

Assessing landscape thresholds for the Siberian flying squirrel

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We examined the relationship between the probability of Siberian flying squirrel *Pteromys volans* occurrence and the amount of mature spruce-dominated forest habitat in a boreal forest landscape in northern Finland. We used three different methods for assessing critical landscape thresholds with reference to spatial scale. First, we carried out a broad-scale landscape analysis to estimate the relationship between mature forest cover and the occurrence of the Siberian flying squirrel regionally. Second, we collected data on the presence/absence status of the species in forest patches in four different study areas. We used these data to determine the critical amount of habitat required for the long-term persistence of the species by applying Lande's demographic model. Finally, we introduced a hierarchical moving window analysis to determine landscape thresholds in a landscape where the species was intensively studied.

Our results suggest that there should be 12–16% spruce-dominated forest habitat for the occurrence of the Siberian flying squirrel. In the regional landscape composition analysis there was > 10% of mature forest covering the area where the species was present. Lande's model suggests that critical extinction thresholds in our four study landscapes are at 11.6–15.6% habitat of the total land area. In a moving window analysis, the landscape threshold for the intensively studied area was 12.2%. Additionally, the probability of occupancy in a landscape window dropped < 0.5 when the amount of unsuitable open areas exceeded 60% of the area. However, it is questionable if the amount of habitat alone in a landscape can be used for assessing landscape thresholds. Additionally, structural landscape connectivity and matrix characteristics are likely to affect the distribution patterns of the Siberian flying squirrel in northern Finland.

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The amount of habitat that needs to be sustained for dynamic populations to persist over a predicted time frame has become a central issue in conservation biology. Habitat loss and fragmentation of natural landscapes have been recognised as a severe threat to biodiversity (Saunders et al. 1991). This has recently prompted a discussion about the critical amount of habitat that should be left intact and about landscape thresholds, below which level of habitat availability populations decline and finally run a risk of extinction (see e.g. Fahrig 1998). Viable populations of all

organisms require habitat where reproduction is successful and conditions for survival at any part of their life history are favourable. However, species vary conspicuously in their habitat affinities (Andrén et al. 1997) making it difficult to assess landscape thresholds for species in general. This question has to be addressed species-wise by focusing first on the rare and most demanding ones (Mönkkönen and Reunanen 1999), which requires a detailed body of knowledge of the species' ecology, including habitat requirements, movement ecology and distribution patterns.

Approaches and theories

One possible way to address critical thresholds in landscapes is to simulate landscape patterns using neutral landscape models (Gardner et al. 1987). Neutral models do not include any explanatory factors, such as ecological processes, that influence the emerging spatial pattern (Caswell 1976). Randomly generated landscapes have, nevertheless, revealed that changes in landscape structure may produce critical thresholds where formerly undivided landscapes turn into fragmented ones with increasing habitat loss. For example, percolation theory suggests that a random landscape becomes disconnected when > 40% of the original habitat is lost (Gardner et al. 1987, With et al. 1997). In fractal landscape models, where spacing and aggregation of landscape elements can be simulated, the corresponding threshold level for the proportion of habitat in landscapes settles between 30 and 50% (With and Crist 1995, With and King 1999a). Also, the hierarchical structure of the landscape patterns is likely to affect the percolation threshold and, hence landscape connectivity (O'Neill et al. 1992). Neutral models serve principally as null models for comparisons with real landscapes and for assessment how changes in landscape structure with increasing fragmentation are likely to affect ecological processes (Caswell 1976, With and King 1997).

Lande's (1987) analytical model is one potential way to estimate a critical threshold for territorial animals in fragmented landscapes. His model is based on a modification of Levins' metapopulation model and requires information on the total amount of focal habitat in an area and the proportion of occupied habitat patches. With this information, the "demographic potential", i.e. the maximum proportion of habitat patches that would be occupied at the equilibrium in original stage of the landscape, can be calculated. Lande's model has been applied, for example, to estimate the amount of habitat required for the long-term persistence of the northern spotted owl *Strix occidentalis caurina* in the Pacific Northwest (Lande 1988).

