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Building and evaluating predictive occupancy models for the Siberian flying squirrel using forest planning data

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Abstract

We analyzed the applicability of forest planning data in predicting the occurrence of the Siberian flying squirrel (*Pteromys volans*) in managed northern boreal forests, in northeast Finland. Forest planning data is a source of information about forest characteristics for forest managers that may be used in estimating the availability of certain habitats for species conservation. Flying squirrel populations have declined in Finland, most probably due to habitat change and loss and maintenance of suitable habitats can be seen as a fundamental task in species conservation. First, we surveyed 715 ha of older spruce-dominated forest consisting of 91 stands, of which 35 were found occupied by flying squirrel. Flying squirrels inhabited larger stands, which had a higher volume of spruce and birch. Occupied stands also had more good quality forests surrounding them than the unoccupied stands. We based the model building on already existing knowledge of the habitat preferences of the species and built four alternative predictive models with logistic regression. Forest planning data seemed useful in estimating the forest quality and the suitability of habitats for the flying squirrel, with a model fit of ca. 72% with the original data. Second, we built the predictive models similarly with data from another study area ($n = 98$) situating ca. 150 km south from the first area. Third, we evaluated the first models using data of the second study area and also using new independent data from three municipalities situating almost in between the two study areas. Moreover, we reciprocally evaluated one model of the second study area using data of the first study area and of the three municipalities. The prediction success of our models indicated some applicability to other areas. The results also showed that the structure of the surrounding landscape is more important in a coarse-grained landscape than in a fine-grained landscape. However, because of some inaccuracies, predictive occupancy models built for the flying squirrel cannot replace field surveys and their generalizations to other areas must be made with caution.

Keywords: Boreal forest; Finland; Forest management; Forest stand; Habitat suitability; Model selection

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1. Introduction

Habitat loss and the diminished quality of habitat patches are the most important threats to species existence (Fahrig, 1997). Species conservation often focuses on preserving suitable habitat and, therefore, the ability to locate these habitats in the landscape is a fundamental task. This is especially important if conservation goals are to be incorporated into forest management planning.

Defining and locating suitable habitat, however, has its problems. First, habitat preferences are usually species-specific. Such information may be difficult to obtain, particularly for rare species, while habitat requirements may even differ between individuals and phases of a life cycle. Second, even though recent ecological research has provided much information on species habitat association, the connection between predictive habitat distribution models (e.g. Guisan and Zimmermann, 2000) and forestry planning are often weak. As a consequence, the most important places for sustaining populations may not be recognized by the foresters and are not maintained.

Moreover, frequently the most important challenge of recognising certain habitats for management is to identify them from large areas. Since extensive field work is practically out of question, characteristics of forests in landscapes may be mapped using remote sensing methods. Hundreds of square kilometres, for instance, can be characterized from a certain species' perspective using satellite images, and furthermore, ecologically meaningful interpretations about species habitat associations in the landscape scale can be discovered (see Reunanen et al., 2002b). On the other hand, information derived from sources, such as satellite images is seldom accurate enough for the forest planning scale, meaning that detailed characteristics of the forests can not be estimated or are not reliable enough (Holmgren and Thuresson, 1998). Stand level forest planning data, however, often include detailed information of the forests, since they are routinely measured for forestry planning purposes and used in forestry planning practises.

We wanted to find out if stand-level forest planning data can be used to locate potential habitats for a predetermined species. In these data, forests are classified as homogenous stand units, if possible, based mainly on soil properties, tree species composition and age class (Uuttera and Hyppänen, 1997). It is possible that some parameters of stand characteristics measured for silvicultural purposes could serve as broad surrogates for certain habitat types. A surrogate variable for a stand, such as probability of the occurrence of a species or a habitat suitability index, could then be used in numerous approaches and incorporated into multi-objective forestry planning procedures (see Pukkala et al., 1997; Kurttila et al., 2002).

We focused on the Siberian flying squirrel (*Pteromys volans*) as an example species, since during the past few years in Finland its ecology has been well studied (e.g. Mönkkönen et al., 1997; Hanski, 1998; Hanski et al., 2000b; Reunanen et al., 2000, 2002a, b; Selonen et al., 2001). The species is classified as vulnerable in Finland, because of a recent population decline (Rassi et al., 2001). This decline is most probably due to habitat change and loss (Rassi et al., 2001), resulting from intensive forest management. Since the 1950s, modern forestry, such as clear-cutting and artificial regeneration of coniferous species, have been established regeneration methods in Fennoscandia (Esseen et al., 1997; Östlund et al., 1997).

The Siberian flying squirrel shows preference for older spruce (*Picea abies*) dominated forests with some deciduous trees, where spruces provide shelter and deciduous trees provide essential food sources (Eronen, 1996; Reunanen et al., 2000, 2002a; Hanski, 1998). Individuals seem to spend the majority of their time in small distinctive core areas with a large proportion of deciduous trees (Hanski, 1998). Total home range size varies greatly, between few to tens of hectares, of which the core areas cover about 10%. In addition, flying squirrel individuals have several nests in use year-round, and about half of them are situated in core areas (Hanski, 1998; Hanski et al., 2000b). Nests are mainly woodpecker-made cavities, usually in large aspens (*Populus tremula*), but also twig dens in spruces.

The aim of our study was to examine how reliably available forest planning data may be used in detecting suitable habitat stands for the flying squirrel. We used presence/absence data of the Siberian flying squirrel in forest stands, and built predictive occupancy models in two study areas, Lakusuo and Kajaani, using knowledge of the habitat selection patterns of the species. In addition, we explored the possibilities of generalizing our models to other areas by evaluating the models using independent data from three municipalities and the two study areas. Lastly, we discuss the applicability of forest planning data for the conservation of this species.

2. Materials and methods

2.1. Forest planning data

We used basic forest planning data as an information source of forest stand structure. In these data, the size and shape of stands are first roughly defined from aerial photographs and base maps, and then adjusted and complemented with measurements in the field (Uuttera and Hyppänen, 1997). Measurements of each tree species are taken from several sample plots per stand and tree volumes are calculated on the basis of diameter or basal area and height of trees. These data are used to calculate stand volume in cubic meters per hectare ($m^3 ha^{-1}$). The minimum size of stands is 0.5 ha in state owned land, and even 0.1 ha in private land.

