has increased the amount of landscape characteristics, such as large open areas and sapling stands, and the dominance of pine in forest landscapes. These habitat types are clearly suboptimal or unsuitable for the Siberian flying squirrel.

For species with highly specialised habitat requirements or even relatively narrow site preferences, degradation of habitats and habitat loss is probably more detrimental for marginal populations than in areas of higher population densities and continuous distribution (e.g. Pimm, Jones & Diamond 1988). The loss of original mixed forest and the general ongoing fragmentation due to human-induced alteration are likely to hasten the decline of marginal Siberian flying squirrel populations and threaten the regional occurrence of this species in northern Finland (Andrén 1994, Bender, Contreras & Fahrig 1998, see also Mönkkönen & Reunanen 1999).

For conservation purposes, it is important to recognise and specify the scale at which most significant alterations in landscape structure are taking place (Wiens 1989), and which combination of landscape factors has the largest impact on the target species (Harrison & Bruna 1999). In terms of forest management practices, it is important to consider regional scale landscape structure in landscape ecological forest management planning. In the present study, landscape connectivity at a very broad scale does not seem to be as important as at smaller scales (*cf.* Reunanen et al. 2000), whereas the amount of mixed forest and its spatial arrangement plays an important role. However, habitat and landscape management should go hand in hand because separate landscape characteristics affect population processes and persistence simultaneously, but at different spatial scales.

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