Spatially explicit simulations have also been used to assess landscape thresholds. These models have indicated that the effects of habitat loss alone are far more important for the extinction risk of species than habitat fragmentation (Fahrig 1992, 1997). Fahrig (1998, see also 2001) showed that fragmentation causes population declines only under relatively limited conditions including factors concerning both landscape structure and species life-history characteristics. According to her simulations, species prone to fragmentation 1) have a limited dispersal ability, 2) prefer habitat, which covers < 20% of the area, 3) do not prefer ephemeral habitats, 4) are territorial and show strong site-fidelity and 5) have a clearly higher mortality rate in the landscape matrix than within the preferred habitat. Habitat loss and the emerging fragmentation effect have also been suggested to be dependent on landscape context (Mönkkönen and Reunanen 1999, Lindenmayer

et al. 1999) and species' habitat affinities and other life-history characteristics (Andrén et al. 1997, Bender et al. 1998).

Empirical approaches

In real heterogeneous landscapes, habitats are often patchily distributed. Human-induced changes in habitat quantity result in a further subdivision of habitat patches in space and create fragmented landscape patterns. So far, too few empirical studies are available to draw firm conclusions on the critical thresholds for population persistence in such landscapes. Andrén (1994) reviewed empirical studies on birds and mammals and suggested that below certain threshold levels in the availability of the original habitat, population densities declined faster than predicted from pure habitat loss. He proposed that when the fragmentation threshold has been exceeded, the relationship between the amount of suitable habitat and the population size is non-linear. Further, other landscape characteristics, such as the spatial arrangement of habitat patches and their isolation, hasten the decline. For birds and mammals in general, this threshold seems to lie somewhere between 10 and 30% (Andrén 1994), but far-reaching recommendations from such estimates for landscape management has to be drawn carefully because of, for instance, significant changes in habitat patterns and landscape context among regions (Harrison and Bruna 1999, Mönkkönen and Reunanen 1999).

An appropriate way to analyse landscape thresholds empirically for a species within a geographic region is to compare several independent landscapes and quantify population densities and the proportion of focal habitat there. Another way is to use a natural habitat gradient, which extends over a region, and then to quantify trends in the amount of habitat and population size. These methods are likely to be useful for some well known taxa only, because of difficulties in censusing the population numbers accurately at broader scales. Also, the replication of habitat patterns at a landscape scale is seldom possible. With modern remote sensing techniques, it is feasible to quantify the habitat in the area, but in order to accurately and reliably determine the status of the species in a vast area requires more sophisticated sampling schemes.

The species

The Siberian flying squirrel *Pteromys volans* is a threatened boreal forest species in Finland and its population has been declining since the 1950s (Hokkanen et al. 1982). Being a rare forest-dwelling species, the flying squirrel has become a focal species in sustainable forest management in Finland and its persistence in commercial forests is considered important. The species is also listed in EU's habitat directive

as a priority species. Therefore, the assessment of landscape patterns and threshold conditions for the species is needed for maintaining viable flying squirrel populations. The prime habitat for the species is mature spruce and spruce-dominated mixed forests, which is the principal habitat type for breeding. Occupied forest sites are typically characterised by closed canopy cover and the presence of cavity trees (Hanski 1998, Reunanen et al. 2002a). The Siberian flying squirrel forages on leaves in summer and hoards catkins for the wintertime. Therefore, the presence of a number of deciduous trees is also typical of occupied forest sites. However, the Siberian flying squirrel regularly visits other mature and middle-aged forested habitat for foraging and when moving between spruce-dominated forest patches. It only avoids open areas and sapling stands (Reunanen et al. 2000, Selonen et al. 2001). The largest male home ranges are > 100 ha, the annual average being 60 ha for males and 8.3 for females (Hanski et al. 2000, Reunanen et al. 2002a). The female home ranges do not overlap, whereas males tend to share habitat patches, especially the ones occupied by the females (Hanski et al. 2000). The young disperse in autumn on average a distance of 2.5 km, with females moving longer distances than males. The maximum observed dispersal distances are up to 9 km (Selonen 2002).

Study objectives

In this paper, our aim is to assess landscape thresholds for the Siberian flying squirrel in northern Finland with reference to different spatial resolution. We report findings of using different methods to assess critical landscape thresholds and discuss their applicability. First, we have carried out a broad-scale landscape composition analysis to determine landscape characteristics that are linked with the species regional occupancy pattern. Here we use data on regional habitat patterns to estimate the relationship between mature forest cover and the occurrence of the Siberian flying squirrel in a region with a spatial extent of several thousands of square kilometres. Second, we collected data on the presence/absence status of the species in forest patches in four study areas, several hundreds of square kilometres in size. Here, we use these data to determine the critical amount of habitat required for the long-term persistence of the species by applying Lande's (1987) model. Finally, in order to tackle the problems of quantifying and sampling an extensive area, we introduce a hierarchical moving window analysis to assess landscape thresholds in an intensively studied landscape (137 km²).

