

## Loss and fragmentation of Siberian jay (*Perisoreus infaustus*) habitats

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Received 7 Oct. 2010, final version received 26 May 2011, accepted 18 May 2011

Muukkonen, P., Angervuori, A., Virtanen, T., Kuparinen, A. & Merilä, J. 2012: Loss and fragmentation of Siberian jay (*Perisoreus infaustus*) habitats. *Boreal Env. Res.* 17: 59–71.

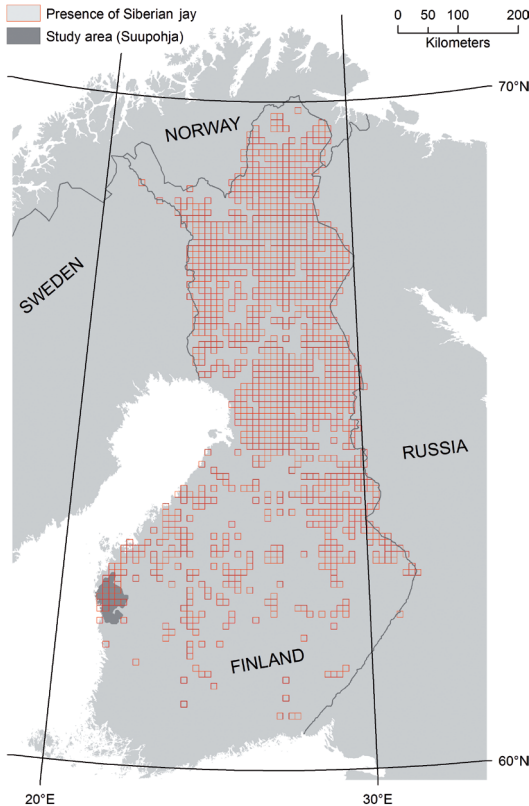
We analyzed forest landscape changes in a western Finnish breeding area of Siberian jays utilizing Landsat MSS and TM satellite images taken during a 29-year period (1976–2005). We found that Siberian jays appeared to favour closed spruce-dominated forest patches, possibly because they provide better visual protection against predators. Such spruce-dominated forest patches became smaller and increasingly fragmented during the study period. According to a 25-m pixel analysis, the total area of spruce-dominated habitats decreased from 14.7% to 11.0% and the mean patch size from 2.0 ha to 1.4 ha during 1987–2005. This was mainly due to intense loggings of spruce forests and a special form of land ownership, which has induced narrow forest estates measuring few dozens of metres in width. The parallel decline in potential breeding habitats as well as Siberian jay population size suggests that loss and fragmentation of key habitats, and possibly related changes in predator community, are the most probable causes for the decline of Siberian jay population in the study area.

### Introduction

Human habitation and economic development have resulted in habitat modification, fragmentation, and destruction on a worldwide scale. Human activities have often been highly selective, impacting some landscape and vegetation types more than others (de Blois *et al.* 2002). For instance, they have created strongly age-structured forests with stand characteristics (as stand density, age structure, species composition, etc.) that differ greatly from those seen in primary forests (Östlund *et al.* 1997). Forestry practices

have also lead to habitat loss, fragmentation and patch isolation, which are the three main factors negatively influencing the occurrence and abundance of forest fauna (Murcia 1995, Kouki *et al.* 2001, Kaisanlahti-Jokimäki *et al.* 2005).

Fragmentation of formerly continuous habitats is a dominating feature of man-modified environments, and understanding its community and population level consequences has become an important issue in ecology and conservation biology (Haila and Hanski 1984, Saunders *et al.* 1991, Harrison and Bruna 1999, de Blois *et al.* 2002). Fragmentation and loss of boreal



**Fig. 1.** Location of the study area in the western coast of Finland and the occurrence of Siberian jay in Finland according to the Atlas of Finnish breeding birds (2008).

forests have generally had a negative impact on boreal bird populations, especially closed-forest specialists (Virkkala 1991, Virkkala *et al.* 1994, Edenius and Elmberg 1996). However, most studies focussing on this topic have covered short time spans, making it difficult to compare pre- and post-harvest situations, as well as long-term impacts of forestry practices (Sallabanks *et al.* 2000, Griesser *et al.* 2007). In addition, long time-series are essential for determining the full effects of habitat fragmentation.

The Siberian jay (*Perisoreus infaustus*) is a good example of a locally endangered, non-migratory bird living in mature, closed coniferous boreal forests. Its preference for closed and layered forest habitats may relate to the fact that its main predators, the northern goshawk (*Accipiter gentilis*) that predate adults, and corvids that predate nests, both rely on visual cues for

prey detection (Griesser *et al.* 2006, 2007, Nystrand 2006, Griesser and Nystrand 2009). Hence, mature and closed spruce forests in our study area may provide better protection for Siberian jays than open pine forests. Furthermore, old spruce-dominated forests have a higher abundance of invertebrates than other types of forests, providing more food for insectivorous birds (Edenius and Meyer 2002). In line with this, Siberian jays have been observed to show habitat utilization preference for spruce-dominated forests (Lillandt 2002, Edenius *et al.* 2004).