2.2. Study areas

Our study areas are located mainly in northeast Finland (Fig. 1). The study area of Lakusuo is located in the municipality of Taivalkoski (Fig. 1b), and covers ca. 10,000 ha of state-owned land. This area belongs to the northern boreal vegetation zone (Ahti et al., 1968), and is dominated by hills covered with boreal coniferous forests, with wetlands (bogs and open fens) between them. Only a few small brooks exist in the area and other watercourses are scarce. There are a few forest roads, but hardly any fields or settlements. The topography varies between 220 and 370 m a.s.l. in the study area. The structure of the forest landscape is somewhat black and white from the flying squirrel's perspective: ca. 28% of the forests are mainly older spruce dominated forests (>100 years), while ca. 65% are young forests (age of <60 years), mostly of Scots pine (*Pinus sylvestris*). The most common deciduous trees are birches (*Betula pubescens*, *B. pendula*) and aspen.

Second study area, Kajaani, is located in the municipality of Kajaani (Fig. 1d), covering ca. 6500 ha of private-owned land. It falls in the middle boreal vegetation zone (Ahti et al., 1968), and boreal forests and farmland characterize the landscape. Forests are mostly managed and dominated by pine but also include some fertile mixed forests. Alder (*Alnus incana*), the preferred food for flying squirrel (Mäkelä, 1996), is a common deciduous tree species, existing along roadsides and edges of agricultural fields together with birches and aspens. A small topographic variation, between 120 and 190 m a.s.l. exists in the Kajaani study area.

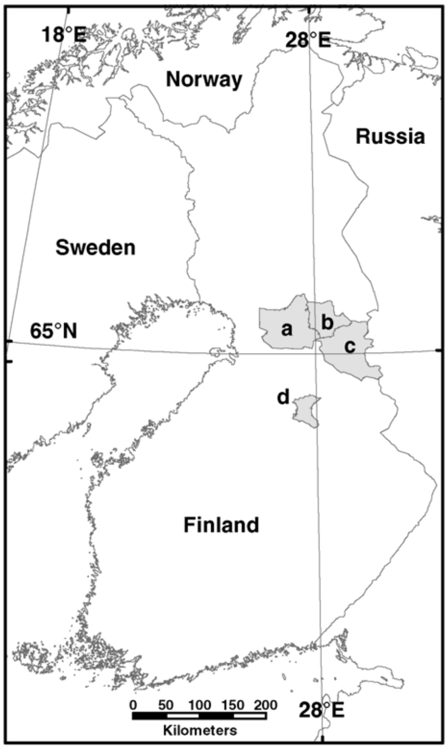

Fig. 1. The study was carried out in municipalities of Pudasjärvi (a), Taivalkoski (b), Suomussalmi (c) and Kajaani (d).

Furthermore, information from adjacent municipalities close to the Lakusuo study area, Pudasjärvi, Taivalkoski and Suomussalmi (Fig. 1a–c), were used in model evaluation. Data from Taivalkoski excluded the stands of Lakusuo study area. They represent typical boreal forest landscapes with forest hills, bogs and small lakes. Pudasjärvi and Taivalkoski fall mainly in the northern boreal vegetation zone or in a transition zone between northern and middle boreal

Table 1
Basic information on productive forests (annual growth >1 m^3 ha^{-1}), of the municipalities in the study (Tomppo et al., 1998)

Municipality	Area of productive forests (ha)	Spruce dominated forests (%)	Pine dominated forests (%)	Birch dominated forests (%)	Over 120 years old forests (%)
Pudasjärvi	362,130	13.5	79.5	5.0	15.9
Taivalkoski	179,290	20.0	73.4	4.2	24.0
Suomussalmi	389,620	14.1	78.7	5.3	21.4
Kajaani	92,850	12.5	78.6	7.3	11.1

zone (Ahti et al., 1968). Suomussalmi, on the other hand, is situated partly in the middle boreal vegetation zone where soils are slightly more fertile. In Pudasjärvi elevation varies between 100 and 430 m a.s.l., in Taivalkoski between 200 and 420 m a.s.l., and in Suomussalmi between 170 and 300 m a.s.l. The municipalities resemble each other in forest type and tree dominance (according to productive forests where annual growth is more than 1 m^3 ha^{-1}, see Table 1 (Tomppo et al., 1998)).

2.3. Occupancy of the flying squirrel and stand selection

We examined the presence of flying squirrel in a stand using its distinctive pellets as indicators (a method first suggested by Skarèn, 1978, and verified afterwards, see Reunanen et al., 2002a). These yellowish, rice grain sized pellets are found at the bases of the largest spruces and deciduous trees. The stands were surveyed thoroughly and the search was terminated when pellets were found. The time of the search was not limited or standardised, and the survey was continued, tree by tree if needed, until the determination of species absence was reliable. We classified a stand as occupied if one or more of these pellet trees were found. Pellets only indicate the use of a stand (Reunanen et al., 2002a), and do not allow any inferences about population density or reproduction. We did not estimate pellet tree density in a stand, because in the case of a priority species classified in a habitat directive of the European Union (Rassi et al., 2001) mere presence is strong enough reason to set the stand aside. Moreover, there is no data to show that pellet tree density correlates with the density of flying squirrels or the reproductive value of a forest stand.

In Lakusuo, we selected spruce dominated stands (>50% of total volume is spruce) that were at least 80-year-old for field survey. We based this stand selection on the forest planning data and on previous knowledge of flying squirrel habitat preferences, i.e. older spruce-dominated mixed forests (Eronen, 1996; Mönkkönen et al., 1997; Hanski, 1998). At the age of 80 years forests are mature, and flying squirrels usually inhabit even older forests in northern Finland (Mönkkönen et al., 1997). We examined 91 forest stands filling our criterion, covering 715 ha. Pellet searching was carried out in June and July 2002 by three experienced persons.

In the Kajaani study area, all forest stands that had a volume of spruce $\geq$35 m^3 ha^{-1} were included in the field survey. Here we used rather flexible criteria in selecting stands for field survey because we did not have prior experience on flying squirrel habitat requirements in this area. The lower limit for the volume of spruce was based on our observations in Lakusuo, where 35 m^3 ha^{-1} was the lowest volume of spruce in an occupied stand. Using this criterion we found 264 stands, covering 483 ha. In Kajaani, pellet searching was conducted during May and June 2003 by one experienced person. We, however, removed stands smaller than 0.5 ha ($n = 53$) from the total data set of Kajaani ($n = 264$), since the smallest stand in the data of Lakusuo was 0.5 ha. As a result, 211 stands remained for testing in Kajaani, of which 49 were occupied. The main drawback of presence-absence models used in ecology is that their results are affected by the prevalence of the target species (Pearce and Ferrier, 2000; Manel et al., 2001). We considered the prevalence in Kajaani data low (0.23), and used a paired approach to equalize presences and absences. We used size-matched pairs since we wanted to eliminate the differences rising from the ownership-related stand size, therefore each occupied stand found in Kajaani was paired with a size-matched unoccupied stand ($n = 98$ used in analyses).

