



# Examensarbete i ämnet biologi

2011:8

## **Is old forest like old forest?**

**Patterns in abundance and species number of resident birds in old boreal forest stands in relation to stand structure and landscape context**

**Ortrud Leibinger**



Photo: Willow Tit *Poecile montanus* (Lars Edenius)



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## **Is old forest like old forest?**

**Patterns in abundance and species number of resident birds in old boreal forest stands in relation to stand structure and landscape context**

## *Är äldre skog verkligen äldre skog?*

*Mönster i förekomst och artantal av stannfåglar i äldre boreal skog i relation till beståndsstruktur och landskapskontext*

**Ortrud Leibinger**

Keywords: resident birds, boreal forest, habitat, declining species

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## Abstract

Forest structure and composition may be, dependent on e.g. soil conditions, human impact and forest age, very different, which might result in differences in abundance and species number of resident forest bird. Because of the adverse effects of modern forestry on resident bird species preferring old growth forest, nature reserves and adapted forest management are needed. However, the planning of such measures requires an understanding of the factors determining occurrence and abundance of resident forest birds. The aim of this study was to identify habitat variables that are particularly important for the abundance and species number of resident birds in old boreal forest patches ( $\geq 80$  years) in the context of two different forest landscapes in northern Sweden.

Habitat variables known to be varying with forest age, productivity and degree of human impact were chosen: basal area, basal area of large trees ( $\geq 40$  cm diameter at breast height), coefficient of variation of basal area, basal area of deciduous trees and forest type (pine vs. spruce dominated forest). Generalized linear models were applied to relate the habitat variables, stand area and the factor landscape to abundance and species number data of resident birds, which were obtained by point counts. Besides total abundance and species number abundances of the most abundant single species (*Parus major*, *Poecile montanus*, *Certhia familiaris* and *Loxia spp.*) and functional bird groups (foliage and trunk gleaners, hole nesters and declining species) were analyzed.

The total species number and the abundance of the declining species were positively affected by basal area, which was used as indicator for the productivity of the forest and tree canopy closure. The basal area of large trees had a positive effect on the total abundance and on the abundance of foliage and trunk gleaners. Because the basal area of large trees was not positively correlated with stand age and site productivity (potential annual timber volume production) it was regarded as indicator for the management intensity of the stands. Total abundance and species number were also positively affected by the area of the investigated stands. Although the total abundance tended to be larger in the less managed landscape, no significant effect of landscape was observed.

The effect of basal area on the total species number suggests that productive forests are needed to maintain the whole spectrum of resident bird species. Moreover, productive forests seem to be important for the declining species among the resident birds in the study area. The effect of large trees on total abundance and the abundance of the foliage gleaners might be explained by the greater structural complexity of forests with low management intensity. The results of this study suggest that resident bird species in the study area would benefit from protection and/or restoration of productive and structural complex forests.

## **Introduction**

### **Why resident birds?**

Due to limited food resources in winter, resident birds preferring old growth forest as habitat are thought to be particularly sensitive to habitat loss and alteration by intensive forest management (Lack, 1954; Fretwell, 1972; Helle & Järvinen, 1986; Virkkala, 1991). Indeed, studies in the boreal forest report a decline of some resident bird species preferring structurally complex old-growth forest (e.g. Virkkala, 1991; Ottvall et al., 2009). Noticing the adverse effects of forestry not only on resident birds but on biodiversity in general, there has been growing effort to maintain biodiversity by creating nature reserves and adapted forest management (Angelstam & Andersson, 2001). However, this requires an understanding of the factors underlying patterns in abundance and species number of resident forest birds. In this study I investigated structural attributes of old forest stands of potential importance to the abundance and species number of resident birds in the context of two different forest landscapes in northern Sweden.

### **Is old forest like old forest?**

The term old-growth forest is a very vague description of how the forest actually looks like. Depending on soil conditions, human impact and forest age e.g. tree volume, the number of large diameter trees, the proportion of deciduous trees, the amount of dead wood and canopy closure may be very different (Liira & Kohv, 2010). In general the structural complexity of the forest, increases with increasing stand age and decreases with the degree of human impact, such as forest management.

The existence of certain structural components of old forests is an important determinant for habitat suitability for many resident bird species preferring old forest. Since winter is regarded to be the critical, population limiting season for resident birds, due to the combination of food scarcity and low temperatures (Forsman & Mönkkönen 2003), food supply might be particularly important. The occurrence of old lichen rich conifers is important for the food hiding behavior shown by some tits (Haftorn 1954, 1956) and the Siberian Jay (Edenius, 2006). The Siberian Jay is dependent the entire winter on the hoarded food. Moreover the abundance and species richness of invertebrates is higher in old lichen rich natural spruce forests compared to younger lichen poor, selectively logged and thinned forests (Pettersson, et al. 1995). Food supply increases also with forest productivity, indicated by a high timber volume (Jokimäki & Huhta 1996). Productivity of the habitat is particularly important for the survival and successful reproduction of resident forest birds in harsh northern conditions.

An important feature of structural complex forests from the bird's point of view is the layering of the forest. A multi-layered forest provides more cover from avian predators, such as the Goshawk, than a single-layered forest (Edenius & Meyer, 2002). According to Griesser et al. (2007), increased predation and nest predation caused by thinning of the forest is a reason for the reduction of reproductive success and decline of the Siberian Jay and possibly many other forest bird species. Furthermore, the number of large living conifers and deciduous trees is reduced in managed forest, due to past and present forestry (Esseen et al., 1997; Östlund et al., 1997). Those trees are important for nest construction by woodpeckers and some birds of prey (Esseen et al., 1997).

## Objective of the study

The objective of this study is to examine the patterns in abundance and species number of resident birds in old boreal forest stands in relation to habitat variables of the investigated stands and in the context of two different forest landscapes. The analysis is aimed to identify those habitat variables that could best explain the observed patterns in resident bird abundance and occurrence. In order to reach this aim, habitat variables known to be varying with forest age, productivity and degree of human impact were chosen. The resident bird species were also grouped into functional groups to be able to study the habitat relationships of the resident bird species more specific.