Landscape threshold as a concept has several alternative meanings. First, it may refer to the level of habitat availability, below which population density and species presence is no longer a linear function of habitat area. This can be called the fragmentation threshold. A second threshold level in habitat availability lies at the point below which a

population is determined to extinction. Because habitat fragmentation can compound the effect of pure habitat loss, populations may go extinct even if suitable habitat still exists. This can be called the extinction threshold. Our approaches are based on qualitative presence/absence status of the species in an area or in a forest patch. Therefore, in this paper, we define a landscape threshold as an estimate of the minimum amount of habitat in a landscape needed for the species to be present there, i.e. extinction threshold.

Methods and results

Regional landscape composition analysis

We compared three different regions in the middle and northern boreal vegetation zones in northern Finland. The total area of this study covered ca 40 000 km² (Fig. 1). The regions were delineated by their topographic variation and edaphic conditions. The westernmost region (West) is situated on flat terrain and is characterised by large amounts of peatlands (open fens, bogs). We defined the eastern region (East) to encompass areas east from the westernmost large lakes in the region (see Mönkkönen et al. 1997, Reunanen et al. 2002b). East and West are located on low altitudes (< 50 m a.s.l.), whereas intermediate higher, hilly areas (> 200 m a.s.l.) characterise the central region (Central).

The three regions differ considerably from each other in the estimated population densities of the species. During systematic old-growth forest inventories on public land in Finland in 1993–1996, the Siberian flying squirrel was recorded in 90 old-growth remnants (Rassi et al. 1996). No observations were made in the West, even though 470 km² were surveyed. In the Central region, 70 old-growth areas were occupied (820 km² surveyed), and in the East the species was recorded in 20 old-growth remnants (1580 km² surveyed). We combined the results from the old forest inventories carried out in 1993–1996 (Rassi et al. 1996) with our fieldwork in 1995–1998 (Mönkkönen et al. 1997, Reunanen et al. 2002b) on a map using 10 × 10 km UTM grid cells. In the West, all the 114 10 × 10 km UTM grid squares were unoccupied, but 46 and 9 of the 129 and 119 squares were occupied in the Central region and in the East, respectively. The three regions differed significantly from each other in terms of the occupancy level ($\chi^2 = 67.7$, DF = 4, $p < 0.001$), and the range of densities, from no observations in the West, through moderate in the East, to relatively high in the Central region could be identified.

Correspondingly, the amount of mature forests (total timber volume > 100 m³ ha⁻¹) vary among these regions from < 10% in the West to 17.2% in the East and 14.2% in the Central region. The proportion of spruce-dominated forests of all mature coniferous forests is highest in the Central region (Fig. 2; Reunanen et al. 2002a, b). In the West, landscapes were generally characterised by open land

