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Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach

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The effects of scale, landscape matrix and habitat structure on birds were studied in forest-dominated landscapes in northern Finland. Abundances of birds correlated with different factors at different scales. No edge effect was observed at the large scale matrix level (4 km^2), even though edge was the most important factor at the small-scale matrix level (4 ha). Matrix components explained up to 47% of the variation in abundances of birds. Fragmentation and amount of edges had a positive relationship with the managed forest species, edge species and habitat generalists. However, virgin forest species and hole-nesters had a negative relationship with edges. Landscape matrix components were more important than habitat components to the managed forest species and the Willow Warbler; whereas habitat components were more important to the migratory species and the Pied Flycatcher. Within a habitat, floristic components were more important than structural components. Habitat generalist species benefited from deciduous forests and virgin forest birds from mixed-tree species composition. Stand age had a positive relationship with species richness, total amount of birds, virgin forest species and hole-nesters. Our results indicate that bird responses to the environment are scale-dependent and individualistic. Bird species composition and abundances are also dependent on factors at larger scales than the individual's immediate habitat.

1. Introduction

The importance of habitat structure for habitat selection in birds has been demonstrated in many studies (Hildén 1965, Cody 1981, among others). As subdivision of natural habitats has increased, many recent studies have pointed out the importance of the landscape matrix in bird population changes, reserve planning and management practices (Janzen 1983, Harris 1984, Väisänen et al. 1986, Hansson et al. 1995). Moreover, fragmentation has been considered one of the most important reasons for the loss of biodiversity (Wilcox & Murphy 1985). Most previous studies of forest fragmentation have been conducted in heavily managed, agricultural landscapes (see Opdam 1991). Since the regional abundance of suitable habitats influences the existence of species, results of these studies may not be applicable to an area where the landscape still consists mainly of forests (Askins et al. 1987, Virkkala 1991a, Angelstam 1992). Previous studies have mainly concentrated on size, shape and isolation of individual patches rather than looking at the entire landscape context (Haila & Hanski 1984, Wiens 1995). However, many species use several different patch types during their life or they may embrace several habitat types in their functional home ranges (Rolstad & Wegge 1987, Hanski & Haila 1988).

Because landscapes are spatially heterogeneous, the structure and changes of landscapes are scale-dependent (Forman & Godron 1986). According to that, differences in the structure of the landscape in which local study plots are situated may produce differences in apparent vertebrate-habitat relationships derived from those local-level observations (Wiens & Rotenberry 1981, Wiens 1989). It is important to consider spatial scale in studies of habitat associations because various factors that affect a bird species may act in different spatial scales. This emphasises a multi-scale approach in bird-habitat relationship studies (Rotenberry & Wiens 1980, Wiens 1981, Virkkala 1991b).

The main aims of our study were to determine the importance of landscape matrix versus local habitat on birds and to study the effects of scale on bird-habitat relationships. In this study, we conducted analyses at three different scales: 1) large-scale matrix (4 km^2), 2) small-scale matrix (4 ha), and 3) within local habitat (≤ 0.79 ha). We had two main study questions. Firstly, do the same environmental variables correlate with bird variables at different scales, as is suggested according to the hierarchy theory (e.g. O'Neill 1989)? Secondly, do different bird species have different responses on landscape and habitat components? Since the evaluation of habitat relationships is an important part of wildlife management and conservation biology (Wiens & Rotenberry 1981, Verner et al. 1986), we also studied how the variations in the abundances of species or ecological groups are associated with certain landscape matrix or habitat characteristics.

2. Material and methods

2.1. Study area

The study was carried out in the Rovaniemi area, in northern Finland (66°N, 25°E), where forests covered about 61% of the landscape. The proportions of different types of forests in our study area were as follows: Scots pine (*Pinus sylvestris*, L.) dominated forests 86%, Norway spruce (*Picea abies*, (L.) Karsten) dominated forests 11% and mixed or deciduous dominated forests 3%. Forests were intermixed with pine bogs (proportion of the landscape 20%) and open areas such as lakes, open bogs, fields and clear-cuts (proportion of the landscape 15%). The mean patch size of our study areas, measured from the topographic maps (1: 20 000) using a frame-scale of 4 km^2, was on average 16 ± 7 (S.D.) ha (N = 20). The mean patch size of different study areas was calculated from the following formula: 400 ha/total number of patches. We defined habitat patch as "a surface area differing from its surrounding in nature or appearance" (see Wiens 1976). As some patches continued outside of the frame-scale, the measurement is an underestimate. The mean age of our study forests was 86 ± 35 (S.D.) years and the mean timber volume was 104 ± 51 (S.D.) m^3/ha (N = 161). In bare areas, the shrub layer was almost missing and the field layer was dominated by red whortleberry (*Vaccinium vitis-idae* L.), heather (*Calluna vulgaris* (L.) Hull) and crowberry (*Empetrum nigrum* L.). In more productive sites the proportions of Norway spruce and birch (*Betula* ssp.) were higher and the cover of the shrub layer was denser. Bilberry (*Vaccinium myrtilus*, L.) was the main dwarf in the field layer. Extensive clear-cutting since the 1950s has increased the area of clear-cuts and young seedling stands (see e.g. Järvinen et al. 1977). As pine has been preferred over other trees species in forest regeneration, large even-aged pine stands dominate the landscape.