### *Functional groups*

The functional trait approach was chosen, because traits shared by many species could give better insights into limiting habitat factors. Foliage and trunk gleaners (hereafter `gleaners`) and cavity and bark nesters (hereafter `hole nesters`) were analyzed separately. According to Järvinen et al. (1977) the total density of the foliage gleaning guild inhabiting mainly coniferous forest habitats declined by ca. 80% from 1945 to 1975. The availability of nest cavities and dead trees for cavity nesting bird species is greatly reduced in managed forests compared to natural forests (Virkkala, 2004). A group consisting of species declining over the ten years period (1997-2006) according to Ottvall et al. (2009) (hereafter `declining species`) were also analyzed. This group was selected in order to investigate if there is a common factor that affects their abundance in the study area.

### *Habitat variables and predictions for their effects from the literature*

The forest habitat variables chosen as independent variables for the analysis are known to be varying with forest age, productivity and degree of human impact (Östlund et al. 1997; Liira & Kohv 2010). The selected habitat variables were basal area, basal area of deciduous trees, coefficient of variation of basal area, basal area of large trees (trees greater than 40 cm diameter at breast height), forest type and stand area.

The basal area was used as proxy for tree stocking, i.e. as an index for the timber volume and tree canopy closure. A high timber volume can be translated in a high number of branches and trunks, which probably favors food availability (Forslund, 2003). Thus the basal area can be used as indicator for forest productivity. A closed tree canopy provides also more cover from predators. Because food resources are crucial for successful overwintering and reproduction (Jokimäki & Huhta, 1996) and predator cover is important for survival, the basal area might have a positive effect on abundance (table 1). The species number might also increase with increasing basal area, i.e. forest productivity. There are several possible mechanisms that might explain the relationship between productivity and species richness (for a good summary see Honkanen et al., 2010 and sources therein).

Liira & Kohv (2010) found the basal area of large trees to be positively related to forest age and negatively to the management intensity of the forest. Since old natural forests are more structural complex than younger managed forests and provide thus higher habitat suitability for resident birds preferring old-growth forest, the basal area of large trees might be positive related to abundances and species number (table 1). The coefficient of variation of basal area indicates the variation in tree canopy closure, which comprises one possible part of habitat heterogeneity in natural forests (Esseen et al., 1997). As habitat heterogeneity is known to be positively related to species richness (MacArthur & MacArthur, 1961; Roth,

1976), the species number might increase with increasing coefficient of variation of basal area (table 1).

Deciduous trees contribute due to their physical structure to habitat heterogeneity in coniferous forest. Thus the basal area of deciduous trees might have a positive effect on the species number (table 1). The effect on the total abundance is unclear, because many resident bird species of northern Sweden prefer feeding in coniferous trees, especially in winter time (Jokimäki & Huhta, 1996; BWPi 2.01, 2008). Spruce dominated forests might have higher abundances than pine dominated forests, because spruces might support due to their physical structure higher insect densities, provide more niches for food hoarding and more cover against predators (Edenius & Meyer, 2002). The higher structural complexity and the higher food supply in spruce dominated forests might also lead to an elevated species number (table 1).

It can be expected that the total species number will increase with increasing stand area, as this is predicted by different underlying theories, such as the island biogeography theory (MacArthur & Wilson, 1963), the area based sampling hypothesis or the habitat heterogeneity hypothesis (Conner & McCoy, 1979) (table 1). However, it is difficult to state a clear expectation about the abundance, because different hypothesis lead to different predictions. The density compensation hypothesis (MacArthur et al., 1972) leads to the prediction that density decreases with increasing species richness, which increases with increasing area. The resource concentration hypothesis (Root, 1973) leads to the converse prediction that the density increases with increasing area of preferred habitat patches.

Finally, the properties of the landscape in which the stands are located can affect resident bird abundance and species number on stand level. Landscapes may naturally differ in overall productivity, forest type composition, altitude, topography and natural fragmentation of forest by e.g. wetlands or water. Additionally depending on forestry impact on the landscape the proportion of old forest and its fragmentation by clear-cuts and young forest may vary between landscapes. This all together may affect bird occurrence and abundance patterns on stand scale. Because the study was conducted in only two different landscapes (i.e. landscape is not replicated), it will not be possible to explain which landscape properties caused a potential effect of landscape. Therefore, I will not make a prediction concerning the landscape effect. However, testing for an effect of landscape in this study can give at least a hint if landscape properties have to be considered, besides stand structure and composition, when planning nature conservation measures.

## **Materials and Methods**

### **Study area and study design**

The study was conducted in Ekopark Rosfors and its more intense managed reference landscape Kloken in northern Sweden (65°35'N, 21°27'O and 65°57'N, 21°7'E, respectively). The distance between the two landscapes, located in the northern boreal vegetation zone (Ahti et al., 1968), was 45 km. The mean altitude and mean site productivity (potential annual timber volume production) in Rosfors is 88 m and 3.6 m<sup>3</sup>/ha and year and in Kloken 165 m and 3.5 m<sup>3</sup>/ha and year. The total forest area in Rosfors is

**Table 1** Predictions from the literature for the effects of independent variables used in generalized linear models relating resident bird abundance and species number to habitat variables at the bird survey points as well as to stand area, forest type and location of the investigated stands (n = 23). Explanations see text. '+'/'-' indicates the expected sign of the effect, '0' that no effect is expected and '?' that no prediction is made.

| Functional group  | Type of dependent variable | BA | BA of deciduous trees | CV of BA | BA of large trees <sup>1</sup> | forest type <sup>2</sup> | area |
|-------------------|----------------------------|----|-----------------------|----------|--------------------------------|--------------------------|------|
| Gleaners          | A                          | +  | ?                     | 0        | +                              | +                        | ?    |
| Hole nesters      | A                          | +  | ?                     | 0        | +                              | +                        | ?    |
| Declining species | A                          | +  | ?                     | 0        | +                              | +                        | ?    |
| All residents     | A                          | +  | ?                     | 0        | +                              | +                        | ?    |
| All residents     | S                          | +  | +                     | +        | +                              | +                        | +    |

