

Landscape level effects of modern forestry on bird communities in North Swedish boreal forests

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Abstract

We address effects of large-scale forestry on landscape structure and the structure and composition of boreal bird communities in North Sweden. Specifically, we ask: after controlling for the effect of patch size, forest age and tree species composition, is there any residual effect attributable to the reduction in area of old forest? Pairs of landscape blocks (25 by 25 km) were selected to maximize area difference in human-induced disturbance, clear-cut as opposed to semi-natural old forest.

Median distance to natural edge (wetlands, open water) from randomly selected points in forest was 250 and 200 m in high and low impact landscapes, respectively, indicating a high degree of 'natural' fragmentation of the pristine boreal landscape in the area. By contrast, median distance to clear-cut in uncut forest was 750 and 100 m, respectively. Clear-cuts in high impact landscapes were disproportionately more common in areas with contiguous forest land than in areas with spatially disjunct forest, implicating that forestry increases natural fragmentation of the landscape by subdividing larger forest tracts.

Point counts along forestry roads showed that species richness and relative abundance of forest birds were higher in landscapes with low forestry impact. These differences can partly be explained by differences in age composition of forest and composition of tree species. After controlling for patch size, forest age and tree species composition, a significant effect of forestry impact remained for Siberian species and the Tree pipit *Anthus trivialis*. Our results thus imply that this group of species and the Tree pipit may be sensitive to forest fragmentation.

In contrast to previous Finnish studies, we found relatively small negative effects on relative abundance of species hypothesized to be negatively affected by large-scale clear-cutting forestry. However, our picture of the present does not contradict results from Finnish long-term population studies. Five factors may account for this: 1) clear-cut areas are not permanently transformed into other land use types, 2) planted forests are not completely inhabitable for species preferring older forest, 3) the majority of species in the regional pool are habitat generalists, 4) the region studied is still extensively covered with semi-natural forest, and 5) our study area is relatively close to contiguous boreal forest in Russia, a potential source area for taiga species.

Introduction

As an important part of modern forestry in the world's boreal forests, large-scale clear-cutting changes age composition in forest landscapes by reducing the area of old growth and increasing the area of young successional stages. In addition, large-scale forestry usually alters size of forest patches and hence the spatial configuration of the forest (Hunter 1990; Mladenoff *et al.* 1992; Syrjä-

nen *et al.* 1994). In the Fennoscandian boreal region a large share of the old and old-growth forest has been converted into managed even-aged stands since World War 2. Not surprisingly, such extensive habitat alteration may lead to regionwide effects on the structure and composition of the avifauna. For example, in North Finland a long-term population decline of birds associated with old growth and a concomitant increase of generalist species are well documented (Jarvinen and Vaisa-

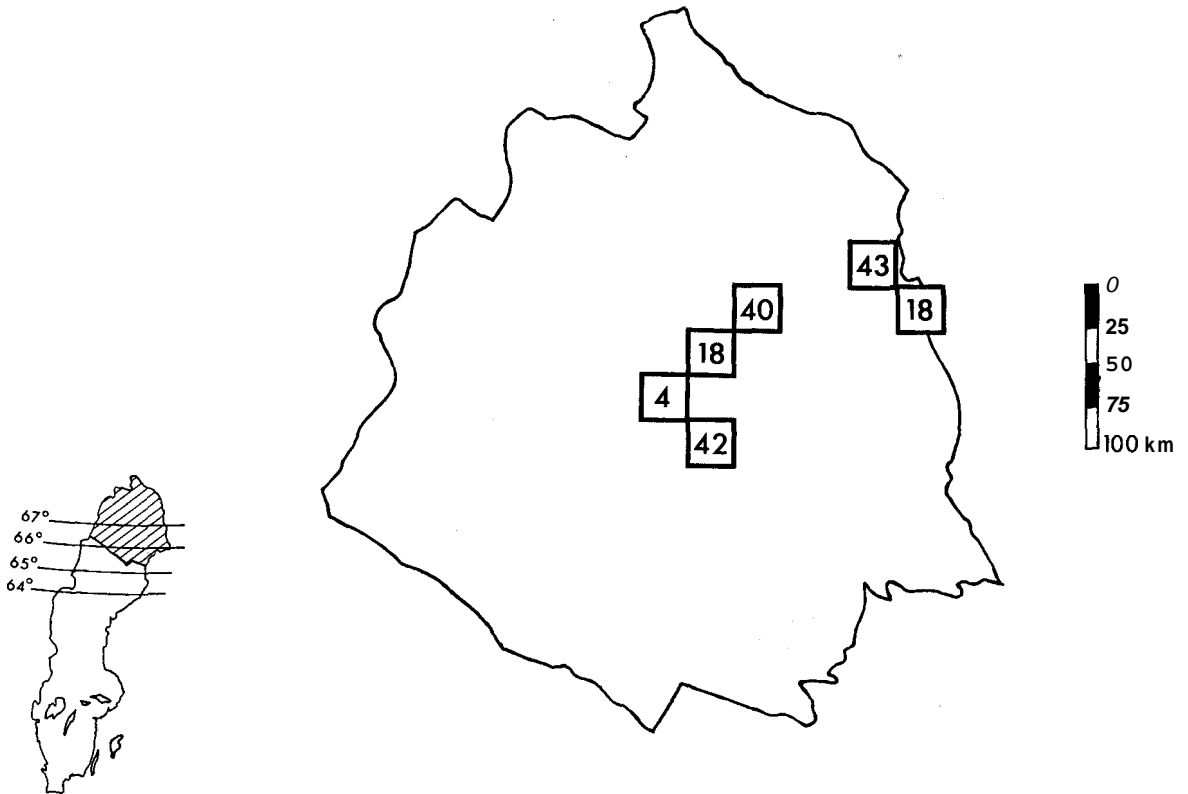


Fig. 1. Landscape blocks selected for testing the effect of forestry on composition and structure of boreal bird communities in North Sweden. Inserted numbers are proportion forest clear-cut since World War 2.

nen 1977; Järvinen *et al.* 1977; Vaisanen *et al.* 1986).

Effects of landscape transformation by forestry on the dynamics of boreal forest bird communities is undisputable, much due to Finnish investigators (*e.g.* references above). Nevertheless, there are few studies combining stand level quantification of forestry impact and composition of bird communities in a certain landscape (but see Helle and Järvinen 1986 for an assessment at a regional scale). To provide management baselines for mitigating negative effects of clear-cutting forestry, it is necessary to quantify relationships between forestry impact and biodiversity.

