



## Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland

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### Abstract

Old-growth forest birds in Fennoscandia have sharply declined in numbers during the last decades apparently due to commercial forest harvesting and fragmentation of old-growth forests. Conservation measures have led to the establishment of a forest reserve network to assure the persistence of forest birds at a regional scale. However, little is known about the effects of landscape structure within and around the reserves on the distribution of old-growth forest birds. We used a hierarchical approach to address the questions of how landscape structure and composition within forest reserves, landscape composition of surrounding areas and reserve location affect the abundance of resident, old-growth forest birds in the Northern Finnish forest reserve network. The positive role of particular landscape features on bird distribution indicates that both the proportion of old-growth forests and the structure of boreal landscape mosaic has an important role in determining the distribution of these birds. The landscape composition surrounding the reserves proved to be only a weak predictor in species distribution models, which argues against the primary role of the surrounding matrix in determining species distribution within forest reserves. Reserves located near the Russian border showed a higher abundance of old-growth birds than more western ones. Once east-west gradients in overall landscape composition had been accounted for, however, reserves did not differ significantly in the number of species present. These results suggest that landscape gradients, rather than ecological processes such as the presence of source areas located along the border with Russia, are the main determinant of the distribution of old-growth forest birds in the Finnish reserve network. We propose that to enhance regional persistence of old-growth forest birds, conservation efforts should be primarily directed towards the protection and enhancement of forest habitat quality and natural heterogeneity of landscapes within targeted areas.

### Introduction

Bird species of old-growth boreal forests in Fennoscandia have steeply declined in numbers during the past 50 years most likely because of habitat loss and fragmentation by commercial harvesting (Helle and Järvinen 1986; Väisänen et al. 1998). This decrease has been particularly pronounced in northern Finland where forest landscapes have also changed markedly since the 1950s (Haila and Järvinen 1990). Many old-

growth forest bird species, such as Siberian Jay (*Perisoreus infaustus*), Siberian Tit (*Parus cinctus*) and Three-toed Woodpecker (*Picoides tridactylus*), have decreased more than predicted on the basis of the decline in the area of old-growth forests (Järvinen et al. 1977). This finding suggests that factors other than pure habitat loss, possibly related to the spatial arrangement of remaining forest stands, might be responsible for the observed population trends. Recent studies in different forest areas across the boreal zone

have stressed the importance of landscape structure and composition in determining bird species distribution and abundance (Jokimäki and Huhta 1996; Schmiegelow et al. 1997; Saab 1999). The configuration of different habitat types in the landscape, including habitat diversity and the density of habitat boundaries, has proved to be an important factor shaping species interactions with their environment at different spatial scales (Jokimäki and Huhta 1996; Sjöberg and Ericson 1997; Villard et al. 1999; Drapeau et al. 2000). Because of the non-linear effects of habitat availability on species distribution, fragmentation effects may appear abruptly after critical thresholds of habitat availability are reached (Andrén 1994). However, the relative effects of habitat composition and configuration on bird distribution may be dependent on the landscape context studied (Mönkkönen and Reunanen 1999). In this case, the type of landscape matrix and the relative proportion of habitat types in the landscape may act in concert to affect bird distribution (Jokimäki and Huhta 1996). There is also evidence for negative effects of isolation on animal populations. Current population ecological theory emphasizes the role of dispersal for population persistence (see Harrison and Bruna (1999)), and therefore, landscape connectivity is a key concept.

Reducing the negative impact that forestry has on the structure of forest landscapes is a central issue in conservation biology (Mönkkönen 1999). Nature reserves constitute the backbone of conservation efforts in Fennoscandian boreal forests even though recent management recommendations emphasize the importance of considering the landscape as a whole (Angelstam 1992; Mönkkönen 1999). For example, an extensive network of nature reserves has been established in northern Finland to assure that representative areas across the region retain their natural habitat structure independent of forestry and landscape management activities that take place elsewhere. For the persistence of regional populations of old-growth forest species, more information is needed about the required extent of conservation areas and their spatial configuration (Virkkala et al. 1994; Cumming et al. 1996). In spite of the concern that this group of species has received lately, very little is known about their specific responses to natural gradients in landscape structure. Nature reserves offer an ideal framework for study because they represent natural landscape mosaics where such responses can be analysed.

In this study, we identify factors affecting the distribution of resident, old-growth forest species inhab-

iting semi-natural boreal forests in the northern Finnish forest reserve network. We used a hierarchical approach to analyse how landscape characteristics within forest reserves, landscape composition of surrounding areas and reserve location affect abundance of resident, old-growth forest bird species in the reserve network.

First, because of their expected association with old-growth forests, we predicted that the abundance of the focal species in forest reserves would be positively related to the proportion of old-growth forest, and negatively related to the amount of unforested and young forest areas. Given the mosaic nature of the boreal forest (Esseen et al. 1997), we also predicted that landscapes with higher forest and landscape diversity would host more old-growth forest bird species than those with low structural diversity (Raivio and Haila 1990). We also studied the role of forest reserve area, asking how area interacts with landscape composition and structure in determining bird distribution.

Second, landscape composition buffering forest reserves might be an important factor contributing to the presence and abundance of forest bird species by affecting the relative isolation of forest reserves. For old-growth forest species, isolation is usually related to distance from large tracts of old-growth forests that could act as source areas (Virkkala 1987). If a reserve is embedded in a landscape where low-quality habitats such as clear-cuts or young forests prevail, one would expect to find a negative effect of isolation on the occurrence and abundance of old-growth forest bird species. Conversely, higher availability of favourable habitat such as old-growth forests in the surrounding landscape might enhance the presence of the old-growth species in the reserves (Virkkala 1991).

Finally, given that the largest tracts of continuous old forest in the region are located in the Russian Karelia along the Finnish-Russian border (Lindén et al. 2000), reserves in Finland located closer to these areas may contain richer old-growth forest bird assemblages (Kouki and Väänänen 2000). If forested areas in Russia function as sources for old-growth forest species in our study region (Source area hypothesis), we would expect to find a larger number of species or higher abundances in reserves closer to the Russian border and decreasing abundances towards the west. Alternatively, natural landscape gradients (i.e., increase in abundance of old-growth forests from east to west) associated with the distance from