2.2. Study design

Firstly, we selected twenty study areas with variable amounts of forest cover using a frame-scale of 4 km^2. This selection was done using aerial photographs from 1985 (1:40 000) and topographic maps (1:20 000). Secondly, within each study area, we established bird census points with variable amounts of forest in the near matrix (4 ha). The immediate surrounding of the census points (within 50 m from the census point) consists of the single forest habitat type. Census points were placed along narrow forest roads, which were used only occasionally by cars. Census points were situated at least 200 m from the roads inside the forest. The distance between individual census points was at least 400 m to minimize the number of recounts of the same individuals (see Fig. 1). Each census point was marked with a wooden tag so that the point was easy to find every study year.

2.3. Landscape matrix and habitat descriptions

2.3.1. Landscape matrix

We determined landscape characteristics both at large (4 km², N = 20) and small (4 ha, N = 161) scales (see Fig. 1). We measured the following landscape matrix variables for both scales: total length of the edges between forests and roads, forest and powerlines and forests and open areas (open bogs, clearcuts, lakes); the proportions of different habitat types: pine-dominated forests, spruce-dominated forests, deciduous-dominated forests, mixed forests, pine bogs, spruce bogs, open bogs, fields, clearcuts, lakes and seedling or sapling areas; and the total number of habitat patches. Large-scale analysis is based on aerial photographs from 1985 (1:40 000) and topographic maps (1:20 000) and small-scale analysis is based on habitat mapping in the field. For that reason, the small-scale analysis is more accurate than the large-scale analysis.

2.3.2. Habitat structure

As both the structure of habitat and floristic composition may affect birds (e.g. Wiens & Rotenberry 1981, Bersied & Mayer 1994), we measured the structure of vegetation within a circle of a 50-m radius (0.79 ha) and floristic composition within a circle of a 3.3-m radius (34 m²) around each census point (N = 161) (see Fig. 1). In our study area, the immediate surrounding of the study points was relatively homogenous. The following structural variables were measured: stand age, height of dominant trees, tree volume (using the relascope method), and the number of barkless trees, snags and decaying trees. Within a circle of 3.3 m in radius, stem frequency distribution series of pines, spruces and birches were measured in five different height categories (1–3 m, > 3–5 m, > 5–10 m, > 10–15 and > 15 m). We used the stem frequency distribution to calculate the tree species diversity (only tree species used) and foliage height diversity (only height categories used) of the stands. Shannon index of diversity was used in all analyses. The structure of the field layer was assessed using four 1-m² plots. Squares were situated four metres from the census point to the principal points of the compass (see Fig. 1). Within each of these squares the cover of grasses, mosses, lichens, dwarfs and barren area (%) was measured. The habitat description method was well standardised since all vegetation descriptions were made by the same forest-technician.