There are both methodological and logistic problems involved in broad-scale spatial comparisons. However, the boreal forest region of northmost Sweden is suited for such studies. First, although the landscape in this region to a large extent is affected by large-scale clear-cutting, substantial areas in natural or semi-natural stages persist. Sec-

ondly, an extensive network of forestry roads gives access to most landscape types. Thirdly, the region is covered by high-resolution vegetation maps allowing unique detailed assessment of vegetation types and forestry impact.

In this paper we address effects of modern forestry in 25 x 25 km landscape blocks, *i.e.* a spatial scale decidedly larger than the individual home-range but much smaller than the distribution range of forest bird species. We here focus on the following questions:

- 1) How does forestry affect landscape structure in terms of distance to edge of uncut forest, and how does this impact vary in relation to landform?
- 2) To what extent do species richness, occurrence, and relative abundance of forest birds differ between landscapes with different forestry impact?
- 3) After controlling for patch size, forest stand age, and tree species composition, is there any effect on relative abundance of forest birds attributable to landscape level forestry impact?

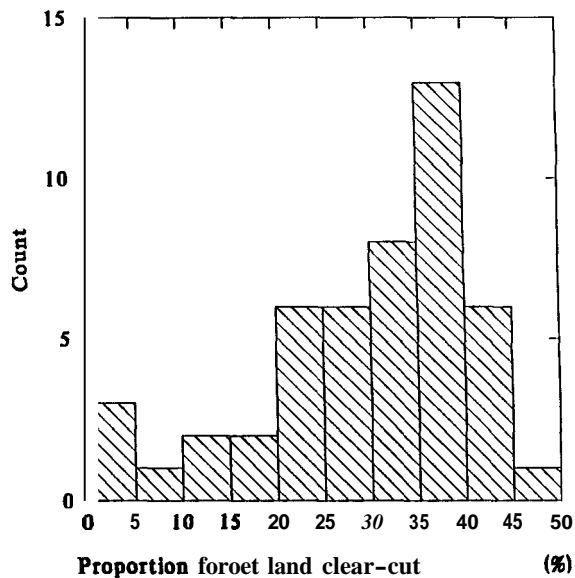


Fig. 2. Frequency distribution of the proportion forest clear-cut in landscape blocks (25 by 25 km) in the County of Norrbotten North Sweden. Only landscapes with > 50% forest land included.

Materials and methods

Study region and landscape blocks

This study was conducted in the County of Norrbotten in North Sweden (Fig. 1), covering about one fifth of Sweden's land area (forest land area in the county is appr. 37,000 km²). Phytogeographically most of the region is in the middle and northern boreal subzones (*sensu* Ahti *et al.* 1968). Vegetation Maps (VM) in a scale of 1:50,000 give detailed information about occurrence and distribution of vegetation types and forestry impact. On the map level, *i.e.* 25 by 25 km, large-scale clear-cutting has transformed 0.2–55% (mean 29%) of the old forest into young forest since about World War 2. Fire has since long been excluded as a functional ecological factor in this part of the boreal region (Zackrisson 1977; Engelmark 1984). Therefore, forestry is now the sole significant large-scale disturbance factor. Earlier cuttings in the study area were chiefly selective removal of large trees (mainly Scots pine *Pinus sylvestris*). Thus, the classes of forest distinguished in VM, 'clear-cuts', *i.e.* trees < 2 m in height, plantations of 'young forest', trees 2–10 m, and 'maturing forest' (trees > 10 m),

reflect different forest histories. Clear-cuts and young forests are generally even-aged, planted monocultures, whereas maturing forest are naturally regenerated stands richer in species and structural diversity. These classes correspond roughly to 0–20, 21–60, and > 60 years. The proportion of these age-classes in the study region is 24, 31 and 45%, respectively (Anon 1994). Note, however, that although the portion of old growth (> 160 years) is comparatively high in the study region (5%; Anon 1994), almost all VM maturing forest has been selectively cut once or a few times. Compared to true old growth, they tend to be impoverished structurally in having only few large standing living and dead trees, snags and downlogs, and they usually lack a multi-layered canopy (Esseen *et al.* 1992). However, they have not experienced clear-cutting and planting and can thus be classified as semi-natural.

We defined landscape blocks as each VM having > 50% forested land. Using the distribution of the proportion forested land clear-cut (Fig. 2) we selected 3 pairs of blocks for proximity and similarity in altitude, relief and proportion of forest land, but as different as possible in forestry impact (Table 1; Fig. 1). To minimize biogeographical differences selection was confined to the northern boreal subzone (Ahti *et al.* 1968).

Assessment of landscape structure

Measurement of landscape structure included a) distance in 50 m units in forest (both cut and uncut) to nearest natural edge (*i.e.* open water, mire or bog), b) distance to nearest clear-cut (in uncut forest), and c) area classification of forest land in three categories: 'forest patch', *i.e.* forest land more or less isolated by open water, mire or bog, either 1) 'small' *i.e.* < 10 ha, 2) 'large' *i.e.* 10–50 ha in size, or 3) 'forest tract', *i.e.* > 50 ha of contiguous forested land (both cut and uncut forest). These measurements were obtained from VM at 35 points in a regular grid system.

Field sites

Within each landscape block, we also selected 35 field sites along forestry roads to obtain data on

Table 1. Characteristics of landscape blocks (25 x 25 km) selected to maximize contrast in forestry impact. Number of field sites in each impact type is 105. Some sites on clear-cuts could not be assigned to forest habitat type. Sites were allocated proportionally to composition of forest age-classes and ground-floor vegetation in each landscape.

Forestry impact	Low (N = 3)	High (N = 3)
Coniferous forest land, mean, %	62 (range 57–69)	66 (range 63–67)
Forest land clear-cut, mean, %	13 (range 4–18)	42 (range 40–43)
Altitude, mean, m	267 (range 160–430)	320 (range 220–380)
Old forest, # of sites	93	61
Young forest, # of sites	12	44
Pine forest, # of sites	44	65
Spruce forest, # of sites	20	8
Deciduous forest, # of sites	17	14
Mixed forest, # of sites	19	12

landscape structure (as above), on forest stand characteristics, and on occurrence of birds. Field sites were stratified in two steps to reflect each VM's proportion of age and forest floor vegetation type. For age we used two classes: 'Young' forest (VM clear-cut and young forest merged) and 'old' forest (VM maturing forest). VM separates height classes on the basis of dominating tree height. Therefore, cut stands with seed trees are classified as either clearcuts or young forest depending on the time since cutting. Forest floor vegetation type combines species composition in the field and bottom layer and reflects the productivity and the expected tree species composition of the site (Hägglund and Lundmark 1977). To avoid edge-effects in bird censusing, forest tracts (*i.e.* > 50 ha of contiguous forest) were preferentially selected when study sites were laid out. The shortest distance between any two sites was 500 m.