BA Basal area, m<sup>2</sup>/ha

CV Coefficient of variation (SD/Mean)

A Abundance

S Species number

<sup>1</sup> log(BA trees > 40 cm diameter at breast height + 0.01)

<sup>2</sup> '+'/'-' indicates significantly higher/lower abundances or species numbers in Norway spruce dominated forest compared to Scots pine dominated forest

2459 ha of which 55% (1354 ha) is old ( $\geq 80$  years), 13% middle aged (20-80 years) and 32% young forest and clear cuts (0-20 years). The respective values for Kloken are 6882 ha, 29% (2015 ha), 48% and 22%. Kloken is dominated by pine forest whereas in Rosfors spruce and pine forests comprise about the same proportion.

For the purpose of this study I defined old forest as 80 years and older and forests with at least 60% spruce or pine as spruce or pine dominated forest. Eight small stands (5-10 ha) and four larger stands (10-17 ha) were selected in each landscape on the basis of forest data provided by Sveaskog (12 stands per landscape = 24 stands in total = 24 replicates in total). The eight small stands were divided in four spruce dominated stands and four pine dominated stands and the four larger stands in two spruce dominated stands and two pine dominated stands. I tried to keep a minimum distance between the selected stands of at least 250 m. However, this was not always possible. Since some previous selected stands were cut or had a not fitting tree species composition, I had to fall back on alternative stands. In the end two small pine stands remained only 67 m apart from another. Therefore I decided to randomly select only one of them for the analyses, which reduced the total number of replicates from 24 to 23. The selection of the stands had to take place for good accessibility rather than random distribution, because the travelling to the stand was made by ski.

One bird survey point was allocated in the small stands and two in the big stands, so that the distance to the edges was maximal, but in no case less than 50 m. The minimum distance between the two bird survey points in the larger stands was set to 100 m. Narrow stands where the compliance of the minimum distance to the edges was not possible were excluded. The location of the bird survey points were selected not randomly, because the size and shape of most stands in combination with the 50 m condition for the distance to the edges left not much leeway for random selection.

The mean age and the mean site productivity (both extracted from the forest data) of the selected stands was 114 years (80-156 years) and 3.5 m<sup>3</sup>sk/ha (2-5 m<sup>3</sup>/ha and year), respec-

tively. The mean site productivity of the selected stands reflects the mean site productivities of the both landscapes reasonably well. The data for stand area can be found in table 2.

### **Bird census and measurement of habitat variables**

Bird data were obtained in single visits by 8 min point counts during the 3<sup>rd</sup> – 25<sup>th</sup> of April 2011, 6 – 10 AM. Five minutes census without song playback was directly followed by 3 min census initiated by 20 seconds song playback of Pygmy Owl *Glaucidium passerinum*. The birds were allowed to settle 1-2 min before the census started. Resident bird species and all other bird species within and outside a 50 m radius from the bird survey point, observations before and after the song playback and overflying birds were recorded separately when first detected. An observation during the second count period (initiated by song playback of Pygmy Owl) was only noted when it was relatively sure that it was a new individual, which was not counted previously. All bird censuses were carried out by the author. I am an inexperienced observer, but I trained intensive with song playbacks and in the field before the study. Since species differ in detectability, the counted numbers should be considered as indices of relative abundance.

Habitat variables were measured by a relascope at the bird survey point and at two additional survey points located approximately 20 m (measured by feet) either north and south or east and west (determined randomly by coin flipping) of the bird survey point. In a few cases the location of one or both additional survey points were subjectively altered, because forest structure and composition at the randomly selected location were not at all representative for the stand or the randomly selected survey points were not accessible (due to a steep slope or a creek). The measured habitat variables were basal area and basal area of trees greater 40 cm diameter at breast height for each tree species separately.

### **Data treatment and statistical analyses**

In order to test the relationships of the bird variables with the habitat characteristics at the bird survey point only observations within the 50 m radius were included in the analyses. The observations from both count periods were added for the analyses. All over-flying birds and uncertain identifications were removed from the analyses. Since the experimental units were the stands, the observations of the two bird survey points in the larger stands were averaged for the analyses (decimals were rounded up). All species with less than five records in total (after averaging the observations of the two bird survey points in the larger stands) were not analyzed at the species level, but these observations were included in the functional groups for the analyses. Because the two *Loxia* species are hard to distinguish in the field, all *Loxia spp.* observations were pooled prior the analyses. The analysis of the declining species was done inclusive and exclusive the Willow Tit, because this species comprised more than half of the individuals in the group and might therefore cover patterns in the other less common species.

The measured habitat variables were averaged across the three survey points in the small stands and the six survey points in the big stands. The coefficient of variation of the total basal area was calculated over the three or six survey points, respectively.

In order to test for correlations between the independent variables the Pearson correlation coefficient was calculated (appendix table 6). There were no correlation coefficients greater than 0.7 among the independent variables and thus the data were regarded as sufficiently



uncorrelated for including them all together in one model. The normality of all variables were also tested (Anderson-Darling-Test). Almost all bird variables deviated from normal distribution, as can be expected from count data of a low sample size. Among the habitat variables only the basal area of large trees was not normally distributed. In order to correct the deviation from normality, this variable was log transformed prior the analyses.