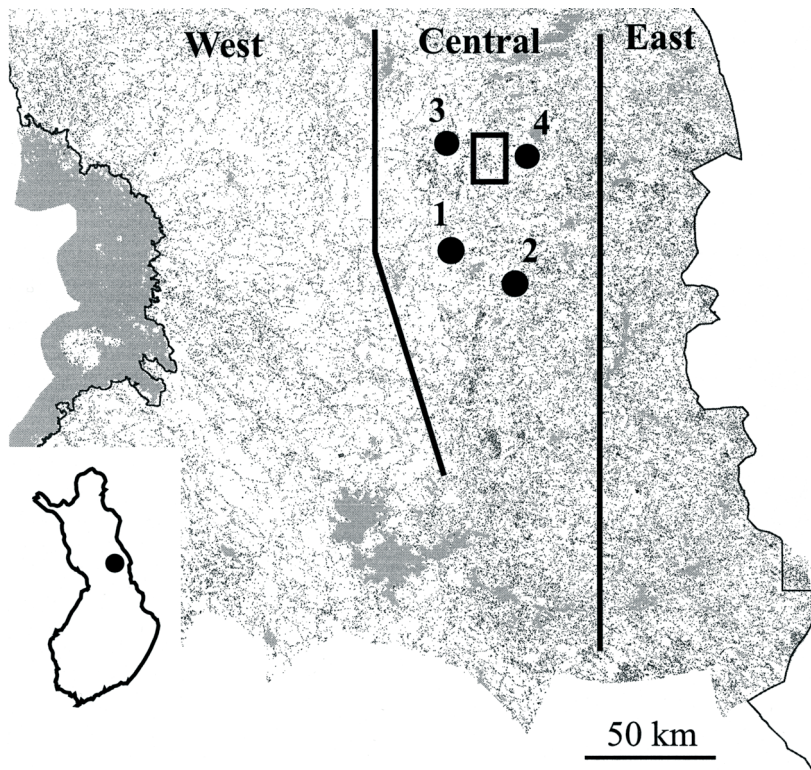


Fig. 1. Our study areas in northern Finland. West, Central and East refer to regional scale studies. Circles denote study areas where independent landscapes were sampled (1 = Puhos, 2 = Metsäkylä, 3 = Syöte and 4 = Salmiunturi). The rectangle shows the location of the intensive study area. Shaded spots in the background indicate mature forest stands.

(wetland areas and bogs, 40% of the land area) and sapling stands (20%). The Central and Eastern regions are principally more forested than the West, but in the Central region spruce-dominated forests cover > 50% of the total area of mature forests (Fig. 2). The regional examination is appropriate to show correspondences between broad-scale landscape patterns and population densities. The above numbers suggest that the overall coverage of mature forests should be above 10% of the total land area for the persistence of the flying squirrel. However, smaller scale examination is needed to more accurately determine critical landscape thresholds.

Comparison of separate landscapes within the Central region

We surveyed four landscapes (spatial extent from 300 to 1260 km²) to characterise patterns of habitat occupancy by the Siberian flying squirrel in the Central region (Reunanen et al. 2002c). All study areas have been managed by clear-cutting since the 1950s and 1–2% of the forest land is presently harvested annually. The areas were selected to ensure large variation in the amount of spruce-dominated forest habitat (Fig. 1, Table 1). In each area, we first identified forest patches characterised by mature spruce forest.

Habitat patches < 1 ha were omitted. Spruce forest habitat was defined by adjusting classification criteria for these specific landscapes (total timber volume > 100 m³ ha⁻¹ and spruce/deciduous tree proportion of the timber volume > 80%) and, therefore, the landscape classification is not exactly the same as in the previous regional scale analyses. In

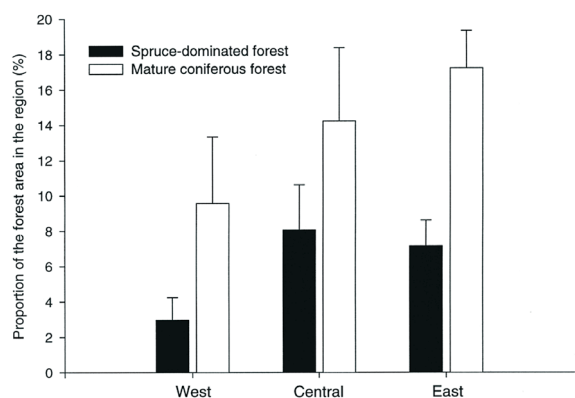


Fig. 2. Proportion of the spruce-dominated forest and the mature coniferous forest (mean and SD) in the regional landscape composition analysis. Note that the bar showing the proportion of the spruce-dominated forest in the regions is included in the bar showing the total amount of mature forest.

Table 1. Study areas in the central region, their size, the amount of preferred habitat for the Siberian flying squirrel and the proportion of occupied patches. Lande's extinction threshold was calculated from the data shown in the table.

Study area	Landscape extent (ha)	Area in patches (ha)	Proportion of the landscape (%)	Number of studied patches	Occupancy (%)	Lande's extinction threshold
1. Puhos	29200	4220	14.5	39	61.5	5.60
2. Metsäkylä	31900	8322	26.0	63	39.7	15.67
3. Syöte	126200	24450	19.3	48	39.6	11.65
4. Salmitunturi	47900	9812	20.5	57	35.1	13.30

these study areas the average patch size ranged from 32 to 56 ha. A stratified random sample of patches was visited in the field and the presence/absence of the species was checked in selected habitat patches. Presence/absence status of the habitat patch was based on faecal droppings that typically accumulate under the spruce and aspen (cavity) trees in occupied forest sites (see Reunanen et al. 2002a). Due to the broad-scale sampling, all inhabited habitat patches were likely to be occupied by different individuals. Our studied landscapes contained 14.5–26.0% of spruce-dominated forest habitat for the Siberian flying squirrel (Table 1). The proportion of occupied habitat patches was fairly constant among the four study areas varying from 35.0 to 39.7% except in Puhos where 61.5% of patches were observed occupied (Table 1).