At each field site we measured tree species composition and abundance of large trees by a relascope 50 m away from the road. Coin-flipping decided which side of the road was used, unless the forest differed much between the sides, in which

case the side most closely resembling the preferred type according to stratification was chosen. Four classes of tree species composition (not to be confused with age classes above) were thus distinguished: 1) Pine forest; Scots pine > 60%, 2) spruce forest; Norway spruce *Picea abies* > 60%, 3) deciduous forest; deciduous trees (mostly *Betula* spp.) comprising > 40% of the basal area, respectively, and 4) mixed coniferous forest; Scots pine + Norway spruce comprising > 60% of the basal area (see Table 1). To increase the number of habitat variables, 100 of the field sites in old forest were later revisited to obtain a detailed description of the forest structure within two 10-m radius circular sample plots. These measurements included stem diameter distribution and the amount of living and dead wood (N. Lindberg, unpublished).

Bird censuses

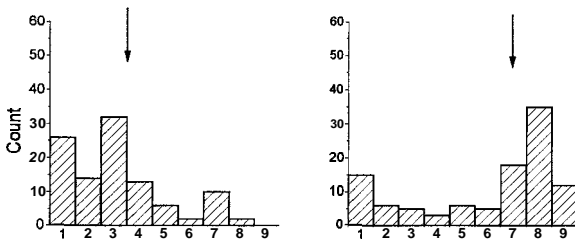
Bird censuses were made as two repeated 5 min point counts 7–12 June 1994, 2–10 AM at each field site. Landscape blocks were censused pairwise so that simultaneous recordings were made in both blocks of a pair in the same morning. Visit order of field sites within a block was reversed in the second census. All censusing was carried out by the authors. The highest number of individuals recorded per field site was used as a measure of species abundance. Since species differ in detectability we regard our estimates as indices of relative abundance.

Data treatment and analysis

Analyses were carried out for all species having forest as their main habitat (following Solonen 1994). We considered overall species richness, occurrence, and relative abundance of individual species, as well as of three functional groups of forest birds (Appendix): 1) species with a long-term decreasing population trend in North Finland coinciding in time with the introduction of large-scale forestry (Vaisanen *et al.* 1986; hereafter 'decreasing species'), 2) sedentary species which might be particularly susceptible to habitat loss and fragmentation due to limited food resources during

1=0-50 m	2=51-100 m
3=101-200 m	4=201-300 m
5=301-400 m	6=401-500 m
7=501-1000 m	8=1001-5000 m
9=>5000 m	

Low forestry impact



High forestry impact

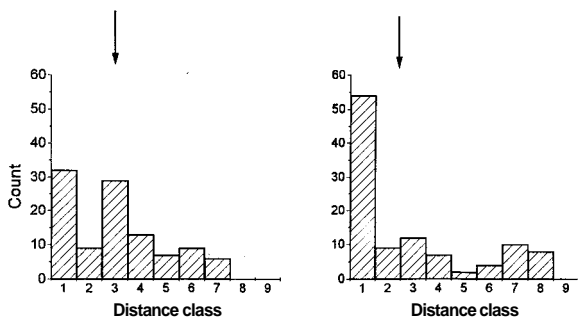


Fig. 3. Distribution of distance to natural edge (left-hand side) and to clear-cut (right-hand side) at randomly selected points in forest in the six selected landscape blocks with different forestry impact in North Sweden. Arrows denote medians. $N = 105$ in each block type.

winter (*e.g.* Fretwell 1972; Järvinen *et al.* 1977; hereafter ‘resident species’), and 3) species belonging to the Siberian or Siberian-Canadian faunal type (*sensu* Voous 1960; hereafter ‘Siberian species’), a group of species which presumably evolved in the boreal forests of the Palearctic and may therefore possess strong habitat affinities (Monkkonen and Welsh 1994). It should be noted that the three functional groups are partly overlapping in composition, and our motive to include them here is primarily to test their suitability as indicators for effects of large-scale forestry.

To control for differences in sample size, we standardized species richness by rarefaction (Simberloff 1978). First, we rarefied pooled data for the low and high impact blocks separately to analyse overall differences. Secondly, we rarefied data for

old and young forest separately to assess differences related to forest age. Thirdly, rarefaction was done separately for each tree species class for assessing the role of habitat.

Most of our analyses were done on the landscape level ($N=6$). Since most of the data were not normally distributed non-parametric tests were regularly employed. In parametric tests residuals of the untransformed and log-transformed relative abundance figures were checked for homogeneity and the model with the best fit was chosen as the final model.

Results

Impact of forestry on landscape structure

Median distance from randomly selected points in forest to natural edge was 200 and 250 m in low and high impact blocks, respectively (Fig. 3); distribution of distance classes being similar ($P > 0.05$; Chi-2 = 8.387, d.f. = 6). By contrast, distance to clear-cut in uncut forest differed significantly between impact types ($P < 0.001$; Chi-2 = 59.174; d.f. = 7; Fig. 3), median distance being 750 and 100 m for high and low impact types, respectively.

In low impact blocks a larger proportion of the points fell in forest tracts (> 50 ha of contiguous forested land) compared to in high impact landscapes ($P < 0.001$, Chi-2 = 16.247; d.f. = 2; Fig. 4a), indicating a higher degree of natural fragmentation of the forest in the latter.

Landscape structure at field sites

Median distance to natural edge at forest field sites was 200 and 150 m for low and high impact blocks, respectively. Median distance to clear-cut at old forest sites in respective types was 450 and 200 m, with a significantly different distribution of distance classes ($P = 0.003$; Chi-2 = 21.505; d.f. = 7; Fig. 5). Distribution of field sites across area-classes was similar between low and high impact blocks (Fig. 4b).