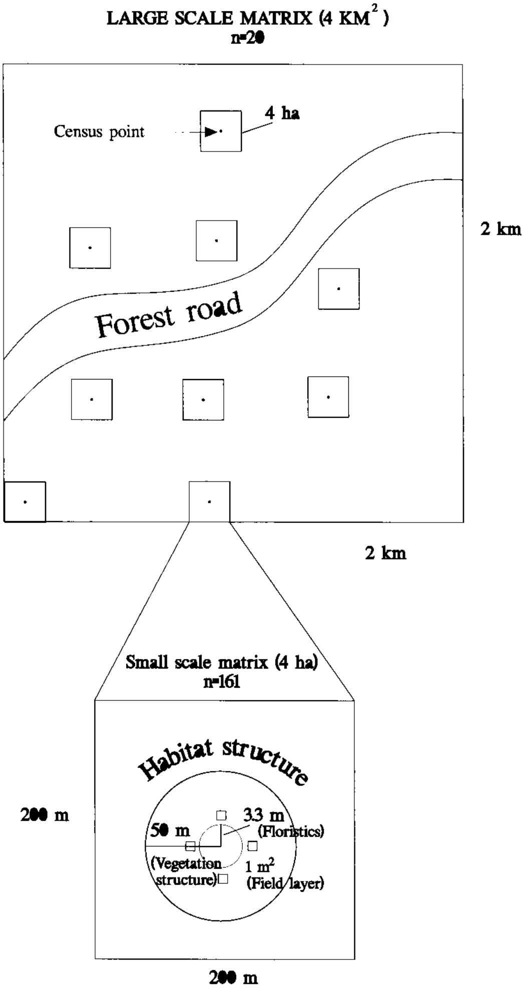

Fig. 1. Study design and the different scales of landscape and habitat structure measurements

2.4. Bird censuses

Most bird populations vary markedly from year to year. It has been suggested that at low density birds may not occupy all available habitats and at high density some poor habitats may also be occupied (e.g. Rotenberry 1985). This may mask differences between preferred and less desirable habitats for the birds. As a consequence, a short-term study based on single-year results will be misleading in studying bird-habitat relationships (e.g. Wiens 1981, 1989). To avoid these problems, data for six years were used in this study.

As the census period of birds is very short in the northern areas, time-consuming census methods, such as territory mapping, were not practical in our case. We surveyed breeding birds using a single-visit point-count method (Hildén et al. 1991) from 1990 to 1995. The single-visit census detects about 60% of breeding pairs and 90% of species in forested areas (Järvinen & Lokki 1978). Because of a short breeding season and simple habitat structure, the census efficiency may be even greater in the north (Järvinen et al. 1978, Helle 1986a). A total of 161 census points were established in an area covering about 250 km^2. The average number of census points per year was 144 (range 106–161) and 117 census points (73%) were visited during every year. Censuses were carried out between 4th of June and 2nd of July in good weather only. The starting date of a census was determined by weather conditions in the spring and all censuses were conducted during two weeks in every year. All censuses were made between 3 and 9 a.m. All birds seen or heard during a 5-min period were recorded separately within and outside a circle of 50 m around the census taker. Each bird was plotted at the distance at which it was first observed. Whenever we were sure that we had already observed the same individual it was not included in results. Flocks of early breeders (e.g. Crossbills, Redpolls, Siskins) are interpreted as fledgling flocks. The number of pairs of these species is calculated by dividing the number of the birds in the flock by the estimated number of one pair plus fledglings; thus 1–6 individuals = 1 pair, 7–12 individuals = 2 pairs, etc. Overflying birds that did not land in trees or on the ground were not counted.

Monitoring specific habitat alterations is most revealing if birds are grouped by habitat use strategies or feeding guilds (Järvinen & Väisänen 1979). Our categorisation of species was based on previous studies. All species were grouped according to their migratory habits (migratory, partly migratory+sedentary; Helle 1985a). Forest birds were grouped into managed/mosaic and virgin forest species according to the type of the habitat where they are most commonly found (Haapanen 1965, Virkkala 1987a, Raivio & Haila 1990). We considered Raivio and Haila's (1990) mature forest generalists and mature forest specialists as virgin forest species and mosaic specialists and mosaic generalists were considered as managed forest species. Moreover, we constructed ecologically important subgroups. A species was considered to be an edge species if it exhibited significantly higher abundance at the edge than in interior parts of the forest (Helle 1983, Helle & Järvinen 1986, Hansson 1994). Habitat generalist species occurred in a wide range of different successional stages (Helle 1983, 1985b, Virkkala 1987b, 1991a). Species groups are shown in Appendix 1.

As the maximum distance of detectability varies between species, we considered point survey results as indices of abundance rather than accurate density. We did not include the Cuckoo in the analyses since most of its observations (99%) come from outside the 50-m study circle. As the overall abundance of birds was so low, we pooled the data from inside and outside the 50-m study circle. The average proportions of the observations of the ten most abundant bird species (see Appendix 1) within a 50-m (0.78 ha) study circle was 19%. Since the same habitat type in most cases continued outside the 50-m study circle, we supposed that even a higher proportion of the bird observations were connected with our habitat structure measurements made within a 50-m circle. As about one-fifth of the total number of observations were made within a 50-m study circle, we supposed that about half of all the bird observations were made within our small-scale matrices (4 ha). In other words, over one-fifth of the bird observations were strictly connected with the immediate habitat and about half of the bird observations were strictly connected with the landscape matrix at the 4-ha scale. As we used both the habitat ($\leq$ 0.78 ha) and the landscape matrix (4 ha and 4 km^2 matrices) variables to explain the abundance of birds, we supposed that the distribution of bird observations was well suitable to our analyses.