The Siberian jay occurs throughout Eurasia between latitudes 50°N and 70°N (Uimaniemi *et al.* 2000). However, in the southern part of its range, the population sizes have declined drastically since the 1940s (Järvinen and Väisänen 1978, Helle 1985, Väisänen *et al.* 1998, Bergholm 2007). Increased forestry activities, fragmentation and loss of mature forests have been assumed to be the main causes behind these declines (Järvinen and Väisänen 1978, Helle and Järvinen 1986, Virkkala *et al.* 1994, Väisänen *et al.* 1998). One possible mechanism is that fragmentation and loss of mature and closed forest habitats may reduce important visual protection against predators (*see* Ekman *et al.* 2001, Eggers *et al.* 2005, Griesser *et al.* 2006, 2007, Griesser and Nystrand 2009). Although the species is not under an immediate threat of extinction (Väisänen *et al.* 1998), it has an important conservation value in southern Finland for two reasons. Firstly, the southern Finnish Siberian jay populations occur at the southern edge of the species distribution range and are isolated from the main population, which is further north (Fig. 1, Väisänen *et al.* 1998, Pihlajaniemi 2006). Thus, the populations in southern Finland may be particularly vulnerable to the effects of demographic and environmental stochasticity. Secondly, over 90% of Siberian jays in southern Finland live outside conservation areas (Pihlajaniemi and Saanto 2005), which may affect their future survival depending on how the non-protected habitats are managed. In a wider perspective, contemporary patterns of species that border their geographic range can provide insights into future changes in core areas (Imbeau *et al.* 2001). Therefore, detailed, quantitative analyses of the effects of recently applied

forestry practices on the amount and configuration of Siberian jay habitats can serve as the first step in the attempts to compromise between conservation and commercial values and, more specifically, in the development of sustainable forestry practices and cost-efficient conservation strategies designed for particular species.

In this study, we focussed on a Siberian jay population inhabiting the Suupohja area in southern Finland (Fig. 1). This population resides at the southern edge of the species' distribution area in Finland, and drastically declined in size over the past three decades, with up to a 60% decline in the annual number of breeding adults (Lillandt 2003, 2004, Bergholm 2007). Our aim was to quantify how Siberian jay habitats in the area have changed during 1976–2005, and to investigate whether these changes can be ascribed mainly to habitat loss or to habitat fragmentation. Considering the improved understanding of the changes of forest landscape, our study should shed light on the possible role of fragmentation and loss of spruce-dominated forests in the recent decline of Siberian jay population in southern Finland.

## Material and methods

### Study area

The study area (approx. 2700 km<sup>2</sup>) covers forest areas along the west coast of Finland (the Suupohja area) between 62°00'N and 62°50'N, and 21°00'E and 22°00'E (Fig. 1). This region is located on the border region of south-boreal and hemi-boreal vegetation zones (Ahti *et al.* 1968) and is characterized as being flat with the terrain elevation ranging from 0 to 30 m above sea level. The choice of this particular area for the study was motivated by the fact that its borders define boundaries of a long-term study of the Siberian jay which has been ongoing since 1976 (e.g. Lillandt 2000, 2002, 2003, 2004, Alho *et al.* 2009, Jaari *et al.* 2009).

The dominant tree species in the study region are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and broad-leaved birches (*Betula pendula* and *B. pubescens*). Forest understory is dominated by dwarf shrubs such as

bilberry (*Vaccinium myrtillus*) and lingon berry (*V. vitis-idaea*). Wood from the forests in this region has been utilized for centuries. Forests with fine sediment soils have been cleared for pastures and agricultural fields. Most (ca. 68%) of the study area is still forested, but influenced by intensive commercial forestry. The majority of the forests are privately owned (85%), though some are owned by companies (< 1%), state (< 2%), and municipalities, or parishes and communities such as foundations and co-operatives (ca. 12%; Finnish Forest Research Institute 2006). Only 0.1% of the state-owned forests in this area is statutorily protected.

### Habitat classification

The landscape was classified for potential breeding habitat, potential dispersal habitat and uninhabitable areas. These classes were defined such that the potential breeding habitat consists of closed spruce-forests (> 1/3 of the wood volume consists of spruce) which have the highest Siberian jay densities and which are the key breeding habitats in the southern edge of their distribution area (Lillandt 2002, Angervuori 2008). Our field classification of habitat suitability of the ground reference points is based on a subjective opinion and many years of practical field experience regarding the bird population in question. To show that our habitat classification can identify the habitats preferred by the Siberian jay, we used generalized linear models to test for the presence or absence of Siberian jay at feeding sites located in different parts of study forests (cf. Lillandt 2000, 2002, 2003, 2004). We found that Siberian jay presence was positively and significantly associated with the fraction of the spruce-dominated forest within a 1500 m radius [we tested several radius lengths (Angervuori (2008))] around the feeders in both years 1987 ( $n = 112$ ) and 2005 ( $n = 558$ ) (Analyses of deviance 1987:  $D = 17.11$ ,  $df = 1$ ,  $p < 0.01$ ; 2005:  $D = 11.36$ ,  $df = 1$ ,  $p < 0.01$ ). Hence, these analyses provide support for the chosen landscape classification, which is based on the occurrence of spruce. Nonetheless, in other areas the effect of spruce dominance on Siberian jay occurrence might be different.