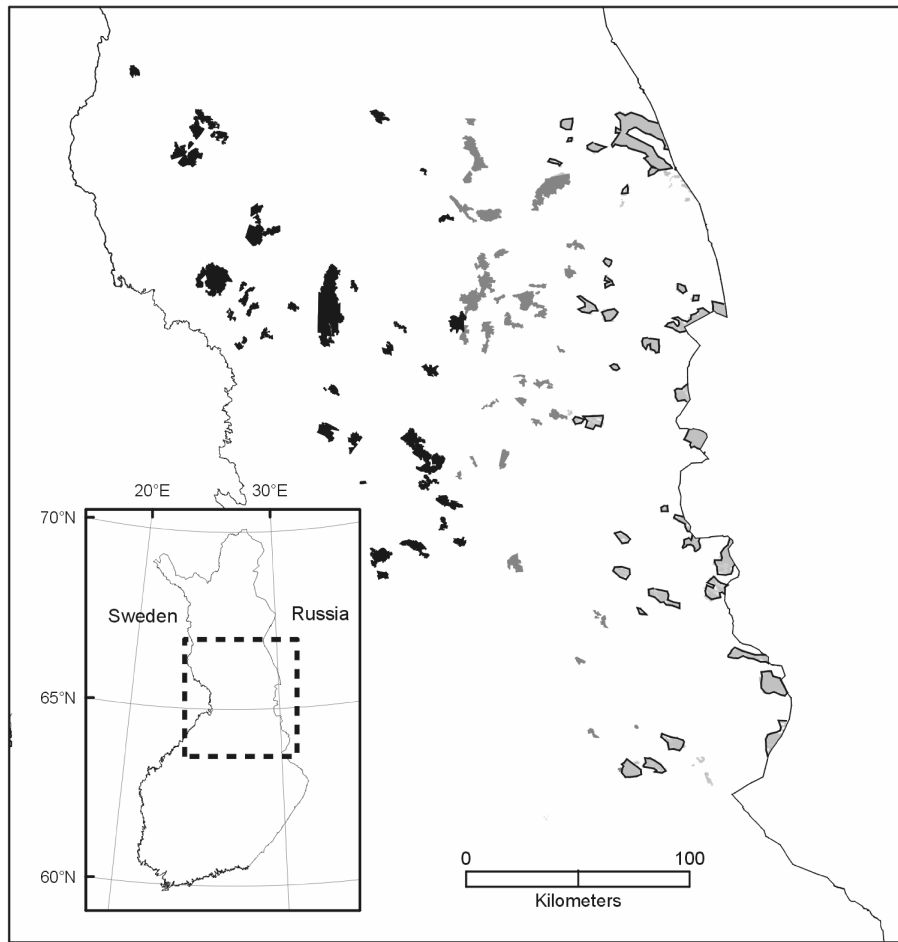


Figure 1. Map of the study area showing the regional location and relative size of forest reserves in northern Finland. Forest reserves in the western region are represented in black, dark grey in the central region, and are outlined light grey in the eastern region.

the hypothetical source area may also explain bird distribution in the reserves.

## Methods

The main purpose of the protected area network in Finland is to conserve pristine environments. In general, alteration of habitats, such as draining mires or cutting forests, is not allowed in protected areas. Because of the centuries long history of forestry in Fennoscandia (see Imbeau et al. (2001)), no pristine forests remain in the area. Present old-growth forests were selectively logged in the late 19<sup>th</sup> and early 20<sup>th</sup> centuries, but remained intact since the 1940s. Forest reserves represent the last remaining semi-natural mosaics of boreal forest in the area, and the area surrounding reserves is intensively managed for silvicultural

purposes. The present study includes 91 forest reserves in northern Finland (Figure 1). The reserves differ in size, with a mean area of 3400 ha (range 200 ha – 28000 ha, S.E. = 492 ha). The reserves belong phyto-geographically to mid-and north-boreal forest zones (Ahti et al. 1968). According to Järvinen and Väisänen (1977), our study region is almost completely within the mid-boreal zoogeographic zone, and is thus fairly homogeneous in terms of the regional bird species pool. Only a few areas in the north-easternmost corner of our study region belong to the north boreal zoogeographic zone.

We concentrated on nine bird species that are mainly resident and associated with old-growth forest habitats (Väisänen et al. 1998; Kouki and Väänänen 2000). The species included in this study are the Hazel Grouse (*Bonasia bonasia*), Capercaillie (*Tetrao urogallus*), Black Woodpecker (*Dryocopus martius*),

Table 1. Number of forest reserves occupied/non-occupied per each species in the three regions analysed in our study. Western region, forest reserves > 100 km from the Russian border. Central region, reserves between 50 and 100 km from Russia. Eastern region, reserves < 50 km from Russia. The total number of individuals detected per species along transect routes is indicated in parenthesis.

Species	Western region n = 28	Central region n = 28	Eastern region n = 33
<i>Bonasia bonasia</i> (230)	11/17	17/13	29/4
<i>Tetrao urogallus</i> (201)	9/19	17/13	26/7
<i>Dryocopus martius</i> (146)	13/15	10/20	21/12
<i>Picoides trydactylus</i> (181)	6/22	16/16	23/10
<i>Parus cinctus</i> (60)	1/27	4/26	15/18
<i>Parus cristatus</i> (150)	3/25	5/25	19/14
<i>Certhia familiaris</i> (253)	9/19	15/15	21/12
<i>Perisoreus infaustus</i> (251)	7/21	13/17	25/8
<i>Pinicola enucleator</i> (53)	0/28	4/26	9/24

Three-toed Woodpecker, Crested Tit (*Parus cristatus*), Siberian Tit, Treecreeper (*Certhia familiaris*), Siberian Jay and the Pine Grosbeak (*Pinicola enucleator*). These are obligatory old-growth forest species (Snow and Perrins 1998; Väisänen et al. 1998) for which the forest reserve network provides high quality core areas of major importance for their long-term regional persistence. Pine Grosbeaks are partial migrants but the other species are strictly resident. Since resident species use the landscape year-round, and winter is the critical period for population regulation (Herrera 1978; Lahti et al. 1998), these species are more likely to respond to changes in landscape structure than migratory species (Bender et al. 1998), in which occurrence is determined to a larger extent by the annual colonisation of new habitats (Haila 1994). Recent population changes of Finnish forest birds indicate that residents in particular have suffered from loss of old-forest habitat and also very likely from fragmentation of the remaining forests (Haila and Järvinen 1990; Mönkkönen and Welsh 1994; Imbeau et al. 2001; Schmiegelow and Mönkkönen 2002). Natal and adult dispersal distances of the species are not accurately known and dispersal abilities differ between species. Genetic studies have shown that at least some species undertake only limited movements (few km at most) during their natal dispersal (Uimaniemi et al. 2000), and therefore, isolation of the preferred habitat may have a strong impact on their distribution patterns.

#### Bird censuses

The data were collected using the Finnish line-transect method (Järvinen and Väisänen 1975) where a prescribed route is slowly (1 km/hour<sup>-1</sup>) walked and all birds seen or heard are tallied using an unlimited radius. The censuses were carried out between 0300 and 1000 in June, which is the peak breeding season in the region, and always in good weather conditions. We aimed at getting representative samples of the breeding bird assemblages in each reserve, and keeping the effort per unit area constant (about 1 km of transect per 1 km<sup>2</sup> of reserve). Transects were located so as to evenly cover the forest reserves. Altogether, 3323 km of transects were conducted in the 91 nature reserves between 1988 and 1997. Overall, we detected 1525 individuals of the selected species (Table 1). This gives a mean of about 0.75 individuals detected per kilometre of transect in forest. This low abundance clearly demonstrates the low density of this group of species in northern forests and emphasizes the need for large-scale monitoring efforts to collect valid information on bird distributions at regional scales. We used the total number of individuals detected per species along transects within each reserve (species abundance) as a dependent variable in the analyses. We also calculated the total number of species present at each forest reserve (total species richness) and the total number of individuals per reserve of the nine studied species combined (total abundance).

Transect length varied with reserve size because of equal sampling effort per unit area. This has an impact on the probability of species and number of in-

Table 2. Landscape structure of forest reserves within the three regions of Northern Finland (see Table 1, Figure 1). Based on ANOVA and subsequent post-hoc tests, regions with the same letter indicate no differences in the landscape variables. Values in parentheses correspond to measures within a 10-km buffer zone around each forest reserve.