2.5. Statistical methods

We made the following transformations of the variables to correct or improve heteroscedasticity and deviation from normality: arcsin-transformation for the percentage variables and log-transformation ($X' = \log_{10}(X+1)$) for the total number of tree trunks; number of trees in different tree height categories; total number of shrubs, deciduous, pine and spruce shrubs, snags and dead trees; the total number of patches; and all bird variables. The normality of variables was tested with the Lilliefors test before any statistical analyses.

We used principal component analysis (PCA) with varimax rotation on the landscape matrix (separately for large (4 km^2) and small (4 ha) scales) and habitat structure variables (separately for structural and floristic). Only components with an eigenvalue greater than 1.0 were accepted for the further analysis. We used PCA factor scores in stepwise multiple regression analysis (SMRA) to investigate relationships between the abundances of selected bird species, or groups of species, and habitat or landscape structure. No variable was entered into models that had $P > 0.05$. Species-level analysis was made for the twelve most abundant species, all having data over 100 pairs. For each bird species, we used the average abundance of birds from different study years per point as the statistical unit for habitat- and small-scale matrix analyses ($N = 161$). At the large-scale analyses, we used the average abundance of bird species from different year per point per study areas ($N = 20$).

All statistical analysis were made with the SPSSx (SPSS Inc. 1988) statistical package.

3. Results

3.1. Principal component analyses

The highest component loadings of the different analyses are shown in Appendix 2. Four large-scale matrix components (4 km^2) had eigenvalues greater than 1.0 and they accounted for 73% of the total variation in large-scale landscape structure. These components described: fragmentation (MLfragm.), proportion of unforested area (MLopen), proportion of spruce forests (MLspruce) and length of edges (MLedge). The fragmentation component had also a high positive loading with the proportion of deciduous forests.

Small-scale matrix (4 ha) variables were reduced to five different components: length of edges (MSedge), fragmentation (MSfragm.), proportion of seedling or sapling areas (MSseedl.), proportion of fields (MSfields) and length of forest roads (MSroads). These components explained 70% of the total variation in small-scale landscape structures. The fragmentation component had also a high positive loading with the proportion of mixed forests.

The floristic variables were reduced to five different components: number of spruces within a circle of 3.3 m in radius (HFspruce), number of deciduous trees within a circle of 3.3 m in radius (HFdecid.), number of pine seedlings within a circle of 3.3 m in radius (HFpseedl.), mixed-tree species composition (HFmixed) and number of large pines within a circle of 3.3 m in radius (HFlpines). These components accounted for 74% of the variation of the floristic composition of the study sites.

Structural variables of the habitat were reduced by PCA into five components: shrub layer (HSshurbs), age (HSage), tree density (HSdensity), amount of snags (HSsnags) and dwarf cover in field layer (HSdwarfs), which explained 75% of the total variation of forest stand structure variation.

3.2. Bird species richness and abundance

A total of 68 bird species and 7 974 pairs were observed during the six-year study period (Appendix 1). The average bird species richness per point was 6.4 and the average number of pairs was 9.2. All the constructed bird–landscape–habitat models are shown in Tables 1 and 2.

No large-scale matrix components were entered into models of species richness and total number of pairs. A greater amount of variation in total abundance of birds was explained by habitat (13%) than small-scale matrix components (5%). The stand age had a positive relationship with the bird species richness and the total abundance of birds (Table 1).

3.3. Ecological groups

3.3.1. Migratory habits

Only small-scale matrix components with poor explanatory powers were entered into models of sedentary birds. The proportion of seedling areas had a negative relationship with the sedentary birds (Table 1).

No large-scale matrix components were entered into the models of migratory birds. Migratory birds had a positive relationship with the amount of edge at the small-scale matrix. A greater amount of the variation in abundance of migratory birds was explained by habitat (14%) than by matrix components (3%). At the habitat level, floristics (10%) accounted for a higher proportion of the variation in abundance of migratory birds than structural components (4%) (Table 1).