We applied Lande's model to assess critical extinction thresholds in these study areas. The equilibrium occupancy of habitat patches can be calculated from the equation:

$$p = 1 - (1 - k)/h, \text{ for } h > 1 - k$$

$$p = 0, \text{ for } h \leq 1 - k$$

where h refers to the proportion of target habitat in an area, p is the proportion of currently occupied territories (patches), and k is the proportion of territories that would be occupied by females in a completely suitable area (the demographic potential). Demographic potential can be estimated if p and h are known:

$$k = 1 - (1 - p) \times h$$

Because all the habitat patches are not occupied at one time, it is possible to estimate the proportion of unoccupied habitat patches and how much the remaining patches cover of the area by solving $(1 - k)$, which is the critical proportion of habitat necessary for long-term population persistence.

Lande's (1987) model suggests that critical extinction thresholds in the study areas are at 12–16% of the total land area, but for Puhos it is at 6%. Lande's model assumes that populations are in equilibrium, i.e. that the present distribution of individuals reflects the current capacity of the landscape to maintain a flying squirrel population. In our areas, logging is an ongoing process and forests in study areas are harvested annually. Therefore, the landscape is under a continuous change and the equilibrium assumption does not necessarily hold true. In addition, a snapshot of a declining trend can be misleading due to a time-lag in population responses to landscape change and may underestimate the critical extinction thresholds. Therefore, threshold values estimated here have to be carefully considered. Lande's model is simple and easy to interpret, but the accuracy and usefulness of the model depends on how precisely the parameters h and p can be estimated empirically.

Moving landscape window analysis

In the moving window procedure we first delineated a landscape of 370 km² (Fig. 1) and determined spruce-dominated forest patches using a similar landscape classification as in the previous landscape comparison. In this study area, we surveyed all patches ($n = 136$) for the presence of flying squirrels. The study area comprises 17.6% spruce-dominated forest habitat suitable for the Siberian flying squirrel. In the study area, the average size of a habitat patch was 48.5 ha and the mean distance to the nearest neighbouring patch 217 m. The mean distance between the two nearest occupied habitat patches was 395 m and, therefore, it is unlikely that the individuals occupy more than one habitat patch. Forty-eight patches (35%) were observed occupied.

To assess critical landscape thresholds for the species in this area, we used a moving window analysis to determine, first, the appropriate scale at which landscape thresholds should be analysed and, second, how much spruce-dominated forest habitat within a moving window there is at that given scale. To approximate the adequate scale we used landscape windows of different sizes (side lengths 100, 200, 500, 1000, 2000, 4000 m). The spatial arrangement of the habitat patches was not quantified. In the moving window analysis, a landscape window was first superimposed on a corner of the study area and then systematically moved over the entire study area. At each step, the proportion of spruce-dominated habitat was quantified and the status of the species recorded. In the consecutive steps, windows did not overlap each other. A landscape window was assigned occupied if it encompassed an inhabited patch or a part of it.

We plotted the proportion of occupied squares at each scale against the size of the window to assess a relevant scale for our landscape analysis (Fig. 3). The idea was that using too large a window would result in all or most windows being occupied, whereas too small a window size would include too low amount of occupied windows. In either case, the power of the statistical analyses would be inadequate. The proportion of occupied squares evidently increases with an increasing size of the landscape window, exceeding 50% at ca 1000 m side length (Fig. 3). Landscape windows (100–200 m in side length) turned out to be too small and mostly contained either close to 0 or 100% of target habitat. Large windows (2000–4000 m side length), in turn, were too large for the observed patch density (actual landscape resolution) in the study area and, thus, became mostly occupied. Therefore, we selected the 1000 × 1000 m window size for further analyses. At this scale, the amount of habitat in a landscape window varies gradually between zero and 90%. This scale also matches well with the home range size and space use patterns in the Siberian flying squirrel.