In adjacent municipalities (Pudasjärvi, Taivalkoski and Suomussalmi), we used existing information on the presence of flying squirrel in state-owned land given to us by the Register of Endangered Species in Finland (maintained by the Finnish Environment Institute). Biologists and forestry personnel have made these observations during forest inventories over the years 1995–2003 and the occupancy is based on pellets at tree bases or, in some cases, on visual observations of individuals. Each observation was already connected to a certain forest stand in the file system of Metsähallitus, a Finnish state enterprise managing state-owned lands and waters. We had information from 247 occupied stands: 34 from Pudasjärvi, 83 from Taivalkoski (Lakusuo stands not included), and 130 from Suomussalmi.

2.4. *Forest variables*

In all study areas, we used basic variables in the forest planning data: stand size (area; ha), stand age (years), volumes ($m^3\ ha^{-1}$) of each tree species (pine, spruce and birch) and total tree volume per hectare in a stand. We used the volume per hectare as an indirect measure of the overall forest structure, since it combines the diameter, length and density of trees in a stand. Larger volumes usually indicate a typical spruce-dominated forest occupied by the flying squirrel (e.g. Eronen, 1996; Mönkkönen et al., 1997; Hanski, 1998).

In study areas of Lakusuo and Kajaani we characterized the surroundings of each inventoried stand by calculating variables to describe the forest quality around it. We used the surroundings within a 500-m distance, measured from the stand's borders. This distance was used for two reasons. Firstly, Hanski et al. (2000b) observed adult male flying squirrels moving on average 292 (±157) m from the nest during a night. Our 500-m would then roughly cover the nightly moving distance within a male's range, and also include the shorter moving distances of females (111 (±33) m on average). Secondly according to Reunanen et al. (2004), about one square kilometre seems to be a suitable area to estimate the surroundings of an individual's range.

As a measure for the quality of surrounding uninventoried stands, we concentrated on stands having $\geq 35\ m^3\ ha^{-1}$ of spruce, and estimated if they were suitable from the flying squirrel's point of view. We ignored all other types of stands. This limit of the volume of spruce in a stand, $35\ m^3\ ha^{-1}$, was based on the minimum volume of spruce observed in an occupied stand in the Lakusuo study area. To estimate the quality of an inventoried stand's surroundings, we used probabilities of occupancy of a flying squirrel as a surrogate for habitat quality of the surrounding stands. We calculated this probability using coefficients from a non-spatial model (the model B in Lakusuo, see Section 3.2; the model Spruce in Kajaani, see Section 3.5).

Furthermore, based on the probability (derived from the model), we divided these suitable neighbor stands into two groups. We used 50% as a limit, and hereafter, stands with a probability of <50% are called low quality stands, and stands with probability of ≥50% high quality stands. From all inventoried stands, we calculated a straight distance to their nearest neighbor, separately to nearest low quality stand (Nnd00; m) and to nearest high quality stand (Nnd50; m). All inventoried stands had at least one low quality stand as a neighbor within 500 m (Nnd00), but some stands (25 in Lakusuo and 15 in Kajaani) did not have any high quality stands within the 500 m radius (Nnd50). For these inventoried stands without any true high quality neighbor, we used an artificial nearest neighbor distance of 600 m.

We also summed the area of suitable neighbor stands situated within a 500 m radius of the stand, separately of low quality stands (Area00; ha), and of high quality stands (Area50; ha). There was variation in the size and the shape of the stands we inventoried, so the area within 500 m radius along their borders gave different sized surroundings for stands. It can be assumed that larger areas are more likely to contain suitable habitats than by chance. To see whether the examined radius of 500 m around each stand mattered, we summed areas of all forest stands within 500 m radius (forest land; ha), despite their quality for the flying squirrel.

Our approach to use a probability of the occurrence to estimate a neighbor stand quality, instead of a limit for a certain original variable, such as for volume of spruce, stems from the idea that important stand level patterns would be similar in a focal stand as well as in a neighbor stand in the study area. Even though logically the quality of neighboring stands depends on the stand level model based on focal stands, from a statistical perspective these variables can be considered independent spatial variables describing the quality of the surrounding landscape (for a similar approach, see e.g. Pakkala et al., 2002).

2.5. Statistical analysis

We used data from Lakusuo ($n = 91$) to build predictive occupancy models, and data from Kajaani ($n = 98$) and adjacent municipalities ($n = 247$) to evaluate these models. In addition, we built the models similarly in Kajaani, and tested one Kajaani model using data of Lakusuo and adjacent municipalities. We first analyzed differences between occupied and unoccupied stands in both Lakusuo and Kajaani study areas. Many of the variables were not normally distributed, and non-parametric Mann–Whitney tests were used. Flying squirrels prefer spruce dominated mixed forests with deciduous trees, usually also in larger forest tracts (Reunanen et al., 2000), so we selected the area of a stand (ha) and volumes of spruce and birch ($m^3\,ha^{-1}$) for further analysis. Selected variables were not correlated with each other.

We used logistic regression with backward elimination to model the occupancy of the species with binomial presence/absence data (Hosmer and Lemeshow, 2000). We first entered the main stand level effects and all two-way interactions in the model, then based on Wald statistics removed the least significant interaction or main variable if it was not in an interaction term, at every step. This stepwise procedure yielded two simple alternative stand level models in Lakusuo where model A included stand area as a predictor but model B did not. In Kajaani, stand size was fixed (matched pairs), and only volume of spruce remained in the model. We used model B in Lakusuo and model Spruce in Kajaani to calculate predicted occupation probabilities for neighboring stands for each focal stand. Based on these probabilities we calculated the spatial variables described above (Nnd and Area). To see if these landscape variables would improve the model fit, we added one spatial variable at a time and both of them together to a stand level model. Landscape variables were only retained in the model if significant. This was to maintain the amount of variables in the final model low and our predictive models as simple and interpretable as possible.

2.5.1. Evaluation of model performance

We evaluated the performance of the models with several statistics recommended by Fielding and Bell (1997). We measured the success of the model by the rate of false positive (sites predicted occupied but observed empty) and false negative (sites predicted empty but observed occupied) cases. We used Kappa K statistics to evaluate the overall agreement between predictions and actual data, comparing if the model predicts the occurrence better than a chance. The K values range from 0 (random) to 1 (all cases correct), and can be ranked according to rate as follows: <0.4 poor, 0.4–0.75 good, and >0.75 excellent agreement with the data (Fielding and Bell, 1997).