Compared with the randomly chosen points, field sites were: 1) closer to a clear-cut ($P < 0.001$ and 0.003; Chi-2 = 33.913 and 21.866; d.f. = 7 and

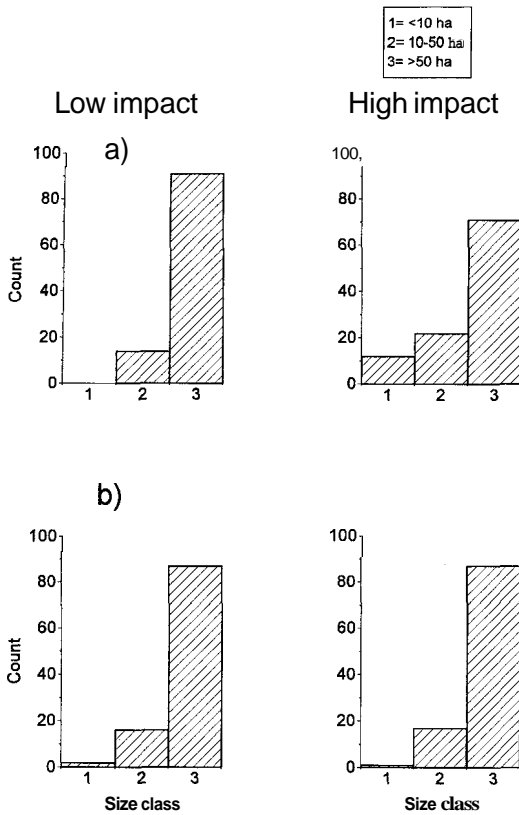


Fig. 4. Distribution of forest area-classes in landscape blocks with different forestry impact. a) Randomly selected points, b) field sites. $N = 105$ in each block type.

7, for low and high impact blocks, respectively), and 2) over-represented in forest tracts in the high impact blocks ($P = 0.003$; $\text{Chi-2} = 11.569$; $\text{d.f.} = 2$; Fig. 4). These differences reflect the effect of taking road-side samples – forestry is concentrated along roads instead of being evenly distributed over the landscape. The over-representation of forest tracts in high impact blocks is in part a result of our ambition to avoid edge-effects when censusing birds.

Habitat characteristics of field sites

Distribution of forest tree species classes (pine, spruce, deciduous and mixed coniferous forest) differed significantly between landscape impact types ($P = 0.016$; $\text{Chi-2} = 10.283$; $\text{d.f.} = 3$; Table 1), pine forest being more common in high than in low impact blocks, and *vice versa* for spruce and mixed

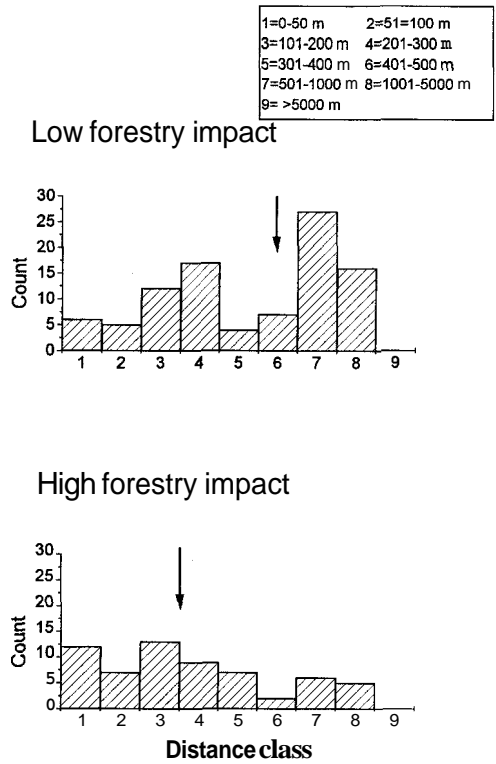


Fig. 5. Distribution of distance to natural edge for field sites (old and young forest). Arrows denote medians. $N = 105$ in each block type.

Table 2. Forest structure at revisited field sites in old forest in landscape blocks with different forestry impact in North Sweden. Means and (S.D.) based on $N = 60$ and $N = 40$ in low and high impact blocks, respectively. Dbh = trunk diameter at breast height.

Difference	Forestry impact		
	Low	High	P-value ¹
# of trees > 30 cm dbh per ha	14 (19)	21 (22)	0.571
# of trees > 45 cm dbh per ha	1 (3)	0 (1)	0.246
Volume of living standing trees; m ³ per ha	80 (36)	93 (39)	0.100
Volume of deciduous trees > 20 cm dbh; m ³ per ha	8 (10)	11 (24)	0.571
Coarse woody debris; m ³ per ha	3 (4)	5 (7)	0.225

¹Mann-Whitney U-test

Table 3. Relative abundance and occurrence of forest birds in landscapes with different forestry impact in North Sweden. Number of records and number of field sites (within brackets) where the species occurred. P-values in bold are significant for $P < 0.1$.

Species	Forestry impact		Difference in Abundance ¹ P-value	Occurrence ² P-value
	low	high		
<i>Aquila chrysaetos</i>		1 (1)	–	–
<i>Tetrao tetrix</i>	2 (2)	4 (4)	–	–
<i>T. urogallus</i>	1 (1)	2 (2)	–	–
<i>Bonasa bonasia</i>	1 (1)	1 (1)	–	–
<i>Scolopax rusticola</i>	1 (1)		–	–
<i>Tringa ochropus</i>	2 (2)		–	–
<i>T. erythropus</i>	11 (7)	23 (21)	0.275	0.013
<i>T. nebularia</i>	25 (24)	18 (18)	0.268	0.398
<i>Columba palumbus</i>	1 (1)		–	–
<i>Cuculus canorus</i>	106 (79)	89 (75)	0.507	0.807
<i>Surnia ulula</i>		1 (1)	–	–
<i>Dendrocopus major</i>	3 (2)		–	–
<i>Picoides tridactylus</i>	1 (1)		–	–
<i>Dryocopus martius</i>	7 (7)		0.037	–
<i>Jynx torquilla</i>	2 (2)	2 (2)	–	–
<i>Corvus corax</i>	31 (33)	24 (22)	0.513	0.892
<i>C. corone</i>	23 (21)	15 (14)	0.500	0.271
<i>Pica pica</i>	7 (7)	1 (1)	0.346	–
<i>Garrulus glandarius</i>		1 (1)	0.346	–
<i>Perisoreus infaustus</i>	20 (7)	7 (4)	0.376	0.378
<i>Parus major</i>	6 (5)	5 (4)	0.796	0.144
<i>P. cinctus</i>	2 (1)		–	–
<i>P. montanus</i>	12 (9)	11 (9)	0.817	1.000
<i>Turdus viscivorus</i>	14 (10)	16 (16)	0.658	0.267
<i>T. pilaris</i>	18 (14)	5 (4)	0.121	0.024
<i>T. philomelos</i>	65 (63)	67 (62)	0.507	0.944
<i>T. iliacus</i>	89 (66)	82 (61)	0.658	0.726
<i>T. merula</i>	1 (1)	1 (1)	–	–
<i>Phoen. phoenicurus</i>	114 (74)	145 (91)	0.050	0.321
<i>Erithacus rubecula</i>	23 (21)	26 (23)	0.825	0.784
<i>Sylvia curruca</i>	1 (1)		–	–
<i>Phyll. trochilus</i>	290 (102)	259 (101)	0.376	0.960
<i>P. collybita</i>	1 (1)	1 (1)	–	–
<i>Regulus regulus</i>	13 (13)	11 (10)	0.822	0.553
<i>Muscicapa striata</i>	17 (17)	12 (12)	0.261	0.384
<i>Ficedula hypoleuca</i>	32 (27)	21 (19)	0.184	0.285
<i>Prunella modularis</i>	6 (6)	5 (5)	0.825	0.769
<i>Anthus trivialis</i>	66 (48)	53 (45)	0.827	0.796
<i>Carduelis chloris</i>	12 (10)	7 (7)	0.507	0.484
<i>C. spinus</i>	109 (65)	116 (68)	0.507	0.839
<i>C. flammea</i>	91 (63)	116 (73)	0.827	0.504
<i>Pyrrhula pyrrhula</i>	38 (30)	15 (13)	0.050	0.018
<i>Pinicola enucleator</i>	1 (1)		–	–
<i>Loxia cuwirostra</i>	128 (22)	70 (5)	0.077	0.002
<i>Fringilla coelebs</i>	33 (29)	18 (16)	0.046	0.078
<i>F. montifringilla</i>	266 (99)	214 (97)	0.513	0.918
<i>Emberiza citrinella</i>	11 (10)		0.121	0.002
<i>E. rustica</i>	14 (12)	4 (4)	0.246	0.054