We regressed presence/absence data against the amount of spruce-dominated forest habitat in a moving window to

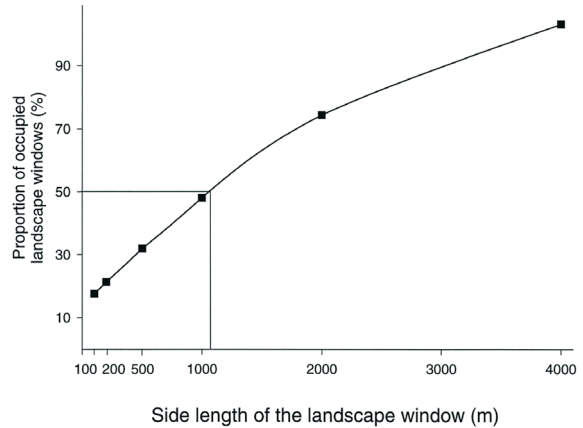


Fig. 3. Proportion of landscape windows that were assigned occupied at different scales. Half of the windows became occupied when the side length of the window was 1063 m.

see how the probability of a window being occupied depended on the habitat availability. We also ran a similar analysis for the combined proportion of open areas and sapling stands to yield estimates of landscape threshold for this habitat type. We excluded those windows from the analysis that did not contain any habitat for the species and were by definition unoccupied.

The results showed that the probability of a moving window to be occupied increases with habitat availability (Table 2, Fig. 4). The probability exceeds 50% when there is 12.2% spruce-dominated habitat in the window (Fig. 4). The relationship was reversed when regressed against the proportion of open areas and sapling stands (Table 2). The probability of finding an occupied patch in a 1 km² landscape window falls below 50% when the amount of those habitat types exceeds 60% (Fig. 5). It is notable, however, that the proportion of spruce-dominated forest habitat yields more accurate predictions of the occupancy status than the proportion of open habitat types. Deviances of the models differ significantly ($\chi^2 = 41.9$, $DF = 1$, $p < 0.001$) and the rate of correct predictions is 76 vs 69% in the models (Table 2). Results of the moving window analysis match surprisingly well with estimates for other study areas in the Central region based on Lande's model (11–16%, Table 1). Lande's extinction threshold for the study area where the moving window analysis was carried out was 11.4%.

Discussion

Population turnover in habitat patches at the broad scale stems from repeated extinction and colonisation events, i.e. classical metapopulation dynamics. At the individual scale, habitat patch turnover reflects birth and death rates in a habitat patch, but also the spatial rearrangement of home ranges. The distinction between the population scale

Table 2. Regression coefficients (B), their significance levels, and the constant term for the variables in the logistic regression models. The deviance indicates the model fit. The models for the proportion of the habitat and open area within the landscape window differ significantly ($\chi^2 = 41.9$, DF = 1, $p < 0.001$). Proportion of correctly predicted cases and the amount of false positive and negative predictions measure the classification accuracy.

Variable in the model	B	DF	Sign.	Deviance	Correctly predicted (%)	False positive (%)	False negative (%)
Habitat within landscape window (%)	8.52	1	0.000	238.68	76.13	17.0	34.0
Constant	-1.08						
Open area (ha)	-0.04	1	0.000	280.61	68.72	27.6	40.6
Constant	2.71						

and the scale of processes that concern individuals is important, because they determine the potential causes leading to true fragmentation effects, i.e. more dramatic population declines than expected by pure habitat loss alone (Andr n 1994). From an individual perspective, a landscape becomes fragmented when habitat patches become too small to contain a home range or the distances between habitat patches are beyond the dispersal capacity of the species. Populations show fragmentation effects when divided into local, relatively independent, sub-populations where survival and reproductive success are dependent on patch size and their recolonisation on isolation. These mechanisms are essential to critical landscape thresholds and the long-term persistence of the populations. In this paper, the regional scale comparison clearly concerns the scale of populations, while the landscape-scale analyses single populations and, hence, habitat patches occupied by individuals.