Variable	Western region	Central region	Eastern region
Cover types (%)			
Mixed pine-spruce > 100 m <sup>3</sup> /ha	5.8 (3.3) <sup>b</sup>	19.46 (7.1) <sup>a</sup>	24.08 (11.5) <sup>a</sup>
Pine > 100 m <sup>3</sup> /ha	2.5 (2.0) <sup>b</sup>	2.5 (2.1) <sup>b</sup>	4.8 (3.9) <sup>a</sup>
Spruce-deciduous > 100 m <sup>3</sup> /ha	3.3 (3.7) <sup>b</sup>	9.8 (3.2) <sup>a</sup>	7.0 (3.0) <sup>ab</sup>
Pine-spruce 25–100 m <sup>3</sup> /ha	7.6 (15.0) <sup>b</sup>	16.0 (11.9) <sup>a</sup>	13.1 (10.3) <sup>a</sup>
Pine 25–100 m <sup>3</sup> /ha	12.9 (20.3) <sup>a</sup>	10.8 (13.8) <sup>a</sup>	9.3 (10.8) <sup>a</sup>
Spruce-deciduous 25–100 m <sup>3</sup> /ha	9.8 (10.4) <sup>a</sup>	12.4 (13.3) <sup>a</sup>	9.9 (10.4) <sup>a</sup>
Pine bogs	32.7 (22.4) <sup>b</sup>	14.3 (16.6) <sup>a</sup>	14.4 (14.9) <sup>a</sup>
Shrubs < 25 m <sup>3</sup> /ha	4.5 (10.4) <sup>b</sup>	6.0 (15.6) <sup>ab</sup>	6.4 (16.7) <sup>a</sup>
Other open areas	21.0 (16.2) <sup>b</sup>	8.6 (16.5) <sup>a</sup>	11.0 (18.5) <sup>a</sup>
Edge density (m/ha)	124.8 <sup>b</sup>	95.7 <sup>a</sup>	114.4 <sup>ab</sup>
Landscape diversity (Shannon index)	1.72 <sup>b</sup>	1.87 <sup>a</sup>	1.93 <sup>a</sup>
Total young forest 25–100 m <sup>3</sup> /ha (%)	30.2 <sup>b</sup>	39.3 <sup>a</sup>	32.3 <sup>ab</sup>
Total old-growth forest > 100 m <sup>3</sup> /ha (%)	11.6 <sup>b</sup>	31.8 <sup>a</sup>	35.9 <sup>a</sup>
Forest diversity (Shannon index)	0.95 <sup>b</sup>	1.29 <sup>a</sup>	1.28 <sup>a</sup>

individuals being detected; larger reserves are expected to have more species and individuals because of greater sample sizes. Therefore, we first removed the effect of sample size in the analyses by including transect length within forest in each reserve (log-transformed) into the models. Since all the species included are forest specialists, transect length across non-forested habitats was not included.

The species included in the present study have little annual fluctuations in numbers (Helle and Mönkkönen 1986). Because not all forest reserves were censused in the same year, however, we checked for possible year-related biases in our data set. We performed an analysis of covariance (ANCOVA) grouping forest reserves censused in the same year and including year as a categorical factor and total transect length through forest as a covariable. Species richness and abundance of old-growth forest species did not differ among years (Species richness,  $F_{8,36} = 0.85$ ,  $p = 0.57$ ; abundance  $F_{8,36} = 0.34$ ,  $p = 0.94$ ). Therefore, we combined data across years and ignored annual variation in bird numbers in the analyses. Annual fluctuations, however, make our analyses more conservative by slightly increasing the probability of Type II errors.

#### Landscape analyses

Land use and cover data for the analyses come from national forest inventory (NFI) of Finland (Tomppo

1993). For each pixel of forested land (25 m × 25 m pixel size), NFI produces an estimate of growing stock volume separately for Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), birches (*Betula spp.*), and all other species as a combined class. Digital maps of non-forest lands (peatland, water, agricultural land, roads and settlements) were used to separate non-forest areas from forest (Tomppo 1993).

We classified the data to obtain nine cover types (Table 2). First, each pixel of forest was classified by timber volume as shrub (total timber volume < 25 m<sup>3</sup>(ha<sup>-1</sup>, corresponding to low-productivity stands within forest reserves, and post-harvesting stands in managed areas around forest reserves), young forest (25–100 m<sup>3</sup>(ha<sup>-1</sup>) and old-growth forest (> 100 m<sup>3</sup>(ha<sup>-1</sup>). Among young and old-growth forests, we made a distinction between pine, mixed pine-spruce and moist spruce-deciduous stands. Other landscape classes were pine bogs (peatlands with timber volume 1–35 m<sup>3</sup>(ha<sup>-1</sup>) and open habitats (including open mires, clear-cut areas and water). Forested landscape around the reserves was analysed using two different radii: 5-km and 10-km-wide belts buffering the outer border of each reserve. To describe the forested landscape around reserves we used the same variables used to describe landscape composition within reserve but we discarded the open habitats category, as it was not considered to describe forest habitat.

A portion of the buffer zones around reserves that were adjacent to or near the Russian border fell out-

side the Finnish land-cover data, and no comparable data from Russia are available. To overcome this problem, we estimated landscape structure in the buffer zone of such reserves by assuming that undisturbed areas along the Russian border have a landscape composition identical to that of the reserve itself. This assumption is reasonable since forest reserves represent natural, undisturbed areas and this corresponds to the state of forest areas along the border with Russia.

We used FRAGSTATS (McGarigal and Marks 1995) to derive measures describing both the proportion of different habitat types and their configuration (Table 2). From each forest reserve we calculated edge density as the length of forest – open habitat edge per unit area. We considered forest to be all areas with timber volume greater than 25 m<sup>3</sup>/ha. Habitat diversity was calculated using Shannon's diversity index. We used only forest habitat classes (> 25 m<sup>3</sup>/ha) when calculating forest diversity, and all habitat classes when calculating overall landscape diversity.

We categorised forest reserves into three groups according to their distance from the Russian border (reserve location, LOC): eastern (up to 50 km west of the Russian border), central (50–100 km), and western region (> 100 km; see Figure 1). This division is based on natural differences in landscape characteristics among the three regions reflecting topographic and edaphic variation (see Reunanen et al. (2002) (in press)). Because of their lowland location, reserves in the western region are more dominated by peatland (and by less old-growth forest) than reserves in the other regions (Table 2). In the central region, relief is more varied and reserves have higher proportions of spruce-deciduous forests than in the other two areas (Table 2), whereas the forests in the eastern region are more pine-dominated. The amount of old-growth forest in the central and eastern regions is considerably higher than in the western region (Table 2). The different landscape structure of the three regions offers a convenient framework to assess the role of natural landscape gradients on bird distributions within forest reserves (for more detailed description of the three regions, see Reunanen et al. (2002) (in press)).

#### *Landscape structure within and around reserves*

In order to reduce the number of variables to be included in the analyses and to describe the main landscape gradients in the study regions, we performed

principal component analysis (PCA) on the landscape variables using Varimax normalised rotation of original factor scores to help factor interpretation (Legendre and Legendre 1998). PCA on the forest variables within reserves yielded five factors explaining 86% of the original variation (Table 3). The first factor was positively related to the cover of old-growth forest in the reserves and negatively related to the amount of peatlands and bogs and the length of edges. Therefore, this factor (OLD) represented a gradient from naturally fragmented areas with abundant bogs and open areas to areas dominated by old-growth forests with high forest diversity. The second factor (YF) was positively associated with the cover of young forest in the reserves. The third factor (PINE) showed a positive relationship with the amount of pine forests, both old and young, in the reserves. The fourth factor (DIV) represented a gradient of increasing landscape diversity within the reserves, whereas the fifth and last factor (SHR) was associated with the amount of shrubby forests.

The variables describing forested landscape composition buffers in forest reserves was summarised in three factors explaining 72% of the total variance (Table 4). Landscape data from 5-km and 10-km buffer zones were highly correlated. The first factor (OLDS) represented a gradient ranging from reserves surrounded by areas with large amounts of old-growth spruce and pine forests to reserves surrounded by mostly peatland and bogs. The second factor (DECS) was positively associated with the cover of mixed deciduous forests, both old growth and younger, and negatively associated with the amount of young pine forests around the reserves. The third factor (YFS) represented a gradient from reserves surrounded by peatlands to reserves surrounded by young pine and spruce forests and shrubs (early successional post-harvest stands or saplings).