¹Mann-Whitney U-test, N = 6

²Chi-2 test, d.f. = 1

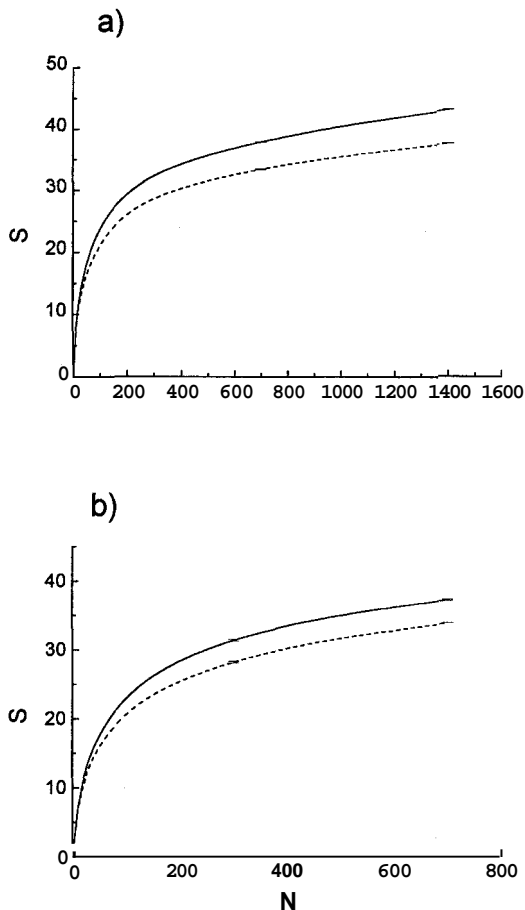


Fig. 6. Rarefaction curves for species richness in a) landscape blocks with different forestry impact, b) field sites in old and young forest. Solid line is low impact landscapes and old forest, respectively, and dashed line is high impact landscapes and young forest, respectively. Bars are ± 2 SE.

coniferous forest.

The inventory of forest structure at the 100 revisited old forest field sites did not indicate any significant differences between impact types in terms of occurrence of large stem diameter trees and volume of different tree fractions (Table 2).

Bird species richness

We tallied 3186 birds of 48 forest species, the latter corresponding to 62% of the regional species pool of forest birds (70% of the passerines).

Species richness was higher in landscape blocks with low forestry impact (Fig. 6a). Species richness was significantly lower in young forests than in old

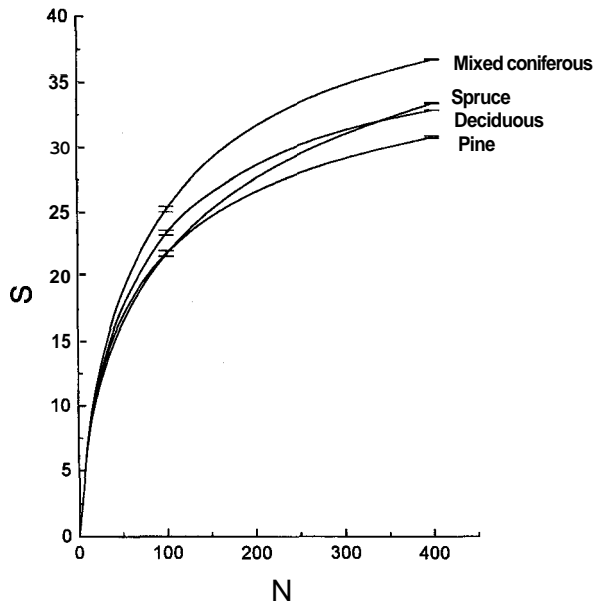


Fig. 7. Rarefaction curves for species richness in different tree species classes. Bars are ± 2 SE.

forests (Fig. 6b), and differed also between forest tree species classes (Fig. 7).

Composition and structure of the avifauna

The five most common species, Willow warbler *Phylloscopus trochilus*, Brambling *Fringilla montifringilla*, Redstart *Phoenicurus phoenicurus*, Siskin *Carduelis spinus* and Common redpoll *C. flammea*, together made up 54% of the total sample. By contrast, resident species accounted for only about 4%.

Occurrence of species differed significantly ($P < 0.1$) between impact type in: Fieldfare *Turdus pilaris*, Bullfinch *Pyrrhula pyrrhula*, Crossbill *Loxia cuwirostra*, Chaffinch *Fringilla coelebs*, and Yellowhammer *Emberiza citrinella* (more sites with occurrence in low impact blocks), and Spotted redshank *Tringa erythropus* (more sites with occurrence in high impact blocks; Table 3). Overall relative abundance of forest birds was higher in low impact blocks (Table 3). In plain numbers 24 out of 32 species with more than 5 records were more abundant in low impact blocks (Table 3), and significant differences ($P < 0.1$) were found for: Black woodpecker *Dryocopus martius*, Bullfinch, Crossbill, and Chaffinch (higher relative abundance in

Table 4. Composition (%) of the bird community with respect to feeding ecology in landscape blocks with different forestry impact.

Group	Forestry impact	
	Low	High
Foliage gleaners	39	39
Trunk feeders	3	1
Air catchers	3	2
Ground feeders	26	31
Granivores	25	24
Others	4	3

Table 5. Number of individuals of different groups of species hypothesized to be negatively affected by forestry in landscape blocks with different forestry impact in North Sweden.