**Table 1.** Information on the satellite and GIS data used in this study.

Data type	Acquired/published	Description	Resolution
Satellite image	25 June 1976	Landsat 2 MSS, path 207, row 16	80 m
Satellite image	20 July 1987	Landsat 5 TM, path 191, rows 16, 17	25 m*
Satellite image	12 July 2005	Landsat 5 TM, path 192, row 16	25 m*
Digital land use map	2005	Corine Land Cover 2000 product (Finnish Environment Institute 2005)	25 m*

\* The original 30 m pixel size was transformed to a 25 m pixel size during the geo-referencing process.

Potential dispersal habitats consisted of all other types of forests including pine forests, broad-leaved forests and finally all seedlings and pre-commercial thinning forests of any tree species (typically under 20 years old). Open areas such as clear-cuts, cultivated areas, open agricultural areas, water bodies, etc. — also forming dispersal barriers for Siberian jays — were defined as uninhabitable. The stand age is in many locations a difficult characteristic to determine because most of the forest stands in our study area are not regularly even-aged, but according to forest evaluation practices we classified the dominant tree layer age into the following classes: 0–10, 10–20, 20–30, 30–50, 50–100, > 100.

To perform this classification, Landsat TM optical remote sensing imagery acquired in 1987 and 2005 was used as the main data source (Table 1). Corine Land Cover 2000 GIS-data

(CLC2000-Finland 2005) was used as a water body mask and to confirm the accuracy of our classification, as well as to delineate open lands such as cultivated areas, water bodies, and constructed areas. For a long time, satellite remote sensing has been considered an ideal data source for large-area landscape and land cover classification (Franklin and Wulder 2002).

Satellite images were geo-referenced to Finnish *kkj3* coordinate system to allow for an overlap with Finnish cartography data. Due to this process, images were re-sampled to a 25 × 25-m pixel resolution. The image of 2005 was subjected to a supervised classification (e.g. Franklin and Wulder 2002). For testing the accuracy of classification, 80 randomly located ground reference field plots were used (Table 2). The same classification was also applied to the image of 1987. In order to do that, we calibrated the reflectance of the images by linear channel-to-channel regression to correspond to each other (Furby and Campbell 2001) with  $R^2$  of 0.63, 0.72, 0.75, 0.91, 0.89 and 0.91 for channels 1–5 and 7, respectively. This is a generally used method and good results can be expected if the images are seasonally close enough to each other (Olsson 1993). The Landsat images utilized in this study were acquired in the middle of vegetative growth season of forest trees with only an eight-day time lag (see Table 1). Classification to different habitat types was performed using a Erdas Imagine software with its maximum likelihood and fuzzy convolution correction tools. Kappa values (Rosenfield and Fitzpatrick-Lins 1986, Landis and Koch 1977) and accuracy (%) were calculated based on 61 (in 2005) or 56 (1987) independent and randomly located field plots (recently logged plots removed from the dataset). The Kappa values for the three class

**Table 2.** General description of the characteristics (mean ± SD) of the 80 ground reference field plots located in forests.

	Spruce-dominated forests	Other forests
Number of stands	40	40
Age of dominant trees	20–100	0–100
Volume (m <sup>3</sup> ha <sup>-1</sup> )		
Scots pine	69.5 ± 65.9	103.7 ± 62.7
Norway spruce	164.2 ± 84.5	3.7 ± 6.4
Broad-leaved trees	27.5 ± 30.9	10.6 ± 17.7
Dead standing trees	0.2 ± 0.3	0.1 ± 0.3
Total	261.4 ± 85.3	120.6 ± 69.5
Crown coverage (%)		
Scots pine	22.1 ± 18.8	76.0 ± 26.3
Norway spruce	64.9 ± 17.6	5.8 ± 8.1
Broad-leaved trees	13.0 ± 9.9	18.2 ± 25.0
Total	55.1 ± 10.6	44.5 ± 15.8

classifications of 1987 and 2005 were 0.68 and 0.80, respectively. The corresponding accuracy percentages were 84% and 89%, respectively. These numbers indicate that the strength of classification agreement was substantial (Landis and Koch 1977).

### **Class proportions: time series between 1976 and 2005**

To increase the temporal coverage of our analyses, we also performed a coarse grain analysis of land cover changes dating back to 1976. The Landsat 5 TM satellite images (years 1987 and 2005) were in spatial resolution of 25 m. In contrast, the Landsat 2 MSS image of 1976 was in resolution of 80 m. Therefore, all Landsat 5 TM images were transformed to coarser resolution of 80 m to avoid any bias in comparisons. The above-described habitat classifications were made simultaneously for coarse resolution images based on a supervised classification of the images of 2005 which was applied to the images of 1976 and 1987. Because the resolution of Landsat 2 MSS images (80 m) is far too coarse for detecting the smallest habitat patches in the study area, the results based on these analyses should be viewed with some caution. This approach is especially sensitive to size of landscape patches and changes of landscape graininess. For this reason, it was also not meaningful to present detailed landscape structure statistics in this resolution. Yet, the adopted approach should give us rough estimates as to how the proportion of different landscape classes have changed during the study period, as well as to how the share of spruce forests, the key habitat of Siberian jays, in the area has changed.