#### *Statistical analyses*

Traditionally, analyses of the effects of landscape variables at different scales on animal distribution have used multiple regression methods to identify the variables that best explain the variation in species richness or abundance. Landscape variables at different scales are often interrelated. Consequently, the best multiple regression model (in statistical terms) in which landscape variables are allowed to enter simultaneously might be misleading due to collinearity across scales (Buckland and Elston 1993).

Table 3. Composite variables derived by principal component analysis (PC1-PC5) describing landscape composition and configuration within forest reserves. Factor loadings of the original variables as well as eigenvalues and proportion of variance explained are also shown.

Variable	PC1 OLD	PC2 YF	PC3 PIN	PC4 DIV	PC5 SHR
Cover types (%)					
Pine-spruce > 100 m <sup>3</sup> /ha	0.87*	-0.27	0.03	0.26	-0.07
Pine > 100 m <sup>3</sup> /ha	0.41	-0.16	-0.67*	0.37	-0.07
Spruce-deciduous > 100 m <sup>3</sup> /ha	0.80*	0.05	0.43	-0.17	0.05
Spruce 25 – 100 m <sup>3</sup> /ha	0.06	0.88*	0.04	0.30	-0.03
Pine 25–100 m <sup>3</sup> /ha	-0.31	0.07	-0.89*	-0.03	0.16
Spruce-deciduous 25–100 m <sup>3</sup> /ha	0.16	0.73*	0.42	-0.29	0.02
Pine bogs	-0.86*	-0.35	0.07	-0.23	-0.10
Shrubs < 25 m <sup>3</sup> /ha	-0.02	0.03	-0.08	0.20	0.96*
Other open areas	-0.73*	-0.48	0.02	-0.16	-0.15
Edge density (m/ha)	-0.84*	-0.19	-0.05	0.30	0.17
Landscape diversity	0.16	0.16	-0.15	0.87*	0.28
Total young forest (%)	-0.02	0.98*	-0.15	0.03	0.06
Total old forest (%)	0.96	-0.20	0.05	0.18	-0.05
Forest diversity	0.74*	0.43	-0.10	0.48	0.05
Eigenvalues	5.14	3.03	1.66	1.64	1.11
Variation explained (%)	37.3	22.1	12.1	12.2	7.9

\* P < 0.05.

We performed hierarchical generalised linear modelling to analyse species richness and total abundance of old-growth forest species in forest reserves, where variables were allowed to enter in groups corresponding to their scale of influence (Model 1). We started with a null model which included the sampling effort within each forest reserve (transect length in forest habitat). Our hierarchical approach was then executed in three steps, each including variables at different spatial scales. Step 1 included the variables describing landscape structure within reserves (5 PC-variables, see Table 3), and their interactions with reserve area (log-transformed, ARE). At step 2, we assessed the effect of reserve location by including the region (LOC) and its interaction with landscape variables. Step 3 included the variables describing the landscape structure surrounding forest reserves (3 PC variables, see Table 4) and their interactions with reserve size and region.

Because we were interested in the additional explanatory power of variables at each step after controlling for the effects of the finer-scale variables, we forced the inclusion of variables proven significant at the previous step before any additional variables were added. At each step, we used a backward removal method to select the best additional explanatory factors of bird richness or abundance starting with the

Table 4. Factor loadings on the principal component axes describing landscape composition and configuration in 5-km (5) and 10-km (10) buffer zones around the forest reserves. Factor loadings of the original variables as well as eigenvalues and proportion of variance explained are also shown for the first three axes.

Variable	PC1 OLDS	PC2 DECS	PC3 YFS
Cover types 5 km buffer (%)			
Spruce > 100 m <sup>3</sup> /ha	0.92*	0.10	0.14
Pine > 100 m <sup>3</sup> /ha	0.85*	-0.23	-0.15
Mixed forests > 100 m <sup>3</sup> /ha	0.10	0.93*	-0.05
Spruce 25–100 m <sup>3</sup> /ha	-0.07	0.00	0.84*
Pine 25–100 m <sup>3</sup> /ha <sup>3</sup>	0.02	-0.59*	0.63*
Mixed forests 25–100 m <sup>3</sup> /ha	-0.49*	0.76*	-0.19
Pine bogs	-0.61*	-0.26	-0.56*
Shrubs and saplings < 25 m <sup>3</sup> /ha	0.17	-0.33	0.70*
Cover types 10 km buffer (%)			
Spruce > 100 m <sup>3</sup> /ha	0.90*	0.05	0.12
Pine > 100 m <sup>3</sup> /ha	0.87*	-0.29	-0.15
Mixed forests > 100 m <sup>3</sup> /ha	0.11	0.92*	-0.12
Spruce 25–100 m <sup>3</sup> /ha	-0.08	-0.05	0.87*
Pine 25–100 m <sup>3</sup> /ha	-0.01	-0.62*	0.59*
Mixed forests 25–100 m <sup>3</sup> /ha	-0.53*	0.70*	-0.25
Pine bogs	-0.63*	-0.17	-0.59*
Shrubs and saplings < 25 m <sup>3</sup> /ha	0.20	-0.30	0.73*
Eigenvalues	5.14	3.03	1.66
Variation explained (%)	37.3	22.1	12.1

\* P < 0.05.

main effects and two-way interactions. We first removed the interaction terms if not significant, and then proceeded to assess the main effects.

We also developed a second series of models that did not include within-reserve landscape variables. In this case, we assessed the associations between landscape composition around reserves and bird distribution (Model 2), and the association between bird distribution and reserve location (Model 3). In this way, we were able to assess the possible effect of intercorrelations between explanatory variables at different spatial scales on the results.

At the level of individual species, the abundance was far from being normally distributed even after log-transformation because no observations were made in many of the reserves (see Table 1). Therefore, we used Poisson regression analysis with backward elimination of non-significant factors to investigate the effect of reserve characteristics and location on species-specific abundances of old-growth forest birds. We used the hierarchical procedure described above. In the case of Poisson regression models, we confirmed the statistical significance of each term in the selected model at each step of the procedure by comparing the residual deviance of the consecutive models with and without a particular variable (Crawley 1993). A term was kept in the model if its removal from the model resulted in an increase in the residual deviance that was significant at the  $\alpha = 0.05$  level. The change in deviance at consecutive steps was calculated using the best model in the previous step as a reference. The final model selected after the three steps was the simplest possible model explaining the largest possible proportion of the variance in the data set. The statistic used to aid in model selection was the Akaike information criterion, which takes into consideration both the change in deviance induced by a model and its degrees of freedom (Chambers and Hastie 1997). At some steps of the procedure the models were overdispersed (i.e., the variance of an observed response variable exceeds the nominal variance given the respective assumed distribution, Crawley (1993)). In such cases, we first adjusted the scale parameter by calculating the ratio of scaled deviance to the degrees of freedom and then refitted the model (Crawley 1993).

## Results

### *Bird distribution and landscape structure within reserves*

After accounting for transect length, within-reserve variables DIV (landscape diversity), OLD (old growth forest cover), and SHR (shrub cover) had significant positive effects on both the total richness and total abundance of individuals of old-growth forest species (Table 5, Figure 2). Reserve area (ARE) was negatively associated with abundance of individuals.

The influence of within-reserve landscape structure on bird distribution in forest reserves was very species dependent. The abundances of Hazel Grouse, Treecreeper, Siberian Jay, Three-toed Woodpecker and Pine Grosbeak were positively associated with the cover of old-growth forest (OLD; Table 6). The interactions of landscape variables with reserve area (ARE) were of minor importance and only the Treecreeper was more positively associated with old-growth forest cover in large reserves than in small reserves.