Generalized linear models (GLM) with Poisson errors and log link were applied for the analyses. Bird abundances and total species number were entered in the models as response variables and the habitat variables and stand area as continuous explanatory variables. Landscape and forest type were included as binary factorial explanatory variables. Modeling was done by backward model simplification. First I did automatic model simplification by using the `step` command in R (R Development Core Team, 2010; R Version 2.12.0), which uses Akaike's Information Criterion (AIC) for dropping factors from the model. Since AIC is not appropriate for low sample sizes, the respective second-order AIC-values (AICc), which adjusts for low sample size, were calculated afterwards using the `AICc.glm` command of the AICcmodavg-package. This AICc-values were used to verify the results obtained by `step`, which revealed that the results obtained by `step` were correct. The model obtained by `step` was checked for non-significant parameter estimates and if necessary further simplified. This was done by removing stepwise the variable where the parameter estimate had the highest p-value (z-test) from the model until only significant parameter estimates remained in the most parsimonious model. The full model and the final model were checked for over-dispersion, but this was not a problem in any case.

## Results

### Habitat variables at the bird survey points

Forest structure and composition at survey points as well as of the whole stands were often very heterogeneous. Thus the proportion of the dominating tree species averaged across the survey points were in seven out of 23 stands below the threshold of 60% originally set for the site selection based on the forest data. The measured tree species composition might be thus not representative for the whole stand. The measured mean proportions of the dominating tree species were 61% (46-75%) and 68% (43-93%) of basal area for Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, respectively. However, Norway spruce or Scots pine, respectively, was still the most abundant tree species. The proportions of basal area of other tree species at the bird survey points in Norway spruce dominated stands were 1-32% Scots pine, 1-38% birch *Betula spp.*, 0-5% aspen *Populus tremula* and 0-1% willow *Salix spp.*. The respective values for Scots pine dominated stands are 4-32% Norway spruce, 0-30% birch, 0-8% aspen and 0-5% willow.

The mean value, standard deviation, coefficient of variation, median and range of the habitat variables at the bird survey points for usage as independent variables in the generalized linear models can be found in Table 2. Scots pine had with 47% the biggest share of the basal area of large trees, followed by aspen (39%), Norway spruce (9%) and birch (4%). Large trees and deciduous trees occurred in 11 and 21 out of the 23 stands, respectively.

The mean stand area of 9.4 ha is probably smaller than the breeding territory of many of the investigated resident bird species. However, for this study is assumed that a bird spends most of the time in the investigated stands and uses the surrounding stands only for insignificant periods of time.

**Table 2** Habitat variables and stand area for usage as independent variables in generalized linear models relating resident bird abundance and species number to habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands (n = 23).

| Variable                    | Mean | SD   | CV   | Median | Range       |
|-----------------------------|------|------|------|--------|-------------|
| BA                          | 23.4 | 6.8  | 0.29 | 24     | 13 - 35     |
| CV of BA                    | 0.19 | 0.10 | 0.51 | 0.16   | 0.06 - 0.40 |
| BA of deciduous trees       | 4.2  | 3.2  | 0.76 | 3      | 0 - 11      |
| BA large trees <sup>1</sup> | 0.54 | 0.75 | 1.39 | 0      | 0 - 2.67    |
| Area, ha                    | 9.4  | 3.8  | 0.40 | 8      | 5 - 17      |

BA Basal area, m<sup>2</sup>/ha

SD Standard deviation

CV Coefficient of variation (SD/Mean)

<sup>1</sup> log(BA trees > 40 cm diameter at breast height + 0.01)

### Bird abundance and species number

In total 268 bird observations of 17 resident bird species were made (both count periods, excl. overflying birds). Out of this, 137 (51% of the total observations) bird observations of 11 species were made within the 50 m radius. Great Tit *Parus major*, Willow Tit *Parus montanus* and Crossbills *Loxia spp.* were with 25%, 25% and 23%, respectively, the most abundant species within the 50 m radius, comprising thus ca. 75% of all bird observations. 10 % of all individuals (incl. short distance migrants) within the 50 m radius remained unidentified and were totally excluded from the analysis. Approximately 50% of the observations within the 50m radius were made during the second count period (initiated by song playback of Pygmy Owl). However, the bird reaction to the song playback was very different and varied from no reaction over moderate reaction to strong reaction. In some cases all observations within the 50 m radius are from the second count period. Thus, the song playback was in general very useful to increase the number of bird observations.

The mean abundance, standard deviation, coefficient of variation, median, range, number of stands with occurrence and designation into functional groups of the species detected within the 50 m radius can be found in Table 3. The corresponding values for the functional groups are given in Table 4.

### Generalized linear model analysis

Five out of nine models revealed significant effects for three of seven independent variables (table 5, appendix table 7). Basal area was the most frequent significant explanatory variable and was included in three models, followed by basal area of large trees and area included in two models. The models for the `declining species`, incl. and excl. Willow Tit, revealed both a positive effect of basal area (both  $P < 0.05$ ). Both models for `all residents` (abundance and species number) included a positive effect of area (both  $P < 0.05$ ), whereas the model of the abundance included additionally a positive effect of the basal area of large

trees ( $P < 0.01$ ) and the model for the species number a positive effect of basal area ( $P < 0.05$ ). The model for the group 'gleaners' revealed a positive effect of the basal area of large trees ( $P < 0.05$ ). The single species models and the models for the group 'hole nesters' revealed no significant effect of one of the explanatory variables.

**Table 3** Total sample size and mean abundance within a radius of 50 m with standard deviation, coefficient of variation, median and range as well as number of stands with occurrence and designation into functional groups of residents bird species detected during 8 min point counts in old boreal forest stands ( $n = 23$ ). For detailed description of the method see text. The data for Great Tit, Willow Tit, Tree Creeper and Crossbills will be used as dependent variables in generalized linear models in relation to stand habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands.