Group	Forestry impact		Difference P-value ¹
	Low	High	
Decreasing species ²	365	305	0.127
Resident species ²	81	50	0.105
Siberian species ²	412	314	0.513

¹Mann-Whitney U-test (N = 6)

²See Appendix for definition

low impact blocks), as well as for Redstart (higher relative abundance in high impact blocks; Table 3).

Species composition according to feeding ecology was similar between impact types (Table 4), except for ground-feeders which were relatively more common in high impact blocks.

Relative abundance of decreasing species, resident species and Siberian species tended to be higher in low impact blocks, but differences were not significant ($P > 0.1$; Table 5).

Differences between oldforest sites

The differences in species richness and species composition between impact types may in part be explained by differences in forest age-class composition and tree species composition. Of particular interest from the view of conservation are the species and groups of species associated with old forest, potentially adversely affected by large-scale reduction of habitat area. To assess the role of forestry impact at the landscape level for these species, we selected a number of field sites from different tree species classes in old forest only, so that an even distribution among landscape blocks

Table 6. Forest age distribution of revisited field sites in old forest in landscape blocks with different forestry impact. Distribution of age-classes was not significantly different between impact types ($P > 0.05$; Chi-2 = 1.602; d.f. = 4). N_{total} = 100.

Age-class, yr	Forestry impact # of sites	
	Low	High
80–100	5	2
101–121	9	8
121–140	20	16
141–160	11	5
> 160	15	9

was obtained. The number was set by the class occurring in lowest frequency in either one forestry impact type. Selection of sites from 'surplus' classes was done evenly between and randomly within landscape blocks. A two-way analysis of variance (ANOVA) was carried out with block type and tree species class as factors. To control for the effects of forest area-class and forest age we performed a second ANOVA excluding all field sites < 50 ha in size (*i.e.* using only forest tracts) and all field sites in old-growth forest (> 160 yrs). This procedure had the additional effect of removing single extra large tracts with long distances to nearest clear-cut (mean distance > 1400 m in old growth). We did not core trees to determine age; instead we used the occurrence of large diameter trees as a proxy for forest stand continuity at the site (Table 6). The relationship between diameter and age was derived from an independent tree material gathered by the National Forest Inventory in the same area.

Among species groups we thus found a significant effect of forestry impact on relative abundance of Siberian species in both ANOVAs (Table 7). A significant effect of tree species composition for decreasing species in the first ANOVA disappeared when area and age was controlled for in the second ANOVA. At the species level, there was a significant negative effect of forestry impact for Tree pipit *Anthus trivialis* (both ANOVAs; Table 8), and for Brambling and Common redpoll (negative and positive, first and second ANOVA, respectively). A significant effect of tree species composition was observed for Redwing *Turdus iliacus* (both ANOVAs), and for Redstart (first ANOVA). The Redwing was most abundant in spruce forest and the Redstart in pine forest.

Table 7. Analysis (ANOVA) of the effect of forestry impact and tree species composition on relative abundance of species in different groups of species hypothesized to be negatively affected by forestry. a) N = 64 (8 replicates x 2 forestry impact types x 4 tree species classes), b) N = 48 (6 replicates x 2 forestry impact types x 4 tree species classes). Significant ($P < 0.05$) differences in bold. b) Differs from a) in the exclusion of field sites in forest patches (< 50 ha of forest) and old growth.

Dependent variable	Forestry impact	Tree species composition	r ² (%)
of	d.f. = 1 P	d.f. = 3 P	
a)			
Decreasing species	0.120	0.020	18.2
Resident species	0.097	0.740	6.5
Siberian species	0.007	0.091	19.9
b)			
Decreasing species	0.634	0.987	7.7
Resident species	0.103	0.145	16.4
Siberian species	0.038	0.087	21.2

Discussion

Impact of forestry on landscape structure

Distance to natural edge was similar in the two impact types, indicating a general and high degree of natural fragmentation due to landform. This agrees with the general view of the boreal forest landscape as a patchwork in a setting of other landforms, predominantly open water and mire (Pastor *et al.* in press). In the County of Norrbotten, open water and mire make up 29% of the forest landscape (according to VM), making this part of the boreal region a spatially heterogenous forest landscape. This has important implications for natural disturbance regimes (Hunter 1993) and, as indicated here, disturbance by man: Clear-cuts were disproportionately more common in areas with contiguous forest than in spatially disjunct forest land. Fragmentation by forestry hence tends to be a phenomenon localized to certain parts of the landscape. One consequence of such nested pattern of forestry may be reduced spatial heterogeneity at the landscape level by reduced variance in size distribution of forest stands (Mladenoff *et al.* 1993). Of course, this hypothesis has to be tested with more sophisticated analytical tools than used here; ideally with direct assessment of patch size distribution in a GIS.

Table 8. Analysis (ANOVA) of the effect of forestry impact and tree species composition on the relative abundance of individual species. a) N = 64 (8 replicates x 2 forestry impact types x 4 tree species composition classes), b) N = 48 (6 replicates x 2 forestry impact types x 4 tree species composition classes). Only species which occurred at > 40% of the field sites are included in the analyses. Significant ($P < 0.05$) differences in bold. b) Differs from a) in the exclusion of field sites in forest patches (< 50 ha of forest) and old growth.

Dependent variable	Forestry impact	Tree species composition	r ² (%)
of	d.f. = 1 P	d.f. = 3 P	
a)			
<i>Cuculus canorus</i>	0.571	0.354	–
<i>Turdus philomelos</i>	0.140	0.969	–
<i>T. iliacus</i>	0.878	0.003	20.8
<i>Phoen. phoenicurus</i>	0.290	< 0.001	35.7
<i>Phyll. trochilus</i>	0.144	0.094	–
<i>Anthus trivialis</i>	0.023	0.893	9.3
<i>Carduelis spinus</i>	0.581	0.431	–
<i>C. flammæa</i>	0.152	0.672	–
<i>Fri. montifringilla</i>	0.047	0.987	6.7
b)			
<i>Cuculus canorus</i>	0.310	0.689	–
<i>Turdus philomelos</i>	0.578	0.238	9.9
<i>T. iliacus</i>	0.424	0.001	31.5
<i>Phoen. phoenicurus</i>	0.482	0.068	16.0
<i>Phyll. trochilus</i>	1.000	0.141	11.8
<i>Anthus trivialis</i>	0.042	0.229	17.1
<i>Carduelis spinus</i>	0.440	0.202	11.4
<i>C. flammæa</i>	0.048	0.317	15.1
<i>Fri. montifringilla</i>	0.139	0.569	9.1

Species richness

The significant difference in species richness between impact types indicated an overall negative effect of modern forestry on forest birds in the study region. As indicated by our results, avian species composition in boreal forests changes during the course of succession through addition of new forest species and exclusion of a few species preferring open habitats, *i.e.* Black grouse *Tetrao tetrix*, Spotted redshank and Greenshank *Tringa nebularia*, leading to a peak in diversity of forest birds in later successional stages (Helle and Monkkonen 1990). Landscapes with much old forest also provide more targets for randomly colonizing species preferring this habitat.