3.3.2. Forest type preferences

No large-scale matrix components were entered into the models of virgin forest birds. At the small-scale matrix level, components describing the amount of forest roads, edges (Fig. 2a) and fields were negatively related to the abundance of virgin forest species. At the habitat level, a greater amount of variation in abundance of the virgin forest birds was explained by floristic (26%) than by structural (6%) components. Components describing the mixed-tree species composition (Fig. 2b), age and amount of snags were the most important positive factors for virgin forest birds (Table 1).

Both the matrix and habitat components were important for managed forest birds. A high percentage of variation in abundance of managed forest species was explained by the large-scale fragmentation (37%) and the amount of edges at the small-scale matrix level (20%, see Fig. 2c). Both components had a positive relationship with the abundance of the managed forest species. At the habitat level, floristics and structural components were equally important for managed forest species. The component describing the amount of deciduous trees was the most important positive habitat factor for the managed forest species (Fig. 2d, Table 1).

Table 1. Bird-habitat relationship models generated by stepwise linear regression analysis for the bird species richness, total number of pairs and groups of birds. "–" after components denotes a negative relationship between that component and the bird variable. The partial R^2 for each component is given in parentheses. $N = 20$ for the large-scale matrix analysis and $N = 161$ for the small-scale matrix, habitat structure and floristical analyses. * $P < 0.05$, *** $P < 0.01$ and *** $P < 0.001$. For component abbreviations, see Appendix 2.

	MATRIX LEVEL		HABITAT LEVEL	
	Large-scale ($4\ km^2$)	Small-scale (4 ha)	Structure	Floristics
Species richness	–	Roads(–)**(6)	Age***(5)	Lpines*(4)
Pairs total	–	Edge*(3) Roads*(2)	Age**(5) Shrubs*(4)	Lpines**(4)
Sedentary birds	–	Fields*(5) Seedl.(–)**(3)	–	–
Migratory birds	–	Edge*(3)	Density**(4)	Decid.*(6) Mixed**(4)
Virgin forest ssp.	–	Roads(–)***(10) Edge(–)****(8) Fields(–)*(2)	Age**(4) Snags*(2)	Mixed***(18) Pseedl.*(8)
Manag. forest ssp.	Frag.**(37)	Edge***(20)	Snags(–)***(8) Density**(4) Shrubs*(3)	Decid.***(13)
Habitat generalists	Frag.*(21)	Edge***(12) Frag.*(2)	–	Decid.***(12)
Edge species	Frag.*(28)	Edge***(14) Frag.***(6) Fields**(4)	Snags(–)***(8)	Decid.***(18) Spruce(–)***(4)
Hole-nesters	–	Frag.(–)***(12) Edge(–)***(11)	Age**(5) Snags*(3)	Spruce(–)***(11) Decid.(–)***(6)