| Species                  | Scientific name              | N <sup>1</sup> | Mean | SD  | CV  | Median | Range | Occ <sup>2</sup> | Group <sup>3</sup> |
|--------------------------|------------------------------|----------------|------|-----|-----|--------|-------|------------------|--------------------|
| Great Tit                | <i>Parus major</i>           | 24             | 1,0  | 1,0 | 1,0 | 1      | 0 - 4 | 18               | H, G               |
| Willow Tit               | <i>Poecile montanus</i>      | 24             | 1,0  | 1,2 | 1,2 | 1      | 0 - 3 | 12               | D, H, G            |
| Coal Tit                 | <i>Periparus ater</i>        | 4              | 0,2  | 0,5 | 2,8 | 0      | 0 - 2 | 3                | D, H, G            |
| Crested Tit              | <i>Lophophanes cristatus</i> | 1              | 0,04 | 0,1 | 3,3 | 0      | 0 - 1 | 2                | H, G               |
| Goldcrest                | <i>Regulus regulus</i>       | 3              | 0,1  | 0,3 | 2,4 | 0      | 0 - 1 | 4                | D, G               |
| Tree Creeper             | <i>Certhia familiaris</i>    | 7              | 0,3  | 0,5 | 1,8 | 0      | 0 - 2 | 7                | D, H, G            |
| Great Spotted Woodpecker | <i>Dendrocopus major</i>     | 3              | 0,1  | 0,3 | 2,6 | 0      | 0 - 1 | 3                | H                  |
| Eurasian Bullfinch       | <i>Pyrrhula pyrrhula</i>     | 4              | 0,2  | 0,5 | 2,8 | 0      | 0 - 2 | 3                |                    |
| Crossbills               | <i>Loxia spp.</i>            | 21             | 0,9  | 1,1 | 1,2 | 1      | 0 - 3 | 12               |                    |
| Hazel Grouse             | <i>Tetrastes bonasia</i>     | 2              | 0,1  | 0,2 | 2,8 | 0      | 0 - 1 | 3                |                    |
| Siberian Jay             | <i>Perisoreus infaustus</i>  | 4              | 0,2  | 0,5 | 3,0 | 0      | 0 - 2 | 3                | D, G               |

N Total sample size after averaging the abundance values of the two bird survey points in the larger stands

SD Standard deviation

CV Coefficient of variation (SD/Mean)

H 'hole nesters' (Cavity and bark nesters)

D 'declining species' [Species declining over the ten years period (1997-2006) in Ottvall et al. (2009)]

G 'gleaners' (Foliage and trunk gleaner)

<sup>1</sup> After averaging the observations of the two bird survey points in the larger stands (decimals were rounded up)

<sup>2</sup> Number of stands with occurrence

<sup>3</sup> All species are pooled in the group 'all residents'

**Table 4** Mean abundance within a radius of 50 m with standard deviation, coefficient of variation, median and range as well as number of stands with occurrence of functional groups of resident bird species detected during 8 min point counts in old boreal forest stands (n = 23). For detailed description of the method see text. Designation of species into functional groups see Table 3. The data will be used as dependent variables in generalized linear models in relation to stand habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands.

| Group                      | Type of dependent variable | Mean | SD  | CV   | Median | Range  | Occ <sup>1</sup> |
|----------------------------|----------------------------|------|-----|------|--------|--------|------------------|
| Gleaners                   | A                          | 2.9  | 1.9 | 0.66 | 3      | 0 - 8  | 22               |
| Hole nesters               | A                          | 2.7  | 2.0 | 0.74 | 2      | 0 - 8  | 21               |
| D incl. <i>P. montanus</i> | A                          | 1.8  | 1.4 | 0.76 | 2      | 0 - 4  | 19               |
| D excl. <i>P. montanus</i> | A                          | 0.8  | 0.9 | 1.12 | 1      | 0 - 3  | 13               |
| All residents              | A                          | 4.3  | 2.5 | 0.58 | 3      | 1 - 11 | 23               |
| All residents              | S                          | 3.0  | 1.4 | 0.46 | 3      | 1 - 5  | 23               |

SD Standard deviation

CV Coefficient of variation (SD/Mean)

D `declining species` [Species declining over the ten years period (1997-2006) in Ottvall et al. (2009)]

A Abundance

1 Number of stands with occurrence

**Table 5** Results of generalized linear models relating resident bird abundance and species number to habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands (n = 23). Indicated are the signs and significance niveaus of the parameter estimates for significant effects, whereas `0` means no significant effect was found (for parameter estimates and other details of the models see appendix table 7).

| species/<br>group    | Type of dependent variable | BA  | BA of deciduous trees | CV of BA | BA large trees <sup>1</sup> | forest type <sup>2</sup> | Area, ha | landscape <sup>3</sup> | reduction in deviance <sup>4</sup> |
|----------------------|----------------------------|-----|-----------------------|----------|-----------------------------|--------------------------|----------|------------------------|------------------------------------|
| Single species       | A                          | 0   | 0                     | 0        | 0                           | 0                        | 0        | 0                      | /                                  |
| Hole nesters         | A                          | 0   | 0                     | 0        | 0                           | 0                        | 0        | 0                      | /                                  |
| Gleaners             | A                          | 0   | 0                     | 0        | + *                         | 0                        | 0        | 0                      | 14%                                |
| D i. <i>P. mont.</i> | A                          | + * | 0                     | 0        | 0                           | 0                        | 0        | 0                      | 17%                                |
| D e. <i>P. mont.</i> | A                          | + * | 0                     | 0        | 0                           | 0                        | 0        | 0                      | 25%                                |
| All residents        | A                          | 0   | 0                     | 0        | + **                        | 0                        | + *      | 0                      | 38%                                |
| All residents        | S                          | + * | 0                     | 0        | 0                           | 0                        | + *      | 0                      | 50%                                |

Significance codes: `\*\*\*\*` < 0.001; `\*\*\*` < 0.01; `\*` < 0.05

BA Basal area, m<sup>2</sup>/ha

CV Coefficient of variation (SD/Mean)

D Species declining over the ten years period (1997-2006) in Ottvall et al. (2009); i./e. *P. mont.* = inclusive/exclusive *Parus montanus*

A Abundance

S Species number

<sup>1</sup> log(BA trees > 40 cm diameter at breast height + 0.01)

<sup>2</sup> `+`/`-` indicates significantly higher/lower abundances or species numbers in Norway spruce dominated forest compared to Scots pine dominated forest

<sup>3</sup> `+`/`-` indicates significantly higher/lower abundances or species number in the Ekopark compared to the managed reference landscape

<sup>4</sup> [(null deviance - residual deviance)/null deviance] \* 100

## Discussion

### Is old forest like old forest?

Indeed, the results of this study show that old forest is not like old forest, but that the investigated old forest patches are not equal in structure and composition and that this is reflected in differences in resident bird abundance and species number. The most influencing habitat variables were basal area and basal area of large trees. However, besides the habitat variables, the stand area had also an effect on resident bird abundance and species number.