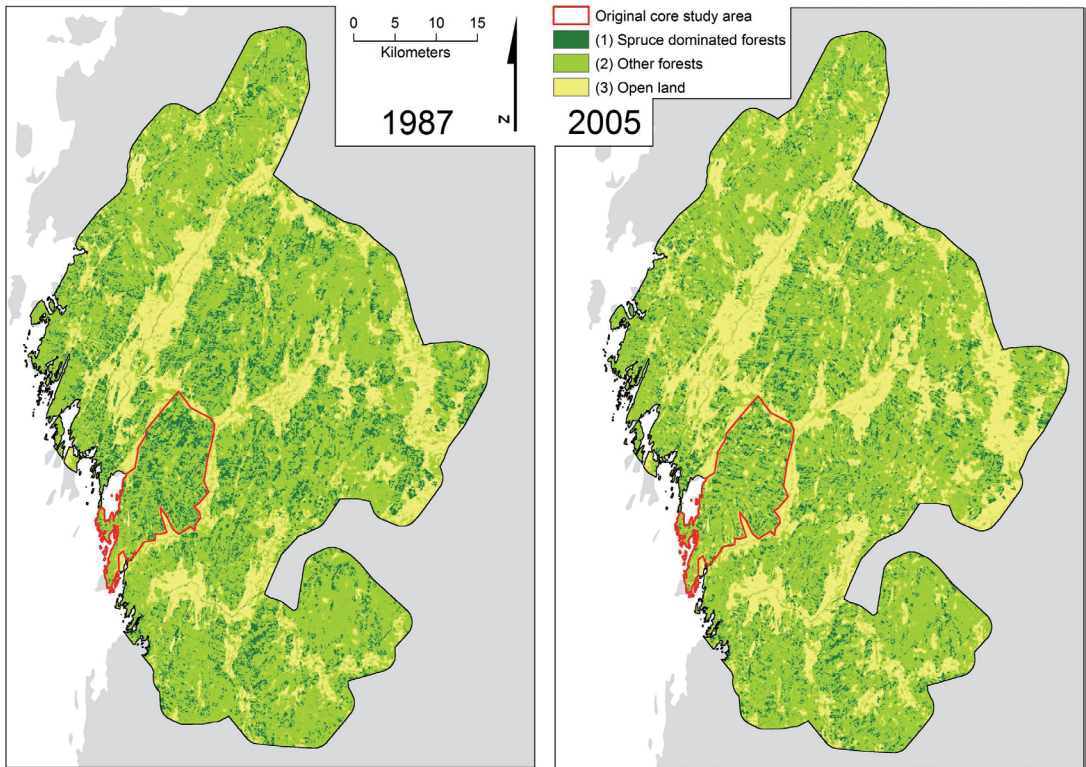
### **Landscape statistics**

To gain insight into the levels and changes in the degree of habitat fragmentation in the study area, the following patch statistics (McGarigal and Marks 1995) were derived for the 1987 and 2005 images: proportion of class area (Class%), patch density (PD) per square kilometre ( $n \text{ km}^{-1}$ ), mean patch size (MPS) (ha), edge density (ED)

( $\text{m ha}^{-1}$ ), and mean nearest neighbour distance to forest patch of a similar kind (MNN) (m) for  $5 \times 5$ -km grid cells over the study region. The edge density was calculated as the sum of patch perimeters in a given landscape type class divided by the total land area in this class. MNN was calculated as the average of the edge-to-edge distances between patches in the same landscape class. When comparing these statistics with other studies, one should bear in mind that especially the edge indices are affected by the resolution of the image (McGarigal and Marks 1995). We attenuated this problem by comparing edge metrics only among images of same resolution, and for that reason, only biases caused by increasing of graininess should be present. The patch statistics were calculated using ArcView 3.2 work package Patch Analyst (grid) 3.0 which is based on a Fragstats-algorithm (McGarigal and Marks 1995).

### **Habitat vs. population decline**

Finally, we also examined how the changes in the amount of spruce dominated forests were associated with changes in occurrence of Siberian jays from 1987 to 2005. To do this, we used calculated landscape patch statistics for  $5 \times 5$ -km grid cells in the 'original study area' (Fig. 2), and summarized observation data of Siberian jay presence (cf. Lillandt 2000, 2002, 2003, 2004) at feeding sites located within these grid cells. In short, occurrences of Siberian jays were observed in autumns at several short term feeding sites located approximately 1–2 km apart. For this analysis, we used an overlapping area of the year 1987 observations ( $n = 112$ ) and the year 2005 observations ( $n = 118$ ). The 1987 observation network was not as extensive as it was in 2005, and the exact locations of observation sites have not remained the same over time. Therefore, we calculated the proportion of positive observations inside  $5 \times 5$ -km squares: i.e. the number of observation sites with observed Siberian jay presence was divided by the number of all observation sites. The effect of changes in proportion of spruce-dominated forests on the Siberian jay occurrence from 1987 to 2005 was tested using a Wilcoxon signed rank test.