We also distinguished the most parsimonious model with Akaike's information criterion, AIC, which is a sum of deviance and two times the number of parameters used in the model (Burnham and Anderson, 2003). The smaller the AIC value, the simpler and better is the model (e.g. Burnham and Anderson, 2003). In addition, we used threshold-independent receiver operating characteristics (ROC) plots to measure the model's discrimination abilities, by plotting true positive rate (the probability that a stand is correctly classified as occupied, i.e. sensitivity) and true negative rate (i.e. 1-specificity) against each other. The outcome of this plot, the area under ROC curve (AUC), provides a single guiding measure of the overall accuracy of the model, which should also be independent of the threshold used. The threshold here means division of probabilities to presence and absence, in other words a cut point. The AUC values range from 0.5, indicating no difference between groups of correctly predicted presences and absences, to 1.0, where there is no overlap between groups, i.e. when performance of the model is perfect.

In Lakusuo, we also investigated the effects of the cut point on model performance more thoroughly. A cut point of 0.5 is often used to classify cases as occupied or empty, but the limit affects the results, and especially, their applications. At an optimal cut point, correct classification rates for presence and absence are maximized (Fielding and Bell, 1997). We estimated the optimal cut point for our models using all cut points between 0.0 and 1.0 with intervals of 0.1 (see also Suárez-Seoane et al., 2002). Also, since false negative cases carry serious consequences in models concerning endangered species (Brito et al., 1999), we checked how lowering the cut point can reduce the risk of false negative cases.

The next task in evaluating our predictive models was to estimate spatial autocorrelation in Lakusuo data, since many of the inventoried stands actually shared a common border. Spatial autocorrelation is a very general property of ecological data where pairs of observations at a given distance are more similar than observations from more distant pairs (e.g. Legendre, 1993; Legendre and Legendre, 1998). This usually indicates a lack of independence between observations, which may increase the risk of rejecting a true null hypothesis.

We determined the mid-points for our stands, and as suggested by Diniz-Filho et al. (2003), generated spatial correlograms based on Moran's I coefficients for actual probabilities and residuals of all four models. We used 10 distance classes, which were selected to make sample size in each group about equal (upper limits were 980, 1600, 2100, 2600, 3200, 4100, 5000, 6500, 8200 and 10,000 m). Moran's I values range from -1 to $+1$ zero value indicating lack of spatial autocorrelation. Since spatial autocorrelation is a problem only if residual values show marked spatial structure, we estimated how Lakusuo models control for the spatial structure of the data by inspecting correlograms made for both, residuals and original probabilities (Diniz-Filho et al., 2003).

2.5.2. *Evaluating the models with new data*

Evaluation with new data from another area is recommended as the most preferred method of model validation (e.g. Fielding and Bell, 1997; Hosmer and Lemeshow, 2000; Kozak and Kozak, 2003). We first evaluated two stand level Lakusuo models with independent data of the occurrence of the flying squirrel in forest stands in adjacent municipalities of Pudasjärvi, Taivalkoski and Suomussalmi. For each of these new occupied stands we calculated a probability of the occurrence using logistic equation and original coefficients from Lakusuo models, and classified them as occupied or empty with two alternative cut points. The idea was that if 95% or more of occupied stands are also predicted as occupied, the model performs well and can be generalized with less than 5% risk to other areas in NE Finland. Second, we tested the ability of all four Lakusuo models to predict the occurrence of the flying squirrel in Kajaani study area by calculating the probability of occurrence for stands of size-matched data using coefficients from Lakusuo models. Third, we tested the performance of one stand level Kajaani model using its coefficients for occupancy data from the three municipalities as well as for data from Lakusuo. Evaluation of the model performances was then based on previous statistics. All statistical analyses were made with SPSS for Windows (version 10.1).

3. Results

3.1. *Univariate descriptions*

We could detect the basic features in forest structure known to be important for the Siberian flying squirrel using forest planning data. In Lakusuo, where 35 of 91 stands were occupied by the flying squirrel, these had larger total tree volume and volume of spruce than unoccupied stands (Table 2). Occupied stands were also larger in size and the proportion of birch was larger, although not statistically significant after Bonferroni correction. However, there were no strong differences in other proportions of tree species at the stand level.

In Kajaani study area, tests showed similar patterns as in the Lakusuo area (Table 2.): the volume of spruce and the proportion of spruce were larger in occupied stands but, surprisingly, birch was not related with the occupancy pattern. The volume of pine, on the other hand, was larger in unoccupied stands. Overall, the biggest differences between these study areas were that, on average, stands were younger in Kajaani, but the total tree volume was larger than in Lakusuo. In addition, stands were 2–3 times larger in Lakusuo than in Kajaani (Table 2).

3.2. *Stand level models, spatial variables and spatial models in Lakusuo*

We chose three non-correlated variables from the Lakusuo data, stand area and volumes of spruce and birch, to reflect habitat preferences of the flying squirrel for the predictions. None of the interaction terms were significant. We were left with two alternative models: Model A, which can be considered as a simple stand level model including area of a stand and volumes of spruce and birch, and Model B, which is a non-spatial model including tree information only (Table 3). The overall accuracy was similar for both: 73.5% for model A and 71.4% for model B.

We then used the non-spatial model B to estimate the forest quality of the surroundings. Comparison

Table 2
Comparison of forest stand level variables as well as of spatial variables between occupied (1) and unoccupied (0) stands in Lakusuo ($n = 91$) and in Kajaani ($n = 98$)