The amount of pine forest in the reserves (PIN) showed less influence on bird distribution than OLD but it was found to affect the abundance of some species (Table 6). The effect of the cover of pine forests was species dependent however. Two species, Crested Tit and Treecreeper showed a positive association with PIN, whereas two other species, Capercaille and Pine Grosbeak, were negatively associated with this variable (Table 6). There were few interactions of PIN with reserve area and only the abundance of one species, the Three-toed Woodpecker, was more positively associated with it in reserves of large size (Table 6).

The amount of young forest (YF) present in forest reserves did not show a consistent influence across species but rather had opposite effects on different species. The abundances of the Black Woodpecker, Crested Tit and Treecreeper were negatively associated with large values of YF in the forest reserves, whereas the opposite was detected for the Siberian Tit, Siberian Jay, Pine Grosbeak and Capercaille (Table 6). Reserve area did not strongly affect specific responses to the amount of young forest in the reserves and we were only able to detect significant interactions between these two variables for the Siberian Tit and the Treecreeper. YF was positively associated with Siberian Tit abundance especially in large reserves, whereas YF was more negatively as-



**Table 5.** Generalised linear models for the number of species and total abundance of old-growth forest species in 91 northern forest Finnish reserves. Model 1 is a hierarchical model including at each step the best predictors from previous steps. Null model included transect length in kilometres. Step 1, within reserve landscape structure; OLD PC1 in Table 3; related to the proportion of old forests, YF PC2; proportion of young forest, PIN PC3; proportion of pine forests, DIV PC4; habitat diversity, SHR PC5; proportion of shrubby forests and their interactions with ARE reserve area. Step 2, reserve location, and interaction with within reserve landscape structure. Step 3, around reserve landscape structure, OLDS PC1 in Table 4; related to proportion of old forests, YFS PC2; proportion of young forests, DECS PC3; proportion of deciduous forests, and their interactions with ARE reserve area and LOC reserve location. See methods for procedures on variable selection. Model 2 does not include within-reserve landscape variables. Model 3 only analyses the effect of reserve location. When the interaction term was significant, main effects of these variables were also included in the models, but for clarity non-significant main effects are not shown.

	Null model $\chi^2$ , df	Step 1 $\chi^2$ , df	Variables	Step 2 $\chi^2$ , df	Variables	Step 3 $\chi^2$ , df
<b>Species richness</b>						
Model 1	179.60, 89	128.54, 86	+ OLD **, + SHR **, + DIV ***	108.75, 80	LOCxOLD <sup>1*</sup> , LOCxSHR <sup>1*</sup>	– –
Model 2		130.74, 87	+ OLDS ***, + YFS ***	123.16, 85	LOCxOLDS*	
Model 3		138.50, 87	LOC <sup>2</sup>			
<b>Abundance</b>						
Model 1	131.84, 89	93.43, 85	+ OLD **, + SHR *, + DIV **, –ARE*	86.88, 81	LOCxSHR <sup>1*</sup>	– –
Model 2		101.32, 86	+ OLDS ***, + YFS ***, –ARE*	–	–	
Model 3		105.89, 87	LOC <sup>2</sup>			

1. The relationship is more positive in reserves far from the Russian border.

2. Higher values of the variable were detected in eastern reserves.

\* P < 0.05, \*\* P < 0.01, \*\*\*P < 0.001.

sociated with the Treecreper abundance in small reserves than in large ones (Table 6).

The cover of shrubs within reserves (SHR) had a positive effect on species richness (Table 5), but its effects on abundance were both positive (total abundance, Hazel Grouse, Black Woodpecker, and Siberian Jay) and negative (Crested Tit, Pine Grosbeak) (Table 6). Area (ARE) interacted with SHR to affect Hazel Grouse, Crested Tit and Pine Grosbeak abundance (Table 6).

Habitat diversity (DIV) had the most consistent positive effect on bird distribution of old-growth forest species in forest reserves. Both species richness and total abundance were positively related to habitat diversity. At the species level, we did not detect any negative associations between DIV and bird abundance and in four species, Hazel Grouse, Siberian Tit, Crested Tit and Siberian Jay abundance was positively associated with DIV (Table 6).

#### *Effects of reserve location on bird distribution*

Distance from Russia was not associated with either species richness or abundance after accounting for within-reserve landscape structure (Model 1, Table 5). On the other hand, the models including only reserve location as an independent variable (Model 3) showed that distance from Russia was significantly associated

with both species richness and abundance, both being higher in reserves in the eastern and central regions than farther west (Table 5, Figure 3). Model 3 did not prove better than Model 1 when analysing either species richness (Model 1, AIC = 299.68; Model 3, AIC = 304.47) or total abundance (Model 1, AIC = 271.50; Model 3, AIC = 278.35), however, suggesting that information contained in reserve location (LOC) alone was largely redundant and already present in the variables describing within-reserve forest landscape structure (Table 5).

In the hierarchical Model 1, we also found significant interactions of LOC with landscape variables, which indicates that landscape effects on bird distribution varied among regions. Variables OLD and SHR had a stronger positive effect on species richness in western reserves, in which overall cover of old growth is lower, and the cover of shrubby, low productive areas higher, than in the other two regions (Table 5, Figure 4). In the central and eastern regions, the relationship between OLD and species richness was very weak and a similar pattern can be observed for SHR for species richness and total abundance (Table 5, Figure 4).

Hierarchical models for individual species, which included reserve location (LOC), and its interactions with bird abundance, proved significant for six species (Step 2, Table 6). For five species we found a

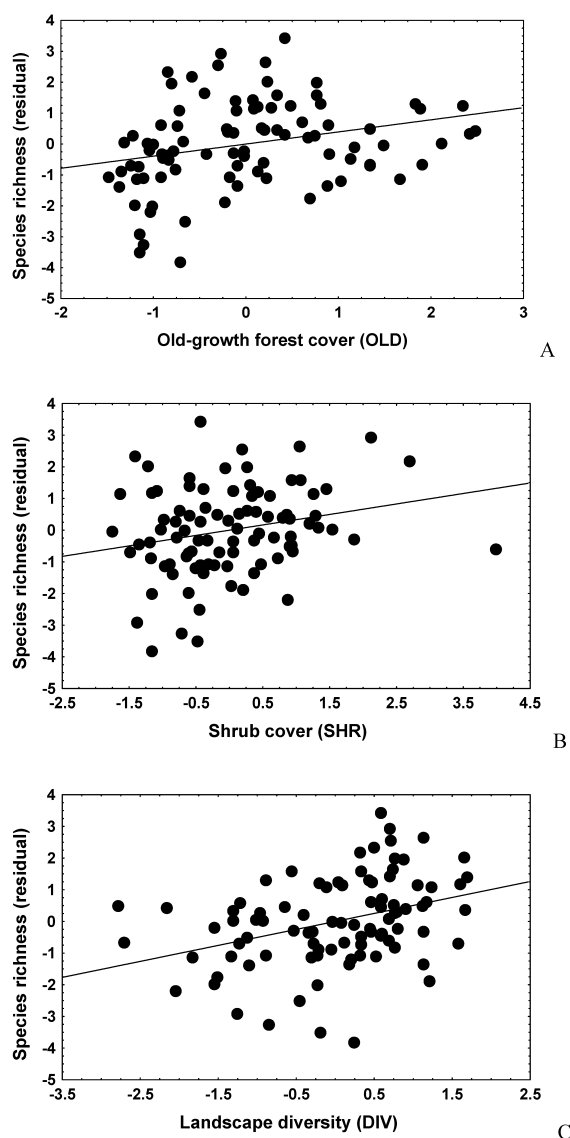


Figure 2. Relationship between residuals of old-growth forest species richness and landscape gradients after transect length and all other significant effects except the one under consideration have been included. A. Habitat diversity (DIV). B. Cover of shrub (SHR). C. Amount of old-growth forests (OLD).

significant main effect of reserve location after accounting for within-reserve landscape variables and their interaction with reserve location. The abundances of Capercaillie, Three-toed Woodpecker, Siberian Jay and Pine Grosbeak were larger in forest reserves located in the central region than in the other two regions. The Crested Tit was more abundant in reserves located in the eastern region close to Russia (Table 6). Reserve location also interacted with with-

in-reserve landscape variables to affect species abundances, but these effects were very species specific (Table 6) and clearly different from interactions involving species richness and total abundance (cf. Table 5).