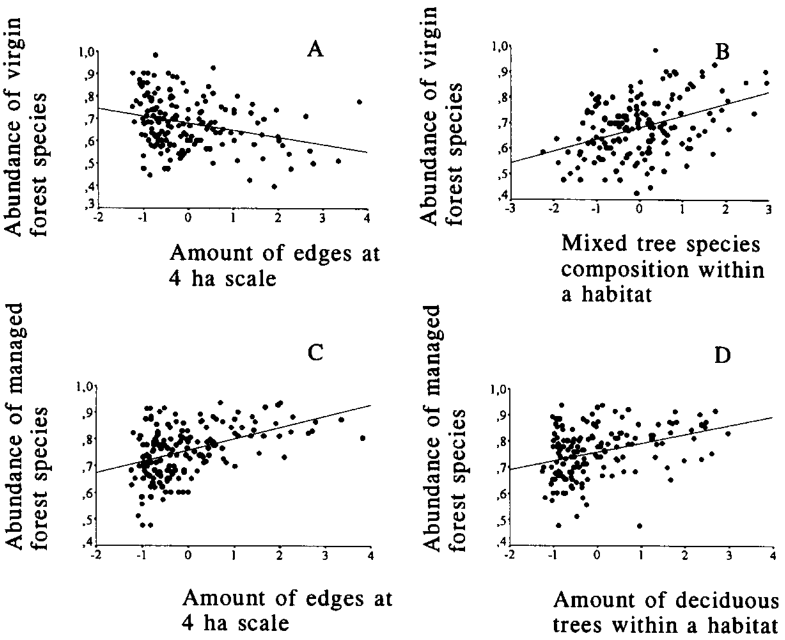

Fig. 2. Relationships between the virgin forest bird species and the amount of edges at the small-scale matrix (Fig. 2a; $R^2 = 7.9$, $b = -0.03$, $t = -3.69$, $p = 0.0003$, $N = 161$); between the virgin forest species and the mixed-tree species composition within a habitat (Fig. 2b; $R^2 = 17.7$, $b = 0.05$, $t = 5.81$, $p < 0.001$, $N = 161$); between the managed forest species and the amount of edges at the small-scale matrix (Fig. 2c; $R^2 = 19.6$, $b = 0.04$, $t = 6.23$, $p < 0.001$, $N = 161$) and between the managed forest species and the amount of deciduous trees within a habitat (Fig. 2d; $R^2 = 12.9$, $b = 0.03$, $t = 4.82$, $p < 0.001$, $N = 161$). Bird variables are $\log_{10}(x + 1)$ transformed and matrix-habitat variables are PCA components.

3.3.3. Habitat generalists

Both the matrix and habitat components were important for the habitat generalists. However, at the habitat level no structural components were entered into models of the habitat generalists. A high percentage of variation in abundance of the habitat generalists was explained by the large-scale fragmentation (21%). At the small-scale matrix level, a greater amount of variation in abundance of the habitat generalists was explained by the amount of edges (12%) than by fragmentation (2%). At the habitat level, the amount of deciduous trees was the only component entered into models. All of these components had a positive relationship with habitat generalists (Table 1).

3.3.4. Edge species

Both the matrix and habitat components were important for edge species. A high percentage of variation in the abundance of edge species was explained by large-scale fragmentation (28%). At the small-scale matrix level, a greater amount of the variation in the abundance of edge species was explained by the amount of edges (14%) than by the fragmentation (6%) and the amount of fields (4%). At the habitat level, the amount of deciduous trees was the most important factor for the edge birds. All of these components had a positive relationship with edge species (Table 1).

3.3.5. Hole-nesters

No large-scale matrix components were entered into the models of hole-nesters. The small-scale matrix components, fragmentation (12%) and amount of edges (11%), explained a great amount of the variation in the abundance of hole-nesters. Both of these components were negatively related to the abundance of hole-nesters. At the habitat level, hole-nesting birds were negatively related to the amount of spruces and deciduous trees, but positively related to the age of stands and the amount of snags (Table 1).

3.4. Individual bird species

Both the matrix and habitat components were important for the Willow Warbler. A high percentage of variation in the abundance of the Willow War-

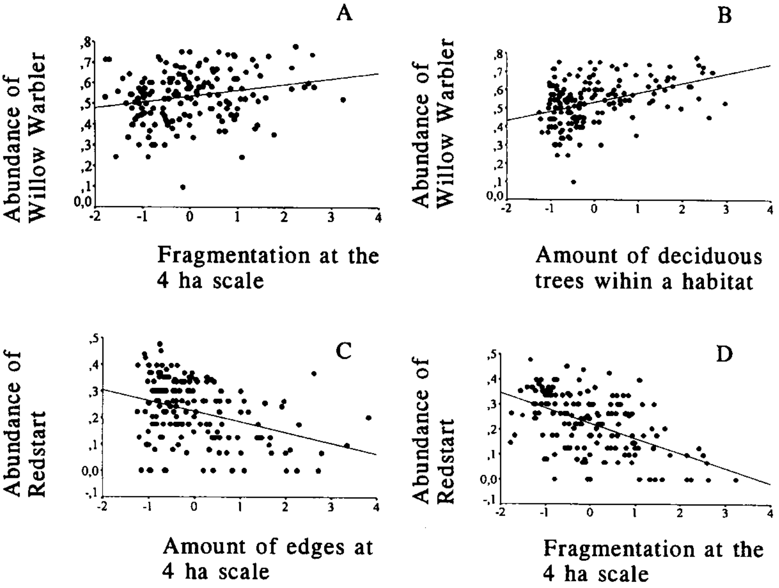

Fig. 3. Relationships between the Willow Warbler and the fragmentation at the small-scale matrix (Fig. 3a; $R^2 = 5.2$, $b = 0.03$, $t = 2.94$, $p = 0.004$, $N = 161$); between the Willow Warbler and the amount of deciduous trees within a habitat (Fig. 3b; $R^2 = 17.1$, $b = 0.05$, $t = 5.69$, $p < 0.001$, $N = 161$); between the Redstart and the amount of edges at the small-scale matrix (Fig. 3c; $R^2 = 11.9$, $b = -0.04$, $t = -4.64$, $p < 0.001$, $N = 161$) and between the Redstart and the fragmentation at the small-scale matrix (Fig. 3d; $R^2 = 27.1$, $b = -0.06$, $t = -7.69$, $p < 0.001$, $N = 161$). Bird variables are $\log_{10}(x + 1)$ transformed and matrix-habitat variables are PCA components.