The regional comparison suggested that at least 14% of the total area should be covered by mature forests for flying squirrel persistence. The species was absent from the western region, where the proportion of mature forests was < 10%. At

the broad scale, landscape composition thus seems to account for the species' absence in the West. Spruce-dominated forest habitat for the Siberian flying squirrel is scarce and embedded in unsuitable open areas (ca 60% of the area in the West is covered by open non-forested habitat). The moving window analysis also suggests that if at the local scale, open areas cover > 60% of the area habitat patches are likely to be unoccupied. These results are parallel with the predictions of the percolation theory. However, very broad-scale examination of landscapes can easily generalise habitat patterns too much and underestimate their spatial variation locally. Local habitat patterns vary considerably due to microclimatic and edaphic conditions. The species is regularly distributed throughout the Central region where the proportion of spruce-dominated forests is highest. Landscape level analyses in this region, based on Lande's model and the moving window analysis, suggest that spruce-dominated forests should cover at least 12–16% of the landscape.

In our four study areas in the Central region, the amount of spruce-dominated forest habitat ranged from 14.5 to 26%. However, the occupancy rate of habitat

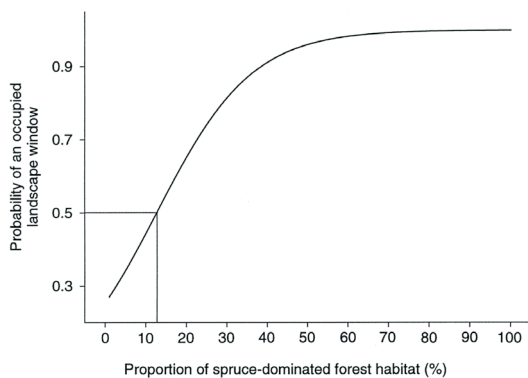


Fig. 4. The proportion of the spruce-dominated forest habitat in a landscape window and the probability of an occupied landscape window. The probability of 0.5 was used as a cut-point in the logistic regression to indicate species occupancy.

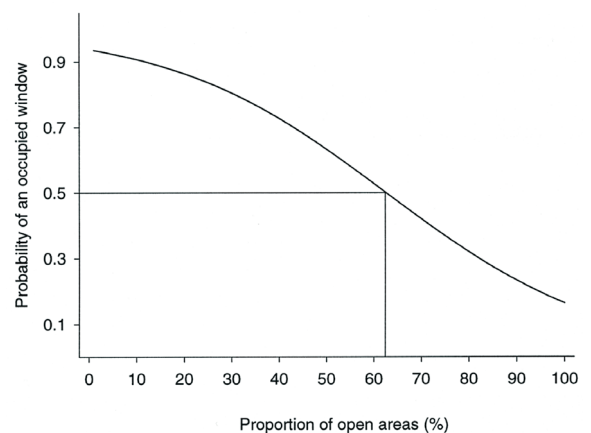


Fig. 5. The proportion of the open areas in a landscape window and the probability of an occupied landscape window. The probability of 0.5 has been used as a cut-point in the logistic regression to indicate species absence.

patches was rather equal among the study areas except in Puhos (35–40%, and 62% respectively). The Puhos area, where the proportion of occupied patches was the highest but the habitat availability the lowest, has the longest history of modern forestry. Large areas were managed already between the 1940s and 1960s, and consequently, young forests comprise a high proportion of the total land area. The young forests are in most cases pine plantations and, therefore, are not likely to be used by the Siberian flying squirrel as a breeding habitat (lack of cavity trees and deciduous trees). The other three areas consist of larger amounts of the spruce-dominated forest habitat and recently harvested stands. The higher amount of young forests (suitable for dispersal) in the Puhos area is likely to increase the landscape connectivity. Our earlier analyses have suggested that landscape connectivity contribute to the spatial pattern of occupied habitat patches (Reunanen et al. 2002c).

Our analyses were based on presence/absence data, which is a potential source of error. Changes in local population densities may take place well before any changes in the patch occupancy emerge. Therefore, presence/absence data may underestimate critical landscape thresholds, i.e. overestimate population viability. However, because two of our analyses were carried out at the scale of individual home ranges, presence/absence data are not likely to cause a major underestimation. Densities are not likely to vary much within smaller habitat patches because particularly females occupy mutually exclusive territories (Hanski et al. 2000). Only in larger patches (several tens of hectares), which may contain several home ranges, changes in density may be difficult to observe in our data. The possibility for underestimation of a landscape threshold must, however, be kept in mind when interpreting the results.