Our study suggests a significant effect of tree species composition on species richness. Earlier

studies in Fennoscandian boreal forests have demonstrated alpha-diversity to vary little between habitat types (Haila *et al.* 1987b; Monkkonen 1994), particularly at northern latitudes (Järvinen and Vaisanen 1976). Among plausible mechanisms accounting for the pattern in our study we suggest altitudinal differentiation of habitat types; spruce and mixed coniferous forest dominate on hillsides and in high terrain where birch often forms an understorey. In contrast, pine forests dominate on drier soils in river valleys at lower altitudes where birch does not thrive.

Occurrence and abundance offorest birds

A higher relative abundance of forest birds in low impact landscapes suggests that there are no positive effects of man-made edges on forest birds in our high impact blocks (cf. Wiens 1989). Distance to natural edge was about the same, but distance to young forest at old forest field sites in high impact blocks averaged half that in low impact blocks. Although not treating explicitly distance to edge, Helle and Järvinen (1986) could explain the long-term changes (positive as well as negative) in population density of abundant northern forest birds in North Finland by the combined impact of altered forest age structure and increased amounts of edge due to large-scale forestry. In our study region, clear-cutting does not produce well-developed ecotones between old forest and young forest, and most man-made edges are of recent origin. These edges may not provide habitat for forest birds. An alternative explanation for the lower relative abundance of forest birds in high impact blocks may be difference in tree species composition. Helle and Jarvinen (1986) did not specifically address this question. Pine forest was more abundant in the high impact blocks, and since pine forests are relatively species poor and have relatively low abundances of forest birds compared to the other tree species classes, landscape level effects may become apparent. Habitat composition in terms of dominating tree species is in part a phenomenon based on natural variation in site characteristics, disturbance regime etc., but to a large extent also an indirect effect of forestry: Pine has been exclusively favoured in forest regeneration following cutting in this part of the boreal region (Kempe *et*

al. 1992). This suggests an additional link between forestry and biodiversity at the landscape level.

It is trivial that relative abundance of many species may be affected by forest patch size- and age-class, as well as by tree species composition. However, our finding that an effect of landscape type remains after controlling for these factors is important, as it implies a landscape level effect of forestry. Thus, for Siberian species and Tree pipit, large scale reduction of habitat area may be a crucial factor. Recent Swedish data suggest that the total population size of the Tree pipit has been reduced by almost 50% in less than ten years (Svensson 1995). The same may apply for the Brambling, for which a significant effect of impact type disappeared when field sites from old-growth forest were excluded.

Jarvinen *et al.* (1977) found the decrease of species associated with old growth in North Finland to be stronger than suggested by the reduction in habitat area alone. They attributed this to fragmentation, and the Siberian species as well as the Tree pipit may in the light of our results be candidates as indicators of forest fragmentation. However, the homogeneity and the functionality of the Siberian group have to be taken into account (Haila and Järvinen 1990). For example, the Brambling's large between-year variation in population density and its low degree of site tenacity (Mikkonen 1983) may speak against using it as an indicator (Landres *et al.* 1988). Moreover, the group is composed of both migratory and sedentary species, which may be subject to different population regulation factors.

Our results suggest that large-scale forestry has relatively small effects on resident and 'decreasing' species. For decreasing species the lack of significance was largely explained by the Redstart. Removing it from the group produced a significant negative relationship. Its relative abundance was clearly associated with habitat (pine forest). Haila *et al.* (1987a) found the Redstart to be area-sensitive in the southern taiga, avoiding small forest fragments. Conditions seem to be different in the north (Virkkala 1987, personal observations), which cautions against generalizing results obtained from one area.

Our selection of field sites along forestry roads resulted in a somewhat biased landscape level sam-

ple, *i.e.* under-representation of naturally fragmented areas, and to a minor extent, of very large tracts of old forest. On the other hand, we have taken samples where forestry has actually been taking place. Hence, our design did not fully cover the range of site conditions in the different landscape types under study. For example, it was not possible to contrast natural landscape mosaics with homogeneous tracts of old forest. At the landscape block level we may thus have underestimated relative abundance of forest interior species, such as Siberian tit *Parus cinctus*. This has to be born in mind when interpreting the results.

Although we tried to avoid edge-effects in sampling of birds by preferentially selecting field sites in forest tracts, it might be argued that our roadside samples introduced such effects. However, this would affect all sites in old forest equally and thus not bias our comparisons. In addition, most sampling in old forest was done along small forestry roads with narrow road corridors.

Conclusions

Our study reveals relatively small differences in the structure and composition of the avifauna between landscape blocks with different forestry impact. One explanation for the similarity in relative abundance of old-growth specialists is that changes in population size may already have taken place, due to regional changes in habitat structure at the stand level. Earlier selective cuttings have long since impoverished these forests in terms of abundance of very large trees, older deciduous trees and snags (Tirén 1937; Linder and Ostlund 1992). It should also be noted that only a small fraction of our field sites were in old growth. Large landscape blocks of old-growth forest may differ considerably from managed forest landscapes in densities of old-growth specialists (Virkkala 1987).

By and large, our results indicate a low present sensitivity of Fennoscandian boreal avian communities to large-scale modern forestry. There are several potential reasons for this. 1) Clear-cut areas are not permanently transformed into other land use forms, *e.g.* farmland, as is often the case elsewhere where fragmentation effects have been demonstrated (see Andrén 1994, for review). 2) Planted

forests in our study area are not totally inhabitable for species preferring old forest, *i.e.* the surroundings of remnant old forest patches can be utilized (Enoksson *et al.* 1995). 3) The majority of species in the regional pool are habitat generalists, as indicated by this study. 4) This part of the boreal region still has many tracts of old forest in natural or semi-natural stage. 5) Our study area is relatively close to contiguous boreal forest in Russia, potentially functioning as a source for taiga specialists. We do, however, recognize that this situation is rapidly changing. We therefore advocate retention of old-growth patches and the maintenance and restoration of legacies such as large trees, older deciduous trees and snags. Nor do we dispute the long-term population changes demonstrated by the Finnish workers. We thus may be approaching a situation when the total amount of old forest is small enough to create threshold effects.