bler was explained by large-scale fragmentation (36%). At the small-scale matrix level, a greater amount of variation was explained by the amount of edges (18%) than by the fragmentation (5%, Fig. 3a) and the amount of fields (5%). At the habitat level, deciduous trees was the most important habitat factor for the Willow Warbler and it accounted for 17% of the variation in the abundance of the Willow Warbler (Fig. 3b). All of these components had a positive relationship with the Willow Warbler (Table 2).

No large-scale matrix component and only one small-scale matrix component with poor explanatory power were entered into models of the Brambling. A greater amount of variation in the abundance of the Brambling was explained by habitat (13%) than by matrix components (3%) (Table 2).

The only component entered into models of the Tree Pipit was the small-scale fragmentation. It was negatively related to the abundance of the Tree Pipit (Table 2).

No large-scale components were entered into models of the Redstart. At the small-scale matrix level, a greater amount of variation in the abundance of the Redstart was explained by fragmentation (27%, Fig. 3c) than by the amount of edges (12%, Fig. 3d) and fields (5%). All of these components had a negative relationship with the Redstart. The interpretation of the negative associations of the Redstart with deciduous and spruce trees is that Redstarts prefer pine forests (Table 2).

Both matrix and habitat components were important for the Siskin. However, no structural components of the habitat were entered into models of the Siskin. A high percentage of variation in the abundance of the Siskin (31%, a negative relationship) was explained by the amount of unforested areas at the large-scale matrix level. Both the small-scale fragmentation and the mixed-tree species composition at the habitat level explained 9% of the variation in the abundance of the Siskin. Both of these components were positively related with the abundance of the Siskin (Table 2).

Only small-scale matrix components were entered into models of the Redwing. The amount of edges, proportion of fields and seedling areas were positively related to the abundance of the Redwing (Table 2).

Both the matrix and habitat components were important for the Chaffinch. The proportion of unforested area was negatively related to the Chaffinch and it explained 21% of the variation in the abundance of the Chaffinch. The amount of forest roads at the small-scale matrix level had a negative relationship with the abundance of the Chaffinch. Both the floristics and habitat structure components were important for the Chaffinch. Mixed-tree species composition was one of the most important positive habitat factors for the Chaffinch and it explained 7% of the variation in the abundance of the Chaffinch (Table 2).

Only small-scale matrix components were entered into models of the Redpoll. The amount of seedling areas explained 6% of the variation in the abundance of the Redpoll. This relationship was negative (Table 2).

No large-scale matrix components were entered into models of the Pied Flycatcher. Mixed-tree species composition and stand age together explained 12% of the variation in the abundance of the Pied Flycatcher. Both components had positive relationships with the Pied Flycatcher (Table 2).

Both the matrix and habitat components were important for the Song Thrush. However, no structural components of the habitat were entered into models of the Song Thrush. At the large-scale matrix level, a high percentage of variation in the abundance of the Song Thrush (22%) was explained by the proportion of unforested areas. Small-scale fragmentation had a positive relationship with the Song Thrush. Both the small-scale fragmentation and the amount of spruces at the habitat level explained 11% of variation in the abundance of the Song Thrush. Both of these components had a positive relationship with the Song Thrush (Table 2).

No large-scale matrix components were entered into models of the Hooded Crow. The proportion of fields at the small-scale matrix level positively affected the Hooded Crow and it explained 9% of the variation in the abundance of the Hooded Crow. Habitat components entered into the model of the Hooded Crow were not

Table 2. Bird-habitat relationship models generated by stepwise linear regression analysis for the individual bird species. "–" after components denotes negative relationship between that component and bird variable. The partial R^2 for each component is given in parentheses. N = 20 for the large-scale matrix analysis and N =161 for the small-scale matrix, habitat structure and floristical analyses. * $P < 0.05$, *** $P < 0.01$ and *** $P < 0.001$. For component abbreviations, see Appendix 2.