#### *Bird distribution and landscape structure around the reserves*

After accounting for within-reserve landscape structure in Model 1, additional steps including variables that described the surrounding area of the reserves did not have further explanatory power (Table 5). On the other hand, the model including only these variables (Model 2), showed that OLDS and YFS were significantly and positively associated with species richness and abundance, suggesting that reserves embedded in forest-dominated landscapes foster a higher richness and abundance of old-growth forest bird species than reserves in more open landscapes. Model 2 did not prove better than Model 1 when analysing total abundance (Model 1, AIC = 271.50; Model 2, AIC = 276.34), but it was slightly better for species richness (Model 1, AIC = 299.68; Model 2, AIC = 299.22). This indicates that although a portion of the variation explaining bird distribution may be associated with landscape characteristics around the reserves, information describing these characteristics was largely redundant and already accounted for by the variables describing within-reserve landscape structure (Table 5).

Although landscape composition around forest reserves was not included in the selected models for overall species richness and total abundance, models for individual species showed that in some cases these variables had additional explanatory power to within-reserve variables in determining old-growth forest bird distribution. These relationships are very inconsistent across species. For example, the amount of old-growth forest surrounding reserves (OLDS) was significantly and positively related to the abundance of Capercaillie, Siberian Tit and Hazel Grouse in the western region. On the other hand, the amount of young forest surroundings reserves (YFS) was positively related to the abundance of Hazel Grouse and Three-toed Woodpecker but negatively related to the abundance of the Treecreeper and Crested Tit (Table 6).

Table 6. Results of Poisson hierarchical regression models best explaining the abundance of the nine old-growth forest species in northern Finnish forest reserves. Variables included at each step are as in Table 5.

	Null model $\chi^2$ , df	Step 1 $\chi^2$ , df	Variables	Step 2 $\chi^2$ , df		Step 3 $\chi^2$ , df	
<i>Bonasia bonasia</i>	153.0, 89	104.61, 84	+ OLD, + SHR, + DIV, ARExSHR <sup>3</sup> , -ARE	94.17, 79	LOCxPIN <sup>1</sup>	64.82, 82	LOCxOLDS <sup>1</sup> , LOCxDECS <sup>2</sup> , ARExYFS <sup>2</sup> , + YFS
<i>Tetrao urogallus</i>	94.2, 89	81.26, 87	-PIN, + ARE	75.75, 85	LOC <sup>5</sup>	67.82, 83	+ OLDS, ARExOLDS <sup>2</sup>
<i>Dryocopus martius</i>	129.5, 89	118.12, 87	-YF, + SHR	-	-	-	-
<i>Picoides trydactylus</i>	185.6, 89	149.08, 85	ARExPIN <sup>1</sup> , + OLD, + ARE	117.42, 80	LOCxYF <sup>2</sup> , LOC <sup>5</sup>	109.09, 78	ARExYFS <sup>2</sup> , + YFS
<i>Parus cinctus</i>	101.1, 89	52.89, 85	ARExYF <sup>1</sup> , + DIV, + YF, + ARE	-	-	48.39, 84	+ OLDS
<i>Parus cristatus</i>	250.4, 89	87.86, 83	ARExSHR <sup>1</sup> , + PIN, -YF, -SHR, + DIV	70.29, 77	LOCxYF <sup>2</sup> , LOCxPIN <sup>2</sup> , LOC <sup>6</sup>	53.66, 77	-YFS
<i>Certhia familiaris</i>	222.1, 89	119.74, 83	ARExOLD <sup>1</sup> , ARExYF <sup>3</sup> , -YF, + OLD, + PIN	-	-	85.13, 74	LOCxDECS <sup>3</sup> , LOCxYFS <sup>4</sup> , -OLDS
<i>Perisoreus infaustus</i>	157.2, 89	123.13, 85	+ OLD, + DIV, + SHR, + YF	103.61, 80	LOCxPIN <sup>4</sup> , LOC <sup>5</sup>	-	-
<i>Pinicola enucleator</i>	145.5, 89	100.41, 84	ARExSHR <sup>1</sup> , + OLD, + YF, -PIN, -SHR, + ARE	41.85, 81	LOCxDIV <sup>4</sup> , LOC <sup>5</sup>	-	-

1. The relationship is more positive in reserves far from the Russian border, or in large reserves.
2. The relationship is more positive in reserves close to the Russian border, or in small reserves.
3. The relationship is more negative in reserves far from the Russian border, or in large reserves.
4. The relationship is more negative in reserves close to the Russian border, or in small reserves.
5. Abundance higher in the central region.
6. Abundance higher in the eastern region.

## Discussion

We found that species richness and total abundance of old-growth forest bird species was strongly related to within-reserve landscape structure and that landscapes surrounding the reserves had little or no influence. Furthermore, these landscape effects were dependent on the geographic location of the reserves, most likely because of variation in topography and edaphic conditions. There was regional variation in how landscape structure was associated with species-specific abundance, suggesting non-linear responses to habitat availability. Large forest reserves closer to

the Russian border fostered more diverse and dense communities of old-growth forest birds. Our results emphasise the importance of multi-scale analyses in regional studies; a mere focus on factors at one spatial scale may yield misleading results.

### *Old-growth forest birds and landscape structure within forest reserves*

As predicted from the ecological characteristics of the species selected, the amount of spruce-dominated old-growth forest (OLD) present in the reserves positively influenced the presence and abundance of this group

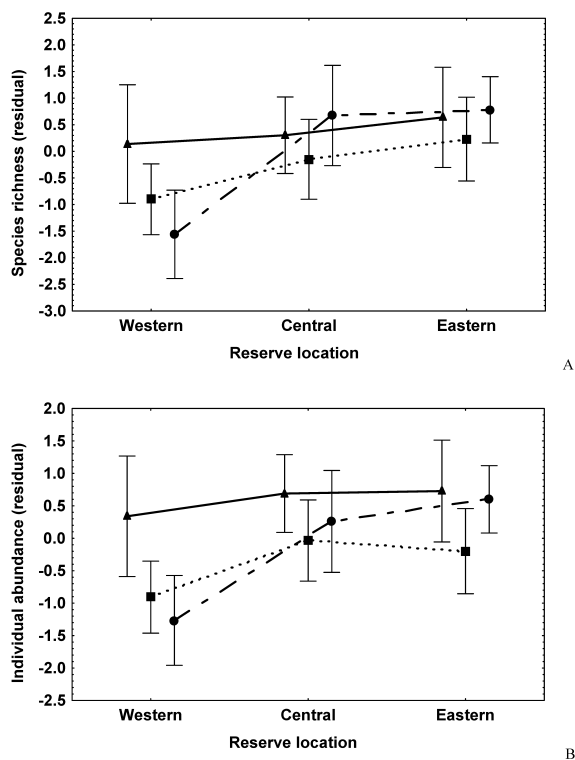


Figure 3. Species richness (A) and total abundance (B) of old-growth forest birds in relation to reserve size and regional location in the network. Both variables are represented as residuals accounting for transect length. Reserve size classes are: small reserves < 1000 ha (triangles), medium sized reserves 1000–3000 ha (squares), and large reserves > 3000 ha (circles).