The basal area, which is indicative for forest productivity and tree canopy closure, was positively related to the abundances of the groups 'declining species' inclusive and exclusive Willow Tit. A positive relationship between bird abundance and productivity has been found in several studies (e.g. Helle, 1985; Jokimäki & Huhta, 1996; Jokimäki & Solonen, 2011). The amount of vegetation, indicated by basal area, is assumed to be positively correlated with invertebrate abundance and overall food supply (Cody, 1981; Helle, 1985), which in turn is positively correlated to bird abundance (Cody, 1981; Jonsson et al., 2011). The invertebrate density might be particularly important for foliage gleaning resident birds – all of the declining species are foliage gleaners –, as most of them are mainly insectivorous. However, the positive relationship with basal area seems to be not consistent for all species in the group, because the abundances of the declining single species Willow Tit and Treecreeper alone were not significantly affected by basal area. This and the fact that the declining species group excl. Willow Tit revealed a positive effect of basal area, suggests that the most influencing species in the group 'declining species' were the species Coal Tit, Goldcrest and Siberian Jay. The Siberian Jay prefers forest with a closed canopy, because it provides cover from predators (Griesser et al., 2007). A productive habitat might be beneficial for the Goldcrest, because its population fluctuations are regulated by harsh winter climate (Väisänen & Solonen, 1997). The positive relationship between basal area and the declining species suggests that these species are particularly dependent on productive forests with a closed tree canopy, which provides sufficient food and cover from predators.

The species number of 'all residents' was positively related to basal area, i.e. productivity of the forest. This result concurs with that of many other studies (e.g. Nilsson, 1979; Haila et al., 1980; Jokimäki & Huhta, 1996; Verschuyt et al., 2008; Honkanen et al., 2010; Jonsson et al., 2011). Total species number was correlated with total abundance ( $r = 0.704$ ,  $P = 0.000$ ), suggesting a mechanism which is density dependent. For example the more individuals hypothesis states, that increasing availability of productive energy can support more individuals and allows species to maintain larger populations (Srivastava & Lawton, 1998). This leads to a lower extinction risk and by this to a higher species number. Another density dependent mechanism is the energy based sampling hypothesis (Carnicer et al., 2008). More productive forests support more individuals and contain thus more species, if individuals are selected randomly from the regional species pool. However, the productivity of the habitat seems to be of importance for the number of resident bird species and also for the abundance of the declining foliage and trunk gleaning species among them.

The total abundance showed a positive relationship to the basal area of large trees. Before I discuss this further, it should be noted that the basal area of large trees was not positively correlated with forest age and site productivity extracted from the forest data ( $r = 0.110$ ,  $P =$

0.617 and  $r = 0.099$ ,  $P = 0.654$ , respectively). Therefore, I will regard the basal area of large trees as indicator for the management intensity of the studied stands rather than representative for forest age or site productivity, as the basal area of large trees was found to be decreasing with increasing management intensity (Liira & Kohv, 2010). Forest structural complexity increases with decreasing management impact, which may be expressed in e.g. a developed understory, multilayered tree canopies, a patchy distribution of trees, a high proportion of deciduous trees and/or the occurrence of snags (Esseen et al., 1997). However, since I did not measure every possible structural feature, which could have been beneficial for bird abundance and species number, it remains at least partly speculation what exactly caused the positive effect of basal area of large trees in the investigated stands. It is unlikely, that the large trees themselves contributed much to the increased resident bird abundance, because they were usually not very abundant. Additionally, the only bird species in this study dependent on large trees for nesting was the Great Spotted Woodpecker and its abundance was not correlated with the basal area of large trees ( $r = 0.127$ ,  $P = 0.563$ ). However, the basal area of large trees was correlated with the basal area of deciduous trees ( $r = 0.453$ ,  $P = 0.030$ ). Thus, it might be that a part of the effect of the basal area of large trees can be explained by a parallel increase in basal area of deciduous trees. Palmgren (1932) showed that numbers and total weights of invertebrates were considerably greater in birch than in spruce and pine during summer. Although most of the resident bird species in northern Sweden prefer coniferous trees for foraging, this might have been one of many reasons for an increased abundance of resident birds in forests with a near natural state. However, the deciduous trees were probably only one part of the overall enhanced structural complexity of the forest patches with low management intensity. In a study of Haila (1996) the majority of the species showed a preference for habitat heterogeneity. Birds have many different requirements during their breeding cycle and those requirements differ between species. Thus, the total abundance is highest in forests where the requirements of the most species are best fulfilled, which is most probable in a heterogeneous forest. Similar to the result of this study, Nilsson (1979) found the proportion of basal area of standing dead wood not correlated with forest age, but to the management intensity of the investigated forest patches. The most intensively managed plot in his study supported only one third of the bird density of the least managed plot.

In contrast to the declining species among the foliage and trunk gleaners, which were positively affected by forest productivity, the group of the foliage and trunk gleaners as a whole was positively affected by the basal area of large trees. As already mentioned above a part of the forest structural complexity, indicated by a high basal area of large trees, may be a developed understory and a multilayered canopy. Both might reflect the various foraging sites that insectivorous foliage gleaning birds use (Cody, 1981). Thus it might be that the different foraging site requirements of the different foliage gleaning birds are best fulfilled in a structural complex forest, which leads to a higher overall abundance of foliage and trunk gleaning resident birds. To summarize structural complexity of forests with near natural state seem to be of importance to support an overall high abundance of resident bird species in the study area.