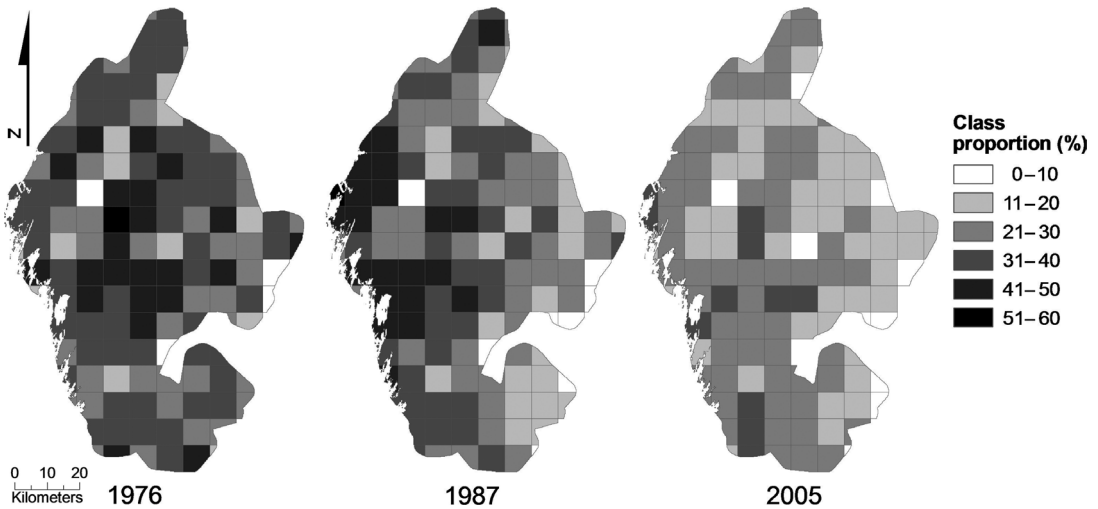
**Fig. 2.** Landscape of the study area in 1987 and 2005. This figure is based on a  $25 \times 25$ -m resolution data. Red polygon shows the area of Siberian jay observations in 1987 and 2005.

## Results

Spruce-dominated forests in the study area declined drastically during the three-decade (1976–2005) study period (Fig. 3). According to the 80-m pixel analysis, the coverage of spruce-dominated forests decreased 9.6% during 1976–1987, and 26.4% during 1987–2005. A finer-grained analysis at a 25-m pixel size during 1987–2005 uncovered qualitatively similar results (Fig. 2). Over this period, the mean patch size of spruce-dominated forests decreased from 2.02 ha to 1.35 ha (Table 3 and Fig. 4) and their coverage from 14.7% to 11.0%, respectively (Table 3). In addition to the decrease in the coverage and mean patch size of spruce-dominated forests, the number of spruce-dominated patches remained the same, and the distance to the nearest neighbouring patch increased while their average edge density decreased (Table 3). These results indicate increased loss and fragmentation of spruce-dominated forests during 1976–2005.

In comparison with spruce-dominated forests, the reduction in the coverage of other forested habitats, which are not the key habitats of Siberian jay, in the study area was much less pronounced (Table 3). Likewise, in contrast to spruce forests, the mean patch density of other forests increased over time, whereas the mean patch size remained unchanged (Table 3). Not surprisingly, the proportion of open land (clear cut areas, cultivated land and built areas) increased during the study period (Table 3). When comparing the changes in different landscape classes during the study period 1987–2005, it is clear that the landscape class of spruce-dominated forests changed the most: only 36.9% of spruce-dominated forests have remained unchanged (Table 4). In contrast, the corresponding numbers for other forests and open land were 78.3% and 84.4%, respectively (Table 4).

The decline of spruce-dominated forests from 1987 to 2005 was paralleled by a decline in the occurrence of Siberian jays (Fig. 5). The



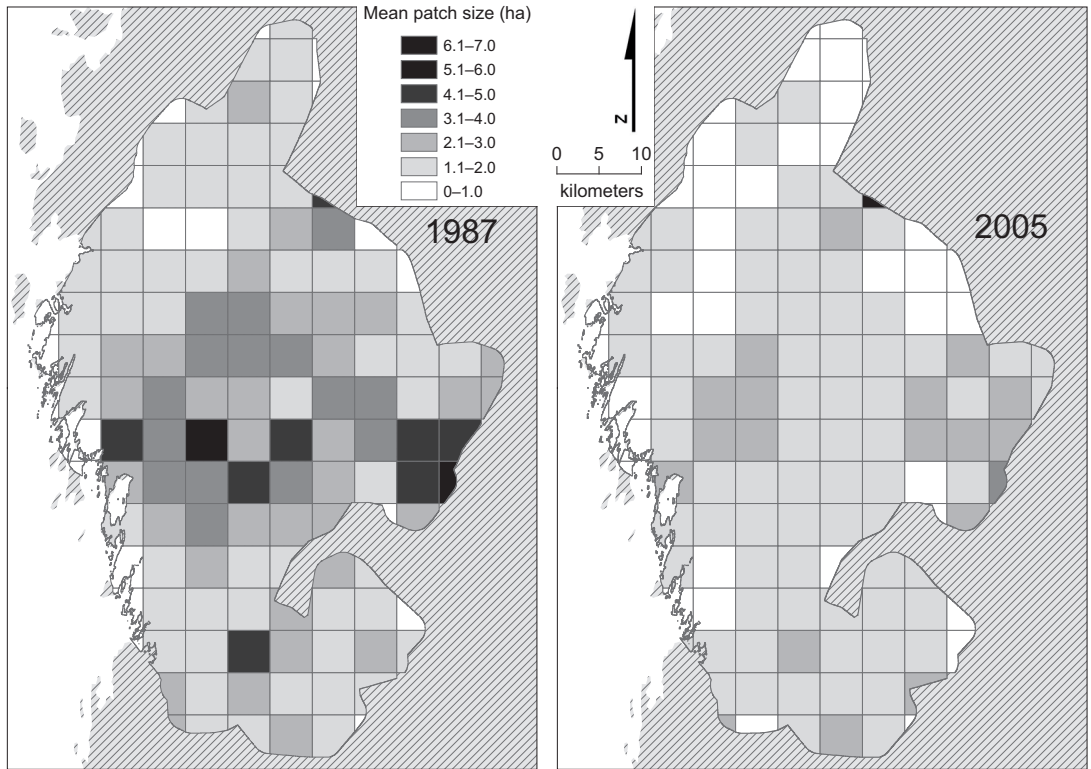
**Fig. 3.** Proportion of spruce-dominated forests in the study area in 1976, 1987 and 2005. The figure is based on a coarse resolution (80 m) data.