	U	Significance	Average (S.D.) of 0	Average (S.D.) of 1
Lakusuo				
Area (ha)	677. 0	0.013	6.5 (6.0)	10.1 (8.8)
Volume (m^3/ha) of spruce	627.5	**0.004**	56.8 (21.5)	75.9 (30.9)
Volume of pine	925.5	0.655	21.5 (22.2)	22.5 (20.5)
Volume of birch	653.5	0.008	15.0 (13.1)	24.0 (17.3)
Volume of all trees	565.5	**0.001**	95.4 (32.7)	123.8 (35.5)
Proportion of spruce (%)	968.5	0.925	62.2 (19.6)	62.8 (20.3)
Proportion of pine	890.5	0.464	21.1 (17.8)	17.8 (15.8)
Proportion of birch	798.0	0.137	14.8 (10.6)	18.3 (10.2)
Proportion of aspen	957.5	0.782	1.9 (5.3)	1.1 (2.5)
Age of a forest (years)	952.0	0.819	163.0 (28.6)	168.1 (16.0)
Nnd00 (m)	641.5	**0.000**	38.3 (80.6)	2.2 (12.9)
Nnd50 (m)	476.0	**0.000**	321.1 (256.9)	93.5 (178.3)
Area00 (ha)	850.0	0.289	74.6 (45.2)	85.1 (35.8)
Area50 (ha)	515.5	**0.000**	17.2 (22.2)	37.7 (29.2)
Forest land (ha)	830.0	0.221	323.0 (76.4)	348.3 (95.7)
Kajaani				
Area (ha)	1185.0	0.912	2.7 (2.6)	3.3 (6.0)
Volume (m^3/ha) of spruce	703.5	**0.000**	79.4 (43.6)	113.0 (52.4)
Volume of pine	782.5	**0.003**	63.9 (41.4)	40.9 (39.2)
Volume of birch	1082.5	0.396	25.6 (26.4)	20.1 (24.6)
Volume of all trees	1107.5	0.509	169.7 (37.3)	175.5 (41.9)
Proportion of spruce (%)	676.0	**0.000**	46.3 (20.4)	63.5 (22.0)
Proportion of pine	829.0	0.008	37.8 (23.5)	24.2 (21.2)
Proportion of birch	1092.0	0.435	15.3 (17.0)	11.5 (12.9)
Age of a forest	1030.0	0.226	109.7 (32.4)	118.4 (32.0)
Nnd00 (m)	1134.0	0.571	59.2 (127.4)	38.8 (83.5)
Nnd50 (m)	1022.5	0.191	204.2 (237.7)	131.6 (200.1)
Area00 (ha)	1068.5	0.348	23.5 (25.2)	24.6 (21.6)
Area50 (ha)	950.0	0.075	8.7 (11.9)	12.1 (14.4)
Forest land (ha)	933.5	0.058	103.9 (52.2)	86.8 (42.4)

Mann–Whitney *U*-test is used and its statistical significance after sequential Bonferroni correction is shown in bold. Averages with standard deviation (in parentheses) are shown.

Table 3
Results from logistic regression models A and B, using forest planning data from Lakusuo ($n = 91$)

	B	S.E.	Wald	Significance	Exp(B)
Model A					
Area	0.065	0.035	3.509	0.061	1.067
Volume of spruce	0.026	0.010	6.870	0.009	1.026
Volume of birch	0.034	0.016	4.398	0.036	1.034
Intercept	−3.338	0.809	17.022	0.000	0.036
Model B					
Volume of spruce	0.026	0.010	7.577	0.006	1.027
Volume of birch	0.034	0.016	4.641	0.031	1.035
Intercept	−2.849	0.723	15.531	0.000	0.058

Table 4
Results from Lakusuo logistic regression models including a spatial variable

	B	S.E.	Wald	Significance	Exp(B)
Model ANND					
Area	0.070	0.037	3.686	0.055	1.073
Volume of spruce	0.020	0.010	3.727	0.054	1.020
Volume of birch	0.007	0.018	0.173	0.678	1.007
Nnd50	−0.004	0.001	7.146	0.008	0.996
Intercept	−1.769	0.944	3.509	0.061	0.171
Model AAREA					
Area	0.057	0.036	2.532	0.112	1.058
Volume of spruce	0.023	0.010	5.283	0.022	1.023
Volume of birch	0.019	0.018	1.127	0.288	1.019
Area50	0.020	0.011	3.484	0.062	1.020
Intercept	−3.311	0.807	16.829	0.000	0.036
Model ANNDAREA					
Area	0.067	0.037	3.247	0.072	1.069
Volume of spruce	0.020	0.010	3.601	0.058	1.020
Volume of birch	0.006	0.018	0.105	0.746	1.006
Nnd50	−0.003	0.002	4.601	0.032	0.997
Area50	0.006	0.012	0.246	0.620	1.006
Intercept	−1.924	0.997	3.725	0.054	0.146

Nnd50 is a distance to closest high quality forest stand, and Area50 is the area of all high quality forest stands surrounding an inventoried stand.

between occupied and unoccupied stands showed that the occupied stands had high quality stands closer to them (Nnd50), and had larger total area of high quality stands (Area50) in their surroundings than the unoccupied stands (Table 2). This larger area of high quality stands in the surroundings of occupied stands was not due to a significantly larger area being studied in the surroundings (see variable Forest land, in Table 2).

Furthermore, we included a spatial variable, Nnd50 or Area50, one at a time in the simple stand level model A (models ANND and AAREA, respectively, see Table 4). We found that the surroundings significantly contributed to occupancy in both of the spatial models. Distance to the nearest high quality stand was clearly significant, while area of high quality stands had a coefficient close to significant in the model. In addition, both of them outweighed the importance of birch. We also included both spatial variables in the model A (model ANNDAREA, see Table 4), but area of high quality stands and volume of birch did not have much impact in this model. We excluded the model ANNDAREA from further analysis since the similar prediction accuracy was achieved using the model ANND.

3.3. Comparison of the Lakusuo models

The comparison of these four models showed that absence was always better predicted than presence, and the overall proportion of correctly predicted cases was quite similar in all models (from 71.4 to 73.5%, see Table 5). Rates of false positive and negative cases,

Table 5
Comparing performances of the Lakusuo models using several statistics

Model	AIC	AUC	Kappa *K*	Correct total (%)	Correct of 0 (%)	Correct of 1 (%)	FP (%)	FN (%)
A	107.2	0.755	0.418	73.5	85.7	54.3	14.3	45.7
B	108.9	0.733	0.355	71.4	87.5	45.7	12.5	54.3
ANND	100.8	0.811	0.410	72.5	80.4	60.0	19.6	40.0
AAREA	105.6	0.780	0.383	72.5	87.5	48.6	12.5	51.4

The smaller the AIC value, the better is the model, and the larger the AUC and the Kappa *K* values, the better is the model (FP: false positive rate, FN: false negative rate).

with a cut point at 0.5, ranged from 12.5 to 54.3% indicating uncertainty in our model performances. However, distance to the nearest high quality neighbor stand, included in the model ANND, seemed to increase the accuracy of predicting the presence of the flying squirrel: 60% of the occupied stands were also predicted as occupied. Other evaluation statistics showed small differences between our models, but they reflected good (but not excellent) fit with the data. However, the model ANND was the best of the four models as evaluated by AIC and AUC values, but Kappa K showed only slight difference between the models A and ANND.