of birds. Necessary resources associated with old-growth forest may either be the decaying wood itself, appropriate for foraging and cavity building (woodpeckers, Fayt (1999)), availability of nesting cavities (in cavity nesting passerines like tits and the Treecreeper, Virkkala (1987)), or berry production associated with this type of forest (Roldstad and Wegge 1989). Some old-growth forest species may be sensitive to variations in dominant tree species (Virkkala 1987). Indeed, the amount of old-growth pine forest (PIN), was positively associated with the abundance of the Crested Tit, Treecreeper and Three-toed Woodpecker in large reserves, which is consistent with the habitat preferences of these species (Snow and Perrins 1998; Fayt 1999). Other species, such as the Capercaille and the Pine Grosbeak, showed a negative relationship with the amount of pine forest in the reserves, however suggesting that species-specific responses to dominant forest type may be especially

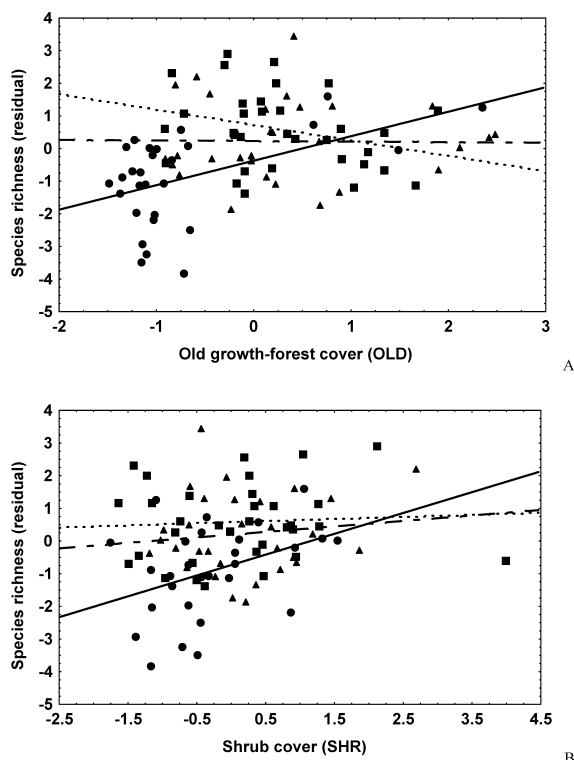


Figure 4. Relationship between residual species richness of old-growth forest bird species (after transect length and all other significant effects except the one under consideration have been taken into account) and old forest gradient (OLD); A, and residual species richness and gradient in shrub cover (SHR); B, separately for the three regions Western region, circles and solid line; central region, triangles and dashed line; eastern region, squares and dotted line.

relevant in determining the distribution of species in pine forests.

Young forests are thought to be low-quality breeding habitats for some old-growth birds in managed forests (Virkkala 1987). This has been associated with the low availability of decaying wood in young forests, which likely reduces the suitability of these areas for woodpeckers and other cavity-nesting birds (Esseen et al. (1992, 1997); Imbeau et al. 2001). The amount of young forest within the reserves (YF) was not a significant predictor of the distribution of old-growth forest birds in the reserves. More extensive stands of young forests negatively affected some species such as the Black Woodpecker, Crested Tit and Treecreeper, which provides partial support for our initial prediction. Our results suggest that in natural boreal forest mosaics, an increase of young forest area is not unambiguously linked with a decrease in the abundance of the old-growth birds studied. Spe-

cies very likely have adaptations to the natural dynamics of these landscapes (Mönkkönen and Welsh 1994) and may adapt to anthropogenic landscape changes as well, given that these do not grossly exceed the range of natural variation. On the other hand, young forests within reserves are structurally very different from silviculturally managed young forests (e.g., in terms of decaying wood, Siitonen (2001)).

In unmanaged forest reserves, forest areas with a total wood volume of less than 25 m<sup>3</sup>/ha are usually low-productivity forests dominated by stunted trees. Within reserves, this habitat class presumably corresponds to areas located along fens and bogs where edaphic conditions inhibit tree growth, or in some reserves, to high-altitude areas where climatic conditions suppress growth. This is because regeneration stands after clear-cutting are very rare within reserves unlike in the surrounding landscape. The finding of a positive relationship between the amount of these shrubby forests and the occurrence of old-growth forest birds does not support the contention that low-productivity forest, usually located in peripheral forest areas, negatively affects species of old-growth forests (Helle and Järvinen 1986; Virkkala et al. 1994). It should be kept in mind however, that the total amount of shrubby forest within forest reserves never exceeded 10% of the total area, which is low compared with the mean cover of this habitat class in the surrounding landscape (5% within forest reserves vs 15% around reserves, the latter including post-harvest sapling stands, Table 2). When a minor component of the landscape, these areas of low productivity may provide important resources for some species, unlike edges between forests and open area, which often are negatively associated with the abundance of old-growth forest birds (Jokimäki and Huhta 1996). Sjöberg and Ericson (1997) suggested that, given their predictability and stability in time and space, forest areas surrounding mires may be important feeding areas for forest birds, thereby favouring the abundance of boreal species.

Recurring disturbances such as forest fires are an essential component of the ecological dynamics of the taiga ecosystem, creating a continuously shifting mosaic of different forest types (Syrjänen et al. 1994; Esseen et al. 1997). Indeed, landscape diversity was one of the variables that was associated with old-growth forest birds within reserves. Bird species inhabiting boreal forests seem to require a combination of habitats on a fairly fine scale, rather than large, uniform forest stands (Haila 1994; Sjöberg and Eric-

son 1997). An example of a strong dependence of boreal birds on original habitat mosaic is provided by the Capercaillie (Roldstad and Wegge 1989). Females forage in swamp forests before egg laying (Storaas and Wegge 1987) and abundant invertebrate resources, which are usually found in insect-rich transitional areas such as shady spruce swamps or sunny pine bogs, is necessary for the chicks during their early development (Sjöberg and Ericson 1997). In later chick development, old-growth forests become especially important.

The structure of northern Fennoscandian forest landscapes has been heavily altered during the last decades (Haila and Järvinen 1990; Esseen et al. (1992, 1997)). In particular, because of forestry practices, forest age structure is strongly biased to young forest stands at the expense of older stands, which are very scarce. Our results, derived from seminatural-forested landscapes, support the hypothesis that a decrease in old-growth forest cover is involved in the recent declines in populations of this group of birds. Furthermore, since mosaic patterns in natural landscapes affect the distribution of old-growth forest birds, we suggest that a general change in landscape diversity in managed forests, decreasing the availability or the combination of particular habitat types in the landscape, may also have played a significant role in the decrease of some of these species. Future forestry practices aimed at mimicking natural landscape disturbance regimes (Mönkkönen 1999) should emphasise the maintenance of particular features, such as natural edges and habitat diversity, in order to create landscapes more appropriate for old-growth bird species.