proportion of spruce-dominated forest decreased significantly (Wilcoxon signed rank:  $z = -2.38$ ,  $p = 0.017$ ) in those  $5 \times 5$ -km squares (totally 8) where Siberian jays were observed in 1987 or in

2005. In parallel, the occurrence of Siberian jays also declined from 1987 to 2005 in all but one  $5 \times 5$ -km square (Wilcoxon signed rank:  $z = -2.52$ ,  $p = 0.012$ ; Fig. 5).

**Table 3.** Landscape statistics expressed as the mean and standard deviation of class area proportion (Class%), mean nearest neighbour distance (MNN, m), patch density (PD,  $n \text{ km}^{-2}$ ), mean patch size (MPS, ha), and edge density (ED,  $\text{m ha}^{-1}$ ) in the study area in 1987 and 2005. The sample sizes (number of polygons) for spruce-dominated forests, other forests and open lands in 1987 were 20404, 8574 and 10014, and in 2005 22865, 6589 and 10434. The equations and units used for the calculation of landscape statistics are in Appendix.  $p$  values at which differences are considered significant are set in boldface.

	1987		2005		$t$	$p$
	Mean	SD	Mean	SD		
(1) Spruce-dominated forests						
Class%	14.7	6.8	11.0	4.6	> 3.5	< <b>0.001</b>
MNN	72.62	27.22	77.25	35.05	2.11	<b>0.036</b>
PD	8.21	3.46	8.61	2.93	1.75	0.082
MPS	2.02	1.11	1.35	0.68	> 3.5	< <b>0.001</b>
ED	52.73	18.14	45.70	15.59	> 3.5	< <b>0.001</b>
(2) Other forests						
Class%	61.7	15.3	60.1	16.0	> 3.5	< <b>0.001</b>
MNN	51.65	20.67	57.97	20.55	> 3.5	< <b>0.001</b>
PD	3.56	3.02	2.85	2.42	> 3.5	< <b>0.001</b>
MPS	36.74	46.90	39.59	38.83	1.00	0.320
ED	95.87	19.41	93.08	21.54	2.87	<b>0.005</b>
(3) Open land						
Class%	23.6	16	28.9	17.2	> 3.5	< <b>0.001</b>
MNN	105.31	31.14	100.29	24.33	2.03	<b>0.044</b>
PD	4.60	4.39	5.08	5.18	2.21	<b>0.029</b>
MPS	9.05	12.38	10.53	14.08	2.44	<b>0.016</b>
ED	43.37	22.32	43.14	16.11	0.20	0.845



**Fig. 4.** Mean patch size of spruce-dominated forests, the key habitat of Siberian jay, in 1987 and 2005 presented in  $5 \times 5$ -km squares. This figure is based on a  $25 \times 25$ -m resolution data.

## Discussion

The key finding of this study was the substantial decline in the mean proportion of the spruce-dominated forests over the 30-year period. Additionally, the increased fragmentation was also revealed, as evidenced by the decline in the mean size of spruce-dominated forest patches on one hand, and the reduced edge density of spruce

dominated forests on the other. Our findings are in good agreement with the regional measurements of Finnish National Forest Inventory on the west coast of Finland, which indicate that the total area of spruce-dominated forests decreased by 25% between 1981 and 2004–2007 (Finnish Forest Research Institute 1992, 2008). However, the data of the Finnish National Forest Inventory provide only average estimated proportions,

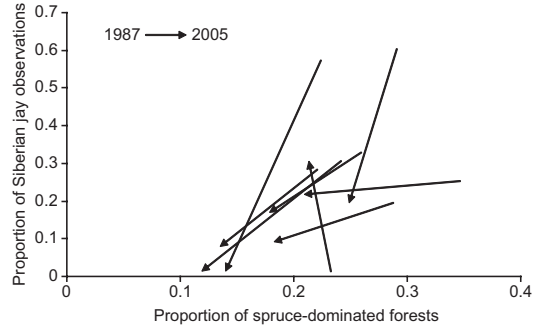
**Table 4.** Changes from one landscape class to another between 1987 and 2005.