We also examined how the cut point affected the outcome of the predictions, and plotted the proportions of correctly predicted cases against each other (Fig. 2). For the models A and B, the optimal cut point, where percentages of presences and absences predicted correctly are maximized, was 0.35. For the model AAREA it was 0.53 and for the model ANND 0.60. Furthermore, as expected, the decrease in the cut point increased the amount of the cases predicted correctly as unoccupied, but it did not remove the problem of false positive predictions. Using a cut point of 0.35 instead of 0.5, the proportion of false negative cases decreased from 45.7 to 34.3% with the model A, and with the model B from 54.3 to 31.4%. With the spatial models the false negative rate also decreased by about 20%: with ANND from 40.0 to 22.9%, and with AAREA from 51.4 to 31.4%.

Inspection of Moran's I values in a correlogram showed that all models seemed to have positive spatial autocorrelation up to 2000 m, and negative autocorrelation between 2000 and 7000 m, before changing back to positive with longest distances of 7000–10,000 m (Fig. 3). Yet our models could control for the spatial autocorrelation since the Moran's I values for residual probabilities were considerably smaller than for original probabilities, especially with the spatial models ANND and AAREA (Fig. 3).

3.4. Evaluation of Lakusuo models

We evaluated two Lakusuo models, A and B, to estimate the grounds for generalizing our results elsewhere in NE Finland. We used these simple models, since differences in the model fit were small

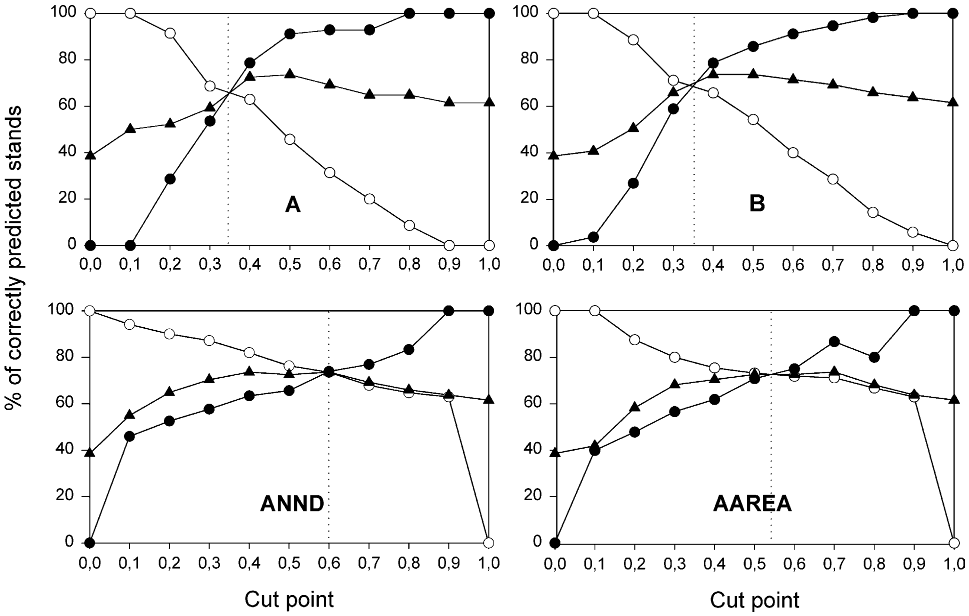

Fig. 2. Adjusting the cut point for models A, B, ANND and AAREA with intervals of 0.1. The intersection is the optimal cut point, where percentage of correctly predicted presences and absences is maximized. Solid circle: correctly predicted presence; open circle: correctly predicted absence; and solid triangle: total correctly predicted cases.

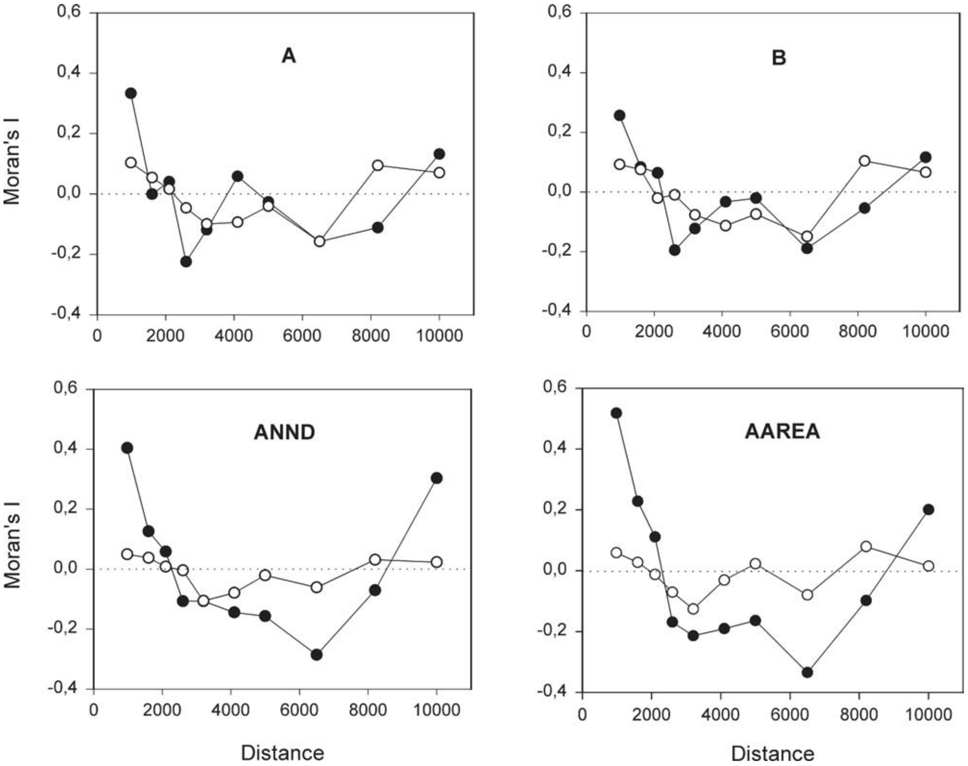

Fig. 3. Spatial autocorrelation defined by Moran's *I* for predicted probabilities (solid circle) and standardized residuals (open circle), separately for models A, B, ANND and AAREA.

compared to more complex spatial models. We used existing information on the flying squirrel from adjacent municipalities of Pudasjärvi, Taivalkoski (excluding Lakusuo study area) and Suomussalmi, and calculated the probability of occupancy for these occupied stands with coefficients from the models A and B. We classified stands as occupied or unoccupied with a cut point at 0.50 and at 0.35.