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References

- Ahti, T., Hamet-Ahti, L. and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Ann Bot Fennici* 5: 169–211.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Anonymous 1994. Statistical yearbook of forestry. Official statistics of Sweden. National Forestry Board, Jonkoping.
- Engelmark, O. 1984. Forest fires in the Muddus National park (northern Sweden) during the past 600 years. *Can J Bot* 62: 893–898.
- Enoksson, B., Angelstam, P. and Larsson, K. 1995. Deciduous forest and birds: the problem of fragmentation within a coniferous forest landscape. *Landscape Ecology* 10: 267–275.
- Esseen, P.-A., Ehnstrom, B., Ericson, L. and Sjoberg, K. 1992. Boreal forests – the focal habitats of Fennoscandia. *In Ecological Principles of Nature Conservation*, pp. 252–325. Edited by L. Hansson. Elsevier, London.

- Hagglund, B. and Lundmark, J.-E. 1977. Site index estimation by means of site productivity. *Stud For Suec* 138.
- Haila, Y. and Järvinen, O. 1990. Northern conifer forest and their bird species assemblages. *In* Biogeography and Ecology of Forest Bird Communities, pp. 61–85. Edited by A. Keast. SPB Academic Publishing bv, The Hague.
- Haila, Y., Hanski, I.K. and Raivio, S. 1987a. Breeding bird distribution in fragmented coniferous taiga in southern Finland. *Ornis Fennica* 64: 90–106.
- Haila, Y., Jarvinen, O. and Raivio, S. 1987b. Quantitative versus qualitative distribution patterns of birds in the western Palearctic taiga. *Ann Zool Fennici* 24: 179–194.
- Helle, P. and Järvinen, O. 1986. Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 46: 107–115.
- Helle, P. and Monkkonen, M. 1990. Forest succession and bird communities: theoretical aspects and practical implications. *In* Biogeography and Ecology of Forest Bird Communities, pp. 299–318. Edited by A. Keast. SPB Academic Publishing bv, The Hague.
- Hunter, M. 1990. *Wildlife, Forests, and Forestry*. Prentice Hall, Englewood Cliffs, New Jersey.
- Hunter, M. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol Conserv* 65: 115–120.
- Järvinen, O., Kuusela, K. and Vaisanen, R.A. 1977. Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. (In Finnish with English summary). *Silva Fennica* 11: 284–294.
- Jarvinen, O. and Vaisanen, R.A. 1976. Species diversity of Finnish birds, II: Biotopes at the transition between taiga and tundra. *Acta Zool Fennici* 145: 1–35.
- Järvinen, O. and Väisänen, R.A. 1977. Long-term changes of the North European land bird fauna. *Oikos* 29: 225–228.
- Kempe, G., Toet, H., Magnusson, P.-H. and Bergstedt, J. 1992. The Swedish national forest inventory 1983–87. Swedish University of Agricultural Sciences, Department of Forest Survey, Umeå, Report 51.
- Landres, P.B., Verner, J. and Thomas, J.W. 1988. Ecological uses of vertebrate indicator species: a critique. *Conserv Biol* 2: 316–328.
- Linder, P. and Ostlund, L. 1992. Changes in the boreal forests of Sweden (In Swedish with English summary). *Sven Bot Tidskr* 86: 199–216.
- Mladenoff, D.J., White, M.A. and Pastor, J. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3: 294–306.
- Mikkonen, A.V. 1983. Breeding site tenacity of the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in northern Finland. *Ornis Scand* 14: 36–47.
- Monkkonen, M. 1994. Diversity patterns in Palearctic and Nearctic forest bird assemblages. *J Biogeogr* 21: 183–195.
- Monkkonen, M. and Welsh, D.A. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Ann Zool Fennici* 31: 61–70.
- Pastor, J., Mladenoff, D., Haila, Y., Bryant, J. and Payette, S. Biodiversity and ecosystem processes in boreal regions. *In* Functional Roles of Biodiversity: A Global Perspective. Edited by H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala and E.-D. Schulze. Wiley Press, New York. In press.
- Simberloff, D.S. 1978. Use of rarefaction and related methods in ecology. *In* Biological Data in Water Pollution Assessment, pp. 150–165. Edited by K.L. Dickson, J. Cairns Jr. and R.J. Livingstone. American Society for Testing and Materials, STP 652.
- Solonen, T. 1994. Structure and dynamics of the Finnish avifauna. *Memoranda Soc Fauna Flora Fennica* 70: 1–22.
- Svensson, S. 1995. Svenska häckfågeltaxeringen 1994. Fågelåret 1995: 11–19. SOF, Stockholm. (In Swedish).
- Syrjanen, K., Kalliola, R., Puolasmaa, A. and Mattson, J. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Ann Zool Fennici* 31: 19–34.
- Tirén, L. 1937. Skogshistoriska studier i trakten av Degerfors i Västerbotten. (In Swedish). *Meddel Skogsfoers Anst* 30: 67–322.
- Virkkala, R. 1987. Effects of forest management on birds breeding in northern Finland. *Ann Zool Fennici* 24: 281–294.
- Vaisanen, R.A., Jarvinen, O. and Rauhala, P. 1986. How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? *Ornis Scand* 17: 282–292.
- Voous, K.H. 1960. *Atlas of European Birds*. Nelson, London.
- Wiens, J.A. 1989. *The Ecology of Bird Communities*. Cambridge University Press, Cambridge.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29: 22–32.

Appendix: Grouping of boreal forest species that could be expected to be negatively affected by large-scale clear-cutting

A. Decreasing species: Species with decreasing population trends in North Finland (*sensu* Vaisanen *et al.* 1986)

Tetrao urogallus
Picoides tridactylus
Dryocopus martius
Garrulus glandarius
Perisoreus infaustus
Parus cinctus
P. montanus
Turdus viscivorus
Phoenicurus phoenicurus
Anthus trivialis
Loxia curvirostra

B. Resident species (*sensu* Solonen 1994)

Tetrao urogallus
Bonasa bonasia
Picoides tridactylus
Dryocopus martius
Corvus corax
Perisoreus infaustus
Parus major

P. cinctus

P. montanus

C. **Siberian species:** Species belonging to the Siberian (or Siberian-Canadian) faunal type (*sensu* Voous 1960).

Bonasa bonasia

Surnia ulula

Picoides tridactylus

Perisoreus infaustus

Parus cinctus

Turdus pilaris

T. iliacus

Fringilla montifringilla

Pinicola enucleator

Emberiza rustica