1987 →	2005	Area (ha)	Percentage
(1) Spruce-dominated forests	Unchanged	12179	36.9
	(2) Other forests	16343	49.5
	(3) Open land	4469	13.5
(2) Other forests	Unchanged	106065	78.3
	(1) Spruce-dominated forests	14061	10.4
	(3) Open land	15336	11.3
(3) Open land	Unchanged	40722	84.4
	(1) Spruce-dominated forests	176	0.4
	(2) Other forests	7370	15.3



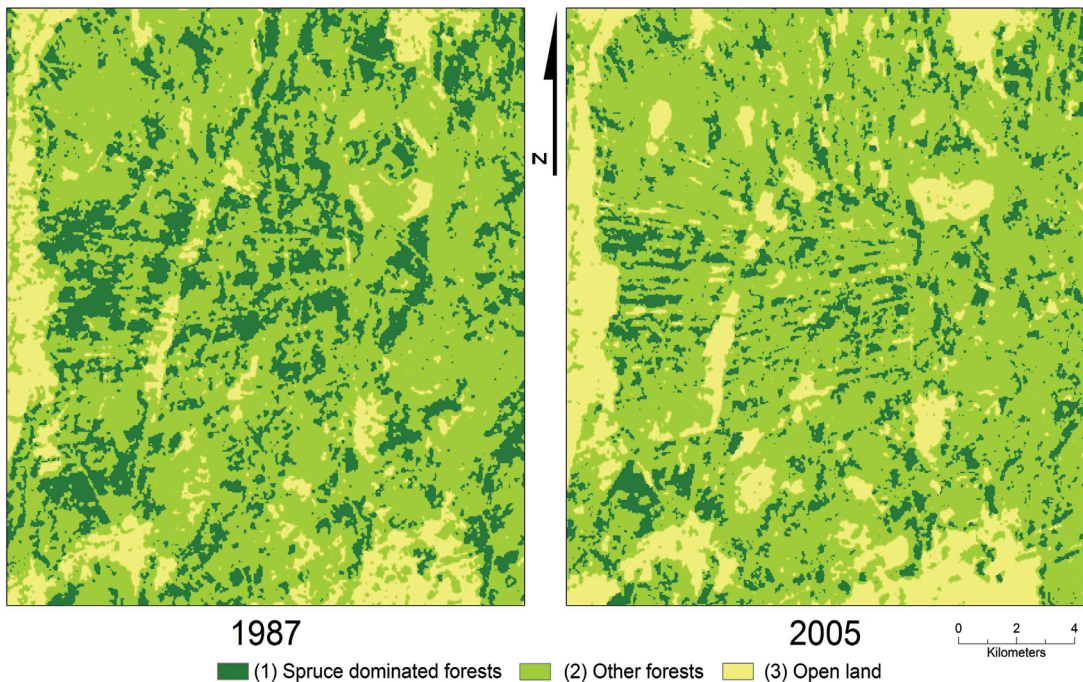
but no information on the landscape structure and fragmentation. In addition, previous general studies dealing with landscape metrics of boreal forests (e.g. Löfman and Kouki 2001) did not differentiate between specific habitat types, such as spruce-dominated forests, which can be of special importance for certain species like Siberian jays at the southern edge of the Finnish distribution area. Therefore, this study is the first to evaluate not only the reduction in the amount of spruce-dominated forests (i.e. key habitats of Siberian jay), but also their degree of fragmentation.

We found that the mean patch size of the spruce forests in the study area declined from ca. 2 ha to 1.3 ha in less than two decades. Although this change is proximately and ultimately due to current forestry practices, it is interesting to note that the small size of forest patches roots back to the special forest ownership typical for the western part of Finland. In the middle of the 18th century, when Finland was a part of the Kingdom of Sweden, the crown carried out a land rearrangement called Great Partition (*Isojako* in Finnish and *Storskifte* in Swedish; Roeck Hansen 1998).



**Fig. 5.** Decline in Siberian jay occurrences (number of observation sites with observed Siberian jay was divided by the number of all the observation sites inside  $5 \times 5$ -km squares in the core study area) and proportion potential breeding habitat (spruce-dominated forests).

In our study area, this created forest and land estates which were arranged in narrow and long strips. The form of these land estates can be still seen from satellite images (Fig. 6), and although some of these strips still support fragments of spruce-dominated forests, most have been totally cleared from them (Fig. 6). Hence, without coordinated management, the current land-ownership



**Fig. 6.** Detailed example of landscape structure changes during 1987–2005. The narrow and long forest estates in east–west direction in the western part of the images are a reflection of the Great Partition during the mid-18th century. This figure is based on a  $25 \times 25$ -m resolution data.

arrangement is likely to promote uncontrollable habitat fragmentation as evidenced by our results and visualized in Fig. 6.

Because our study was based on two to three time points only, it is difficult to assess when exactly the habitat fragmentation and loss has taken place, but nothing indicates that it would be halted in the near future either. In addition, the most rapid period in the landscape transformation in Finnish forests had already occurred between the 1940s and the 1960s (Löfman and Kouki 2001), which is outside our study period. Yet, the overall trend of annual removals has increased during the past decades, and spruce forests have been logged more intensively than other forests (Metinfo 2008). These intensive loggings and peculiarities of the forest ownership (cf. Great Partition) provide an explanation for the observed fragmentation and loss of spruce-dominated habitats.