#### *Old-growth forest birds and landscape composition around forest reserves*

Landscape characteristics around forest reserves might have a significant, but secondary role in determining species distribution within forest reserves. The proportion of old-growth forest surrounding reserves was positively associated with the occurrence or the abundance of species such as the Siberian tit, Capercaillie, and Hazel grouse, especially in the western region where old-growth forests are more scarce. Therefore, the availability of old-growth forests surrounding the reserves may interact with intrinsic reserve characteristics in determining its species pool (Virkkala 1991). A larger availability of old-growth forest around reserves may facilitate dispersal,

thereby increasing the probability of individual immigration into the reserve (Desrochers et al. 1999). Overall models of species richness and total abundance of individuals did not include any variable describing landscape structure surrounding forest reserves however, indicating again that either the effect of buffer zones on bird distribution is limited, or, as suggested by species-specific models, that its effects are not consistent across species. Variation in the effect of the amount of young forest present in the areas surrounding the reserves on old-growth forest bird distribution, reflects differences among species in the capability of using young forests as adequate breeding habitat (see above), or dispersal habitat (Desrochers et al. 1999).

#### *Reserve area and location*

Overall, the abundance of old-growth birds was negatively related to reserve area. Large reserves were, on average, situated on less-productive soils than small reserves (Nilsson and Götmark 1992; Virkkala et al. 1994) which could contribute to higher densities in small reserves. This is supported by our data which showed that small forest reserves have more mixed spruce-deciduous forests than larger reserves ( $F_{1,89} = 4.105$ ,  $p < 0.005$ ,  $r = 0.21$ ). Not all species abundances were higher in small reserves however; the Capercaille, Three-toed Woodpecker, Siberian Tit, and Pine Grosbeak were more abundant in large reserves, suggesting a positive effect of area on their numbers (Virkkala et al. 1994).

The significance of interactions between reserve location and landscape variables on the occurrence or abundance of species stresses the importance of landscape context in determining species' distributions (Mönkkönen and Reunanen 1999). Landscape-specific responses of species to habitat availability are likely to arise if the habitat availability is related non-linearly to the density of the species (Andrén 1994). Andrén's original result was that in landscapes with more than 30% of habitat available, habitat availability is the only factor affecting species occurrence, but below 10–30%, patch size and isolation effects start appearing. In our study, the amount of old-growth forest within reserves was more positively associated with species richness in the western region, far from the Russian border, than in the regions closer to Russia, where the relationship was sometimes negative. Because total old-growth forest cover varies with distance from the Russian border (see Table 2), our re-

sults suggest a non-linear response by the old-growth forest birds to habitat availability. In the eastern and central regions, the total coverage of old-growth forest was above 30%, whereas in the western region it was only about 12%. Therefore, although a higher proportion of old-growth forest generally had positive effects on the species studied, our results suggest that above a certain threshold level, the amount of old-growth forest is not a clear determinant of the occurrence or abundance of these species, which is supported by other studies in boreal forest (Edenius and Elmberg 1996).

Our results also indicated the positive effect of increasing shrub cover on old-growth forest birds was stronger in reserves located in the western region. This suggests that in habitat mosaics with high proportions of peatland and bogs, the presence of small amounts of shrub stands may have a significant effect on bird distributions. Species considered most dependent on old-growth forest however, were scarce in the western region (Siberian Tit, Crested Tit, Pine Grosbeak) and tended to be negatively related to the amount of shrub forest. Therefore, it may be that the positive effect of shrub cover in such areas was derived from the rest of the species being positively associated with the amount of shrub. This is partially supported by the species-specific effect of shrub forests on bird abundance (see Table 6). The additional effects of reserve location on the relationship between the amount of old-growth forest or shrub and bird distribution were not seen in many species, suggesting a cumulative effect of species preferences.

#### *Russian forests as a source for old-growth forest birds*

Source-area hypothesis predicts that the distance to the intact boreal forests of Russia would remain a significant predictor of bird abundance after other landscape and isolation variables have been included in the model (Kouki and Väänänen 2000). Our results showed increasing species richness and total abundance of old-growth forest species toward the Russian border, independent of reserve area. After including landscape gradients however, we found that only one species was still relatively more abundant in the eastern region, whereas four species were relatively more abundant in the central region and none in the western region. The finding of a relatively higher abundance of some old-growth forest birds in reserves located in the central region may be attributed to its

special landscape features and edaphic conditions. Reunanen et al. (2002) (in press) studied the same regions included in our study and found that the Flying squirrel (*Pteromys volans*), an arboreal mammal typical of old-growth forests, was more abundant in the central region, because of the larger proportion of mixed old-growth forest, where deciduous trees played an important role.

The amount of old-growth forest and landscape diversity are the most important factors affecting the distribution of old-growth forest birds. These variables showed clear east-west gradients in our study region, such that stronger positive associations were found in eastern reserves closer to the intact boreal forests of Russia. This suggests that even large reserves in the western parts of Finland are suffering a loss of boreal species if the overall cover of old-growth forest is small and fragmented. Therefore, the existence of natural east-west gradients in species distribution and the changes in landscape structure associated with distance from the Russian border, confounds the relationship between the distance from a hypothetical source area (intact boreal forests of Russia) and bird abundance. The Russian Karelia does not appear to be a widespread source for old-growth forest birds in northern Finnish forest reserves. To test this further, the source-area hypothesis would need a more fine-grained, population level study focussed on the population dynamics and the movement patterns of individuals at shorter distances from the hypothetical source areas. Still, large tracts of old-growth forests in Russia have an intrinsic high conservation value and may function as a regional corridor for old-growth forest species, favouring the occurrence of species in certain regions (Lindén et al. 2000), rather than increasing their abundance at more local levels.

An alternative explanation to the lack of a significant relationship between bird distribution and distance to the Russian border might be the role that large forest reserves have as source areas for old-growth forest birds. Habitat availability at the regional level may help to maintain higher regional densities of birds for reasons linked to source-sink effects and/or to enhanced dispersal abilities (e.g., from Russian forests). We could not separate the effects of regional-level habitat availability and reserve location effects because these two are intercorrelated. Future demographic studies analysing the possible role of old-growth forest-dominated landscapes as source areas for old-growth forest birds, both in and outside forest reserves, are required to assess to what

degree these areas may sustain source populations at the regional scale.

#### *Concluding remarks*

The results obtained in this study provide new insights for the design and implementation of conservation networks for old-growth forest birds. First, our results suggest that regional differences in landscape structure should be taken into account. The positive effect of the amount of old-growth forests on the distribution of bird species was stronger in areas with a low overall availability of old-growth forest in the landscape (western region). Increasing old-growth forest in such a landscape is likely to be effective for maintaining old-growth forest birds. In regions where habitat availability is not a limiting factor for forest birds (central and eastern regions) it would be more effective ensure the continued existence of natural habitat mosaics (i.e., landscape diversity). This would include landscape elements such as 'soft' edges between forest and open habitat (shrubby, low-productive forests).

Second, we observed only weak (but generally positive) effects of the amount of surrounding forest buffering reserves on old-growth forest bird distribution, suggesting that the immediate surroundings of the reserves are secondary to within-reserve landscape composition. Therefore, retaining intact old-growth forest remnants is effective even though located within a severely harvested matrix. The overall landscape structure where reserves are embedded certainly has an effect on the composition of bird assemblages in forest reserves (Väisänen et al. 1986), but this effect seems to work on a regional (rather than local) scale. Virkkala (1991) suggested that in very large boreal forest reserves (> 1000 km<sup>2</sup>), bird populations are buffered against impacts from the surrounding area.

Third, our results showed that the source-strength of the extensive old-growth forest bird populations of Russia may not be as strong as previously suggested. This emphasises the importance of maintaining a national reserve network for Finnish bird populations (but does not undermine the importance of Russian Karelian forests as the westernmost large remnant of once continuous taiga). Sustaining old-growth forest bird populations in northern Finland primarily depends on preserving habitat availability and quality within Finnish landscapes.

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