In our study areas, the Siberian flying squirrel does not perfectly fit to the five conditions for a fragmentation prone species as suggested by Fahrig (1998). 1) The average dispersal distance of the Siberian flying squirrel is 2.5 km, which is six times longer than the average distance between two nearest occupied habitat patches (ca 400 m) in our study area, and suggests that the species is a better disperser than a fragmentation-prone species. 2) 17.6% of the study area consists of good quality habitat for the species, which is < 20%. 3) Breeding habitat of the Siberian flying squirrel, i.e. mature spruce-dominated forest, is in principle not ephemeral from the perspective of an individual or a few generations. 4) Females seem to be territorial and occupy the same breeding area annually. 5) Survival probabilities of the Siberian flying squirrel in different habitats are not known precisely, but survival is very likely lower in landscape matrix than in the prime habitat.

Three of these conditions hold for the Siberian flying squirrel, but regarding the dispersal ability and survival in landscape matrix, it seems that the species is not as demanding as species susceptible to fragmentation. Therefore, according to these criteria the Siberian flying squirrel

can be considered moderately prone to fragmentation of its prime habitat. The species' ability to disperse relatively long distances and its use of various habitats, indicates that it is not much affected by fragmentation and is adapted to move in landscapes that are to some extent fragmented. Reunanen et al. (2002c) found that not only patch size and quality, but also landscape connectivity are important landscape characteristics increasing the probability of a habitat patch being occupied. This suggests that there might be a threshold distance the species is not likely to cross in non-forested areas. Therefore, successful patch occupancy dynamics may depend on landscape context and sharp contrasts between forested habitat types and open areas, which, in turn, are not directly related to the amount of target habitat in the area.

It is, therefore, likely that the proportion of spruce-dominated forest habitat alone, is not the only determinant of the capacity of a landscape to maintain sustainable populations. The landscape matrix plays an important role in population dynamics and in inter-change of individuals among habitat patches. Quality of the landscape matrix improves connectivity, thus, promoting dispersal of many species (Taylor et al. 1993, Merriam 1995, With and King 1999b). However, the contrast between habitat types in a landscape and the permeability of habitats is dependent on how species perceive them (Lima and Zollner 1996). Therefore, landscape structure in general and the sharpness of landscape boundaries (Wiens et al. 1985) is likely to affect the critical amount of habitat in a landscape. At a regional scale, the amount of open areas i.e. landscape context, rather than spruce-dominated forest habitat tend to account for the absence of the Siberian flying squirrel.

Assessment of critical landscape thresholds normally refers to the habitat availability only, while information on dispersion and spatial arrangement of key habitat patches is not used in analyses. It is somehow paradoxical that only the habitat availability but not the spatial arrangement of the habitat is considered, because the definition of the critical landscape threshold is based on the premise, that below the fragmentation threshold the spatial arrangement of habitat patches becomes an important determinant for population persistence. Ecological conditions, such as landscape context and contrast between two habitat types, may be critical to some species even though there would be much habitat left. Depending on the landscape characteristics and species responses to them, it would be more adequate to speak about a threshold zone. The landscape threshold zone allows the landscape threshold value to vary for a given habitat availability, with the spatial context of that habitat in the landscape. There is a consensus that there are differences in species' habitat affinities and their habitat requirements are likely to affect species' critical landscape thresholds. Therefore, habitat loss effect is always species-specific, but due to variation in landscape patterns, may also be landscape-specific (Mönkkönen and Reunanen 1999).

Our regional scale analysis was carried out at the scale of populations, whereas landscape analyses at habitat patch scale focused on individuals. Regional scale analysis gives an overview of landscape characteristics that are likely to be good candidates to explore in more detail in the landscape threshold analysis. Population viability, however, stems from reproductive success and survival of individuals, and, therefore, local scale information of critical landscape characteristics is more important to apply in forest landscape planning. Our results suggest that home ranges are not established if there is < 12–16 ha of spruce-dominated forest habitat within a one square kilometre block of forest landscape. Our results suggest that it is likely that a landscape threshold for the Siberian flying squirrel exists, but it is unclear to what extent other landscape characteristics, such as landscape matrix, affect landscape threshold estimates. Management recommendations stemming from the current analysis should also include information on temporal changes in population size and environmental stochasticity, which may cause local extinctions even if habitat availability is above the extinction threshold. Therefore, we suggest that the amount of spruce-dominated forest habitat should cover > 12–16% of the total forest area, say, 25–30% (the probability of occurrence is 0.9 when 38% of the landscape window is covered by the focal habitat) to allow the long-term persistence of local populations of the Siberian flying squirrel in northern Finland.

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