Besides forest productivity and structural complexity the total abundance and species number were also positively affected by stand area. Because I averaged the abundances of the two bird survey points in the larger stands, the positive relationship between stand area and abundance can be regarded as density-area relationship in this study. However, this positive density-area relationship is probably an artefact, because of three reasons. Firstly, because the averaged numbers of the two bird survey points in the larger stands were

always raised when rounded, the abundances of the larger stands are overestimated. Secondly, since the sampling effort was higher in the larger stands (two bird survey points) than in the smaller stands (one bird survey point), the probability to detect an individual was higher in the larger stands. This might have led also to an overestimation of the abundances in the larger stands. Thirdly, the investigated forest patches were always directly adjacent to at least one other old forest stand with sometimes similar structure and composition. Thus it is possible that the density-area relationship found in this study is influenced by the surrounding stands. If there is a real positive density-area relationship it might be best explained by the resource concentration hypothesis (Root, 1973). According to this, the increased area of preferred habitat leads to a concentration of critical resources, such as food, habitat heterogeneity or safety from predators. Individual density increases with increasing area of preferred habitat, because species can remain in the patch to reproduce and do not need to visit other patches whereas in small patches they would have to. However, the potential positive relationship between stand area and resident bird 'density' is only valid for a stand area range from 5-17 ha and cannot be extrapolated to larger stands. Similarly to the potential density-area relationship found in this study Virkkala & Rajasärkka (2006) found higher mean densities of bird species preferring old-growth forest in larger than in smaller areas of old forest.

Since no effect of landscape was observed, it seems to be that the landscape context of the stands plays a minor role in determining the resident bird abundance and species number patterns in the investigated landscapes compared to structure and composition of the stands. However, the total abundance tended to be higher in Rosfors (mean = 5.3 individuals) than in Kloken (mean = 3.3 individuals).

### **Conclusions and recommendations for forest management and conservation**

The results of this study show that both forest structural complexity as well as forest productivity positively affects the resident bird abundance and species number in Ekopark Rosfors and its reference landscape. Therefore, I recommend to preserve and/or to restore productive and structural complex forests in the study area. Species preferring structurally complex old forests, such as the Willow Tit or the Tree Creeper continue to decline most among all forest birds (Ottvall et al, 2009). Hence, the need to preserve or restore structural complex old forests is unchanged. According to the result of this study productive forest is needed to maintain the whole spectrum of resident bird species. Moreover, especially for declining species the forest has to have a certain productivity, to be able to support high individual numbers. This emphasizes the need to create forest reserves in productive forest land.

Finally, a note about the generalizability of the results of this study. The generalizability of the results of this study is restricted to landscapes with similar properties than Ekopark Rosfors and Kloken in the same area, because differences in e.g. forest structure, climate or soil conditions between landscapes and regions might influence the importance of different factors. For example, Verschuyt et al. (2008) found bird species richness on continental scale in North America dependent on productivity, whereas this was not always the case on landscape scale. Forest productivity was the most important factor in low energy landscapes and forest structural complexity was the most important factor in high energy landscapes.

## Sources of bias and improvements

Since I was very restricted in time, the obtained bird abundances might suffer from stochastic variation due to single visits. A second visit would have raised probably the species number and individual number in some stands, because it is very likely that a present bird was not counted just because it was not active during the count time. The counted bird numbers might also suffer from bias due to the different reaction to the song playback. A further source of bias might be a not random selection of the investigated stands. The consequence of this might be that the variation of stands present in the landscapes was not completely covered by the selected stands, because well accessible stands relative near to forest roads had to be selected, which might be different from stands farther away from the forest roads. This might be particular a problem in Kloken, because Kloken is more than twice as big as Rosfors and because the road network is less dense in Kloken than in Rosfors. I had to select also stands which were relative near to each other so that they could be sampled during one morning, which caused that especially the stands in Kloken were allocated in clusters which might have reduced the spatial independence of the stands. The abundance estimate of the Goldcrest is probably biased by its partial migration, because I heard it not singing in the first half of the census period.

More replicates on stand scale would improve the data quality, because this would increase the number of observations. Thus, it would have been also possible to study more species at the species level. The study design could be improved by more replicates on landscape level. This would allow the explanation of a possible effect of landscape and thus to study landscape level factors more specific. Since boreal forest birds might select their breeding territory randomly in an area of the coarse habitat that they prefer (or not avoid) (Haila et al., 1996), the results could be altered if I would have carried out the study in another year. Hence, the best way would be to collect data over several years.

It should be also noted at this point that the explanatory variables are to some extend ecologically and statistically dependent from each other, despite they were not highly correlated ( $> 0.7$ ). This is reflected in some Pearson correlation coefficients greater than 0.4 (appendix table 6). Because collinearity between explanatory variables might affect the size and significance of parameter estimates (Kutner et al., 2005), the results of this study might be affected by the correlation between some of the explanatory variables used in this study. This might be particular the case for the effects of basal area and the basal area of large trees, which were correlated with each other ( $r = 0.455$ ,  $P = 0.029$ ). There is no model in which both variables revealed a significant effect (table 5), probably because the correlation between them lead to the mutual exclusion of the respective other variable, although the excluded variable might have a significant effect alone. Thus it is difficult to judge the relative importance of basal area and the basal of large trees.