Since many boreal forest plants, animals and fungi are dependent on (mature) spruce forests (e.g. Berg *et al.* 1994, Niemelä 1997), the observed trends suggest that many spruce forest specialists in this area may soon suffer from well-established negative consequences of habitat fragmentation and loss (e.g. Hanski 2000). Tikkanen *et al.* (2006) argued that of all the boreal tree species, spruce harbors the greatest number of red-listed species. This would apply to species such as the Siberian jay, which show a preference for closed and mature forest habitats (Edenius and Meyer 2002, Bergholm 2007, Angervuori 2008), which in our study area are predominantly related to spruce dominance. This preference was also shown in our study: apart from the strong dependence of the occurrence of Siberian jays on the proportion of spruce-dominated forests, the parallel decline of Siberian jay observations and coverage of potential breeding habitats suggests that spruce-dominated habitats are important for Siberian jays in our study area. Yet, as our data cannot prove causality, we cannot rule out the possibility that loss of spruce dominated forest is correlated with some yet unidentified factor(s) that is (are) responsible for the patterns seen in Siberian jay and forest data. For example, a parallel reduction in visual cover or increased abundance of predators or competing species might have occurred simulta-

neously. Previous studies suggest that decreased visual protection (i.e. layered and closed forest habitats) against predators have a negative impact on Siberian jay populations (Ekman *et al.* 2001, Eggers *et al.* 2005, Griesser *et al.* 2006, 2007, Griesser and Nystrand 2009). However, based on the knowledge that Siberian jays in our study area favour spruce-dominated habitat, and that we detected significant fragmentation and loss of these preferred habitats, habitat loss and fragmentation and related changes in predation and other ecological interactions remain the primary suspects behind the Siberian jay population decline.

The distribution of Siberian jay in southern Finland is not continuous (Fig 1.), and the populations can be fairly isolated (Väisänen *et al.* 1998, Pihlajaniemi 2006, Bergholm 2007) thus, particularly vulnerable to demographic and environmental stochasticity. Increased thinning of Norway spruce may also decrease the survival of young birds as well as immigration of individuals (Bergholm 2007), and partially thinned or partially clear-cut forest areas have been found to remain unoccupied by Siberian jays more often than unmanaged areas (Griesser *et al.* 2007). In addition, closed forests provide better protection (concealment of nests) from nest predators (Eggers *et al.* 2005). For these reasons, Siberian jays living in areas affected by forest management experience a significantly lower breeding and nesting success than those breeding in old-growth forests (Griesser *et al.* 2007). Therefore, the observed decline of spruce-dominated key habitats in our study region may provide an explanation for the simultaneous population decline of Siberian jay. However, the possible role of other factors such as climate change cannot be excluded. Therefore, this issue warrants future research, with the next logical step being jointly analysing the time series of Siberian jay demography with the forest landscape data presented in this paper.

In conclusion, the results of our analyses of landscape changes in the forests of western Finland show that the spruce-dominated forests became reduced and more fragmented during the past decades. These changes are likely to be detrimental to many species depending on spruce forests, such as the Siberian jay. Interestingly, the historical foundation for the present

day forest fragmentation patterns observed in this study can be traced back to 300 year-old land-ownership arrangements: by constraining the forestry practices, the narrow, long forest strips seem to predispose western Finnish forests to a greater degree of fragmentation than forests elsewhere.

*Acknowledgements:* This study was supported by Maj and Tor Nessling Foundation (grant to JM) and Academy of Finland (grants to PM, AK, JM). Partial support was also obtained from Finnish Forest Research Institute (research project 'Interlinkages between forest biodiversity and carbon sequestration'; PM). We are also grateful to Mr. Bo-Göran Lillandt for his participation in the field-work and access to Siberian jay data, and Jaquelin DeFaveri for comments and linguistic corrections.

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**Appendix.** Patch statistics used in this study (McGarigal and Marks 1995).

Landscape statistics	Equation	Unit
Proportion of class area	$\text{Class\%} = \frac{\sum_{j=1}^i a_{ij}}{A} \times 100$	Percent (%)
Patch density	$\text{PD} = \frac{n_i}{A}$	1 per square kilometre
Mean patch size	$\text{MPS} = \frac{\sum_{j=1}^{n_i} a_{ij}}{n_i} \times 100$	Hectares (ha)
Edge density	$\text{ED} = \frac{\sum_{j=1}^{n_i} p_{ij}}{A}$	Metres per hectare ( $\text{m ha}^{-1}$ )
Mean nearest neighbour distance	$\text{MNN} = \frac{\sum_{j=1}^{n_i} h_{ij}}{n_i}$	Metres (m)

$i$  = type of patch (class  $i$ ),  $j$  = patch in class  $i$ ,  $a_{ij}$  = area of patch  $j$  in class  $i$ ,  $A$  = total area,  $p_{ij}$  = perimeter of patch  $j$  in class  $i$ ,  $h_{ij}$  = edge-to-edge distance from patch  $j$  in class  $i$  to the nearest patch also in class  $i$ .