The predictions were successful with an overall accuracy of over 80% in the pooled data (Table 6). However, the accuracy seemed to vary among the municipalities and only in Suomussalmi were >95%

Table 6
Evaluation of the Lakusuo models A and B, using presence-only data of the flying squirrel from all adjacent municipalities (All: pooled data, $n = 247$; PJ: Pudasjärvi, $n = 34$; TK: Taivalkoski, $n = 83$; SS: Suomussalmi, $n = 130$)

	Model	Cut point 0.50 (%)	Cut point 0.35 (%)	Spruce ($m^3\ ha^{-1}$)	Birch ($m^3\ ha^{-1}$)	Area (ha)
All	A	84.2	89.9	128.1 (53.9)	23.4 (16.9)	13.0 (23.1)
	B	81.0	87.9			
PJ	A	67.6	73.5	113.5 (50.4)	16.9 (24.2)	10.5 (15.5)
	B	70.6	76.5			
TK	A	78.3	86.8	108.0 (51.9)	23.7 (16.3)	22.3 (36.3)
	B	68.7	80.7			
SS	A	92.3	96.2	144.8 (50.8)	24.9 (14.6)	7.8 (6.0)
	B	91.5	95.4			

Proportions of correctly predicted cases, with a cut point 0.5 and 0.35, and averages (with standard deviation) of variables used in the models are shown.

Table 7
Evaluation of the four Lakusuo models in Kajaani ($n = 98$), using several statistics (a cut point 0.5)

Model	AUC	Kappa K	Correct total (%)	Correct of 0 (%)	Correct of 1 (%)	FP (%)	FN (%)
A	0.632	0.102	55.1	57.1	53.1	42.9	46.9
B	0.631	0.143	57.1	55.1	59.2	44.9	40.8
ANND	0.680	0.286	64.3	71.4	57.1	28.6	42.9
AAREA	0.670	0.204	60.2	73.5	46.9	26.5	53.1

of the stands correctly predicted as occupied with a cut point at 0.35, using both models (Table 6). In Suomussalmi the volumes of spruce and birch were higher, but stands on average were smaller in size than in other municipalities. In Pudasjärvi, having the lowest predictive success from 68 to 77%, the volume of birch was on average smaller, whereas in Taivalkoski, with a predictive success of 78–87%, the volume of spruce was on average smaller than in other regions. Stand size was on average the largest and most variable in Taivalkoski. However, even though we had presence-only data for testing, predictive success can be considered relatively high: in original Lakusuo data, presences were correctly predicted in only about half of the cases (Table 5).

We also evaluated all Lakusuo models with Kajaani data (size-matched pairs of stands, $n = 98$). The performance of Lakusuo coefficients in Kajaani was almost as good as guesses using models A and B (Table 7). The landscape variables in spatial models ANND and AAREA slightly improved the performance, particularly the rate of false positive predictions dropped, but some inaccuracy remained in the fit with the data (Table 7).

3.5. Building and evaluating Kajaani models

Correspondingly, model building was carried out in Kajaani using paired data ($n = 98$) and uncorrelated variables: size of a stand, and volumes of spruce and birch. Interaction terms and the stand size were insignificant. The effect of spruce on flying squirrel prevalence was strong ($B = 0.015$, $p = 0.003$; constant $= -1.266$), but birch was not significant in this model ($B = -0.005$, $p = 0.544$). Volume of spruce alone, called the model Spruce, explained 68.4% of the occurrence (spruce $B = 0.015$, $p = 0.002$; constant $B = -1.414$) in Kajaani, again absence better than presence (73.5 and 63.3%, respectively). There was some inaccuracy in the Spruce model fit with the Kajaani data (FN = 36.7%, FP = 26.5%, AUC= 0.707, Kappa $K = 0.367$, AIC = 126.286).

The model Spruce was used to estimate the stand quality for calculating the spatial variables Nnd00, Nnd50, Area00 and Area50 in Kajaani similarly as in Lakusuo (Table 2). The values of spatial variables, however, did not significantly differ between occupied and unoccupied stands (Table 2). As such, neither Nnd50 nor Area50, alone or together, were significant when entered into the models with spruce volume (all $p > 0.35$).

The model Spruce was tested with Pudasjärvi, Taivalkoski and Suomussalmi data, and also with Lakusuo data, having a cut point at 0.5. The coefficients of Spruce explained 67.7% of the occupancy correctly in Pudasjärvi, 56.6% in Taivalkoski, and 85.4% in Suomussalmi. In Lakusuo, 69.2% of the occupancy status of stands was explained correctly, absence better than presence (98.2 and 22.9%, respectively), but there was inaccuracy in the model fit (FN = 77.1%, FP = 1.8%, AUC = 0.680, Kappa $K = 0.245$).

4. Discussion

4.1. Usefulness of the forest planning data

Our results suggest that forest planning data can be used in locating potential habitats of the Siberian flying squirrel. In the Lakusuo study area, flying squirrels were associated with mature spruce-dominated stands of larger size, having a mixture of larger volumes of spruce together with birch. These results concur with earlier studies on the habitat use of the species (Eronen, 1996; Hanski, 1998; Selonen et al., 2001). In addition, occupied forest stands were surrounded by more high quality forests also supporting earlier findings from the landscape scale (Reunanen et al., 2000, 2002a, b). Therefore, volumes of spruce and birch in a stand and the existence of high quality forest in the surroundings can be used as guiding features when estimating the habitat suitability for the flying squirrel. Our models, based on the knowledge of flying squirrels' preferences of forests and their surroundings, seemed to grasp the most typical features of suitable habitats, i.e. spruce-dominated mixed forests. In Lakusuo the overall accuracy of over 70% and agreement of other statistical values (AIC, AUC, Kappa *K*), for all our models, indicated a good fit with the data. However, the absence of the species was much better predicted than the presence: our models do relatively little to determine the occupancy status. In addition, the misclassifications (FP and FN rates in Table 5) revealed some inaccuracy in predictions.

Despite misclassifications with the original data, our simple stand level Lakusuo models performed well with the data from adjacent municipalities: correct classification rate was about 80% in pooled municipality data. This indicates general applicability in NE Finland. The prediction success was also fairly good for individual municipalities, from 67 to even 96%, but differences between them are still worth consideration. This dissimilarity may be because of a gradient in the forest structure: Pudasjärvi and Taivalkoski fall mostly within the northern boreal zone, whereas Suomussalmi is situated within the transition or even in the middle boreal vegetation zone. These locations may be reflected in the prediction success because, for instance, model accuracy was weakest in Pudasjärvi, where volume of birch was on average the least, while the predictions performed the best in Suomussalmi having on average the highest volume of spruce and birch.