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## Appendix

**Table 6** Pearson correlations between continuous independent variables of generalized linear models relating resident bird abundance and species number to habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands.

|                          | BA of deciduous trees | CV of BA  | large trees <sup>1</sup> | area     |
|--------------------------|-----------------------|-----------|--------------------------|----------|
| BA                       | 0.447 *               | -0.612 ** | 0.455 *                  | -0.425 * |
| BA of deciduous trees    | /                     | -0.173    | 0.453 *                  | -0.200   |
| CV of BA                 | /                     | /         | -0.173                   | 0.294    |
| large trees <sup>1</sup> | /                     | /         | /                        | -0.181   |
| area                     | /                     | /         | /                        | /        |

Significance codes: ‘\*\*\*’ < 0.01; ‘\*’ < 0.05

BA Basal area, m<sup>2</sup>/ha

CV Coefficient of variation (SD/Mean)

<sup>1</sup> log(BA trees > 40 cm diameter at breast height + 0.01)

**Table 7** Detailed results of generalized linear models relating resident bird abundance and species number to habitat variables at the bird survey points as well as to area, forest type and location of the investigated stands (n = 23). Indicated are the signs of the effects and the parameter estimates with significance niveaus and standard errors. `0` means no significant effects were found.

| species/species group     | Type of dependent variable | Intercept                | BA                     | BA of deciduous trees | CV of BA | BA large trees <sup>1</sup> | Forest type <sup>2</sup> | Area, ha               | Landscape <sup>3</sup> | AIC (AICc)     | Residual deviance | Null deviance |
|---------------------------|----------------------------|--------------------------|------------------------|-----------------------|----------|-----------------------------|--------------------------|------------------------|------------------------|----------------|-------------------|---------------|
| <i>Parus major</i>        | A                          | 0                        | 0                      | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | /              | /                 | /             |
| <i>Parus montanus</i>     | A                          | 0                        | 0                      | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | /              | /                 | /             |
| <i>Certhia familiaris</i> | A                          | 0                        | 0                      | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | /              | /                 | /             |
| <i>Loxia spp.</i>         | A                          | 0                        | 0                      | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | /              | /                 | /             |
| Hole nesters              | A                          | 0                        | 0                      | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | /              | /                 | /             |
| Gleaners                  | A                          | + 1.327 ***<br>(± 0.156) | 0                      | 0                     | 0        | + 0.105 *<br>(± 0.052)      | 0                        | 0                      | 0                      | 93,0<br>(93.6) | 25,9              | 30,0          |
| D i. <i>P. mont.</i>      | A                          | 0                        | + 0.051*<br>(± 0.024)  | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | 76,8<br>(77.4) | 22,7              | 27,5          |
| D e. <i>P. mont.</i>      | A                          | - 2.506 *<br>(± 1.063)   | + 0.093 *<br>(± 0.038) | 0                     | 0        | 0                           | 0                        | 0                      | 0                      | 53,5<br>(54.1) | 19,4              | 26,0          |
| All residents             | A                          | + 1.183***<br>(± 0.279)  | 0                      | 0                     | 0        | + 0.127**<br>(± 0.045)      | 0                        | + 0.056 *<br>(± 0.026) | 0                      | 97,9<br>(99.2) | 18,6              | 29,2          |
| All residents             | S                          | 0                        | + 0.043 *<br>(± 0.021) | 0                     | 0        | 0                           | 0                        | + 0.081 *<br>(± 0.033) | 0                      | 79,4<br>(80.6) | 7,2               | 14,4          |

Significance codes: '\*\*\*' < 0.001; '\*\*' < 0.01; '\*' < 0.05

BA Basal area, m<sup>2</sup>/ha

CV Coefficient of variation (SD/Mean)

D Species declining over the ten years period (1997-2006) in Ottvall et al. (2009); i./e. *P. mont.* = inclusive/exclusive *Parus montanus*

A Abundance

S Species number

<sup>1</sup> log(BA trees > 40 cm diameter at breast height + 0.01)

<sup>2</sup> `+`/`-` indicates significantly higher/lower abundances or species numbers in Norway spruce dominated forest compared to Scots pine dominated forest

<sup>3</sup> `+`/`-` indicates significantly higher/lower abundances or species number in the Ekopark compared to the managed reference landscape

## SENASTE UTGIVNA NUMMER

- 2010:8 Human attitudes toward large carnivores bear, wolf, lynx and wolverine. A case study of Västerbotten County.  
Författare: Robert Mannelqvist
- 2010:9 The distribution of Moose (*Alces alces*) during winter in southern Sweden: A response to food sources?  
Författare: Mikael Wallén
- 2010:10 Training identification tracking dogs (*Canis familiaris*): evaluating the effect of novel trackdown training methods in real life situations.  
Författare: Erik Håff
- 2010:11 Hotade arter i tallmiljöer på Sveaskogs mark i Västerbotten och Norrbotten. Skötsel förslag och analys av potentiell habitatutbredning.  
Författare: Karin Lundberg
- 2010:12 Migration losses of Atlantic salmon (*Salmo salar* L.) smolts at a hydropower station area in River Åbyälven, Northern Sweden.  
Författare: Stina Gustafsson
- 2010:13 Do grizzly bears use or avoid well-sites in west-central Alberta, Canada?  
Författare: Ellinor Sahlén
- 2011:1 Pre-spawning habitat selection of subarctic brown trout (*Salmo trutta* L.) in the River Vindelälven, Sweden.  
Författare: Erik Spade
- 2011:2 Vilka faktorer samvarierar med användandet av viltkött, vildfångad fisk, bär och svamp i svenska hushåll? – Stad vs. Landsbygd.  
Författare: Jerker Hellstadius
- 2011:3 Konsekvenser av födoval och minskande sorkstammar för populationer av sorkätande ugglor och rovfåglar.  
Författare: Katie Andrie
- 2011:4 Tjäderns (*Tetrao urogallus* L.) vinterdiet i norra Sverige: Är gran (*Picea abies*) viktig i vissa habitat?  
Författare: Staffan Öberg
- 2011:5 Grey-sided vole and bank vole abundance in old-growth forest patches of different size and connectivity.  
Författare: Niklas Paulsson
- 2011:6 *De novo* sequencing and SNP discovery in the Scandinavian brown bear (*Ursus arctos*).  
Författare: Anita J Norman
- 2011:7 A genetic approach to identify raccoon dog within a large native meso-carnivore community.  
Författare: Dan Wang