A similar pattern of area-specificity existed in the Kajaani study area. The same characteristics of spruce-dominated forests provided ca. 70% accuracy in Kajaani, but birch did not influence strongly in the occupancy pattern. Deciduous trees may perhaps be more abundant outside the stands in Kajaani because of road sides and field edges, but this was not discernible in the data. Furthermore, spatial variables did not seem to explain the occurrence of flying squirrels in Kajaani. On the other hand, the original Lakusuo coefficients of spatial models performed better than stand level models in Kajaani, which indicates some importance of the landscape structure there after all. The performance of Kajaani's simple Spruce model in three municipalities and in Lakusuo study area was weaker than those of Lakusuo models.

These differences in model performances may be due to Kajaani's more southern location well within the middle boreal vegetation zone, but most probably due to the overall structure of the landscape, i.e. the grain size (Levins, 1968), since the average stand size varied markedly between study areas. From this perspective, the Lakusuo study area, where forest stands were on average larger and about the size of a home range of one female (ca. 8 ha, see Hanski et al., 2000b), can be considered as a coarse-grained landscape for the flying squirrel. With much smaller stands Kajaani study area represents a fine-grained landscape. In principal, one flying squirrel individual most likely could to use several stands to gain the same amount of resources in a fine-grained landscape. This idea was not supported by our data as no spatial variable describing the stand surroundings significantly improved the model performance in Kajaani. However, it is obvious that in a fine-grained landscape, properties of one stand are not so indicative of presence/absence pattern as in a coarse grained landscape, where a single stand may form a home range (see also Hanski et al., 2000a). In the coarse grained landscape of Lakusuo stand surroundings affected stand occupancy, which reflects the higher relative importance of connectivity (ability to disperse among stands) in coarse-grained than in fine-grained landscape. The idea that species responses to landscape structure differ between coarse-grained and fine-grained pattern is intriguing as it suggests that the effects of habitat loss and fragmentation on species depend on the spatial scale of landscape change (see also Rolstad and Wegge, 1987).

4.2. Aspects to the data

The correlograms for original observations are typical when spatial variation is structured in patches (Legendre and Legendre, 1998). Our graphs suggested a spatial structure in occupancy (i.e. stands having similar probabilities for the occurrence of the flying squirrel) where clusters of stands within a 2 km radius were similar, as were clusters situated more than 7 km apart. This actually coincides with the structure of the forest landscape in Lakusuo where clusters of larger mature forest areas are embedded in young sapling stands and open land, which dominate the landscape. Our models, to a large extent, controlled for spatial autocorrelation between observations because correlograms for residuals indicated only small, if any, spatial structure (Diniz-Filho et al., 2003).

Forest planning data itself may, however, not be applicable in general. For example, stand borders may be delineated purely for forestry purposes (Uuttera and Hyppänen, 1997) and may not follow biologically meaningful borders in the landscape. Further, heterogeneity within the forest stand level may be more important to many species than among-stand variability, i.e. stand level information is not able to describe the variation and resolution of resources that is important for the species. For flying squirrel, stand level forest planning data seemed to work, perhaps because spatial requirements by this species match with the spatial scale where stands are delineated.

Earlier studies have pointed out the importance of aspen, particularly large individuals, for flying squirrels (e.g. Reunanen et al., 2002a). Large aspens often grow as scattered clumps of few trees and therefore, estimation of their volume is subject to high sampling variance. We could not use information on aspens in our models, because measurements of living aspens in a stand were often missing from the data. Other additional information, if available, could then be used to augment forest planning data in estimating small-scale features within a stand: false color aerial photographs, for instance, could be used to locate potential cavity trees and groups of big aspens (e.g. Uuttera and Hyppänen, 1998).

Snapshot data on presence and absence of the flying squirrel disregards population dynamics in time. Without information about variation in the occupancy among years, we cannot estimate the effects of possible dynamics in the area, or detect reliable thresholds for the stand quality. Sometimes even good habitats may seem empty, and as Tyre et al. (2003) pointed out, it would be wise to survey sites several times to get a good picture of the occurrence. However, Tyre et al. (2003) were concerned mainly with visual observations on moving mammals where it is important to be at the right place at the right time, whereas we based our observations on pellets accumulating in sites mostly used by flying squirrels. In our case, the risk of not noticing the actual presence should be rather small, since pellets often remain for months and in addition, the pellets accumulated during the previous winter are still visible in early summer when our field work was carried out.

4.3. Applicability of the predictive models

Reunanen et al. (2004) suggested that about 15% cover of suitable forests would be enough to maintain Siberian flying squirrel persistence. Our present results indicate that forest planning data with predictive occupancy models can be used to locate such suitable forest stands. This is important because earlier works suggest that the flying squirrel is sensitive to habitat loss (Selonen et al., 2001), but also to fragmentation effects (Mönkkönen et al., 1997; Reunanen et al., 2000, 2002b). In fact, landscape patterns have been found to be more important in northern Finland than in southern Finland (Reunanen et al., 2002b; Selonen et al., 2001; Selonen and Hanski, 2003). This difference most probably arises because of the different grain size of the landscape structure (Hanski et al., 2000a), which is fine-grained in the south and more coarse-grained in the north from flying squirrel perspective. This idea is supported by our results from Lakusuo versus Kajaani.

Even though the model accuracy varied among municipalities, we were encouraged that both, stand level and spatial models can be used in estimating suitable habitats for the flying squirrel. They can be generalized to NE Finland and in adjacent regions, however, with some caution (see Cardillo et al., 1999; Reunanen et al., 2002b). Before forest planning data and predictive occupancy models are applied and generalized to forest management planning, factors, such as vegetation zone and landscape structure must be considered.

We also emphasize, that habitat models alone cannot completely replace field surveys. Relatively high false negative rate may become a problem for a species classified as vulnerable (see Brito et al., 1999) if, for instance, clear cutting or thinning operations are permitted in forest stands predicted empty but actually occupied by the species. To diminish these problems, we suggest using a lower cut point level for predicted probabilities when estimating potential forest stands for the flying squirrel, and stress the need to confirm the absence by field surveys. Finally, we agree with Åberg et al. (2003), that when the accuracy of forest planning data improves, it can probably be used even more accurately in predicting many biodiversity related nature values, like the occurrence of different species in managed forests.

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