	MATRIX LEVEL		HABITAT LEVEL	
	Large-scale (4 km^2)	Small-scale (4 ha)	Structure	Floristics
Willow Warbler	Frag.**(36 Spruce***(10)	Edge***(18) Frag.**(5) Fields**(5)	Snags(–)***(10)	Decid***(17))
Brambling	–	Fields(–)*(3)	Snags**(8)	Lpines*(2) Mixed**(5)
Tree Pipit	–	Frag.(–)**(4)	–	–
Redstart	–	Frag.(–)***(27) Edge(–)***(12) Fields(–)***(5) Seedl.(–)**(3)	–	Spruce(–)***(20) Decid.(-)***(15)
Siskin	Unforest(–)*(31)	Frag.***(9) Roads(–)*(3)	–	Mixed***(9) Spruce**(4) Decid.*(3)
Redwing	–	Seedl.***(7) Fields*(3) Edge*(2)	–	–
Chaffinch	Unforest*(–)(21)	Roads(–)***(13) Frag.***(6)	Density***(7) Dwarfs*(4)	Mixed***(7)
Redpoll	–	Seedl.(–)**(6)	–	–
Pied Flycatcher	–	Frag.*(4)	Age*(2)	Mixed***(10)
Song Thrush	Unforest*(22)	Frag.***(11) Roads(–)**(4)	–	Spruce***(11)
Hooded Crow	–	Fields***(9)	Snags(-)**(7)	Pseedl.(–)*(3)
Crossbill	–	Frag.**(4) Edge(–)*(2)	–	–

ecologically meaningful for the Hooded Crow (Table 2).

Only small-scale matrix components were entered into models of the Crossbill. Small-scale fragmentation positively affected the Crossbill and it explained 4% of the variation in the abundance of the Crossbill (Table 2).

4. Discussion

4.1. Importance of scale

Some studies have found conflicting (e.g. Wiens et al. 1987, Steele 1992) and other equivalent (e.g. Ambuel & Temple 1983, Swenson 1993) patterns of habitat selection at different scales. In our study, abundances of bird species or groups of birds correlated with different environmental factors at different scales. For example, we did not find any edge effect at the large-scale matrix level even though the edge effect was one of the most important factors entered into bird-habitat relationship models at the small-scale matrix level. Moreover, many bird species had positive relationships with the mixed-tree species composition (mixed-tree species composition was included in the MSfrag-component) at the matrix level, whereas the same species favoured deciduous trees within a habitat (e.g. edge species, habitat generalists, Willow Warbler). These observations are not compatible with the hierarchy theory (e.g. O'Neil 1989), which predicts that the same environmental components should be correlated with bird variables at different scales. Our results suggest that it is difficult to extrapolate bird-habitat relationships derived from one scale to other scales.

We suggest that the overall structure of the landscape may determine the occupancy of birds at the regional level, but birds may locate their territories according to the quality of local habitats. Also, Rotenberry and Wiens (1980) concluded that birds of shrub-steppe habitat responded to elements of a general landscape at a large-scale, but within a habitat type their responses were associated with the details of habitat floristics. In our study, managed forest birds benefited from fragmentation at the large-scale, but the amount of edges was the most important factor at the small-scale. Within a habitat, the amount of deciduous trees was a positive component for the managed forest species. Fragmentation of coniferous forests by clear-cutting increases the amount of edges and young-aged successional stages with a high amount of deciduous trees or shrubs. Managed forest species may preferentially settle down in fragmented landscapes and locate their territories so that the amount of deciduous trees or shrubs are maximised, i.e. near the edge. Thus, both large- and small-scale phenomena affect habitat selection patterns of birds. The results are consistent with the view that a multiscale approach is essential in bird-habitat relationship studies (e.g. Rotenberry & Wiens 1980, Virkkala 1991b).

According to our results, the matrix features were more important than the structure of local habitat for some species or groups of birds (e.g. for managed forest species, habitat generalists, edge species, Willow Warbler), whereas the opposite was true for the other species (e.g. for migratory species, Pied Flycatcher). Based on this, birds' responses to landscape and habitat features were quite individualistic. The results by Pearson (1993) from bird communities wintering in Georgia, USA, support that view.

4.2. Importance of matrix

Large-scale matrix components explained 20–37% and small-scale matrix components explained 3–47% of the variation in the abundance of individual bird species or groups of birds when the matrix components were entered into the models. These observations are compatible with the results of Pearson (1993) and McGarical et al. (1995). In their studies, the landscape matrix variables accounted typically for about 50% of the variation of the individual bird species. Thus, species composition and abundances are dependent on factors at larger scales than the individual's immediate habitat. According to these observations, bird-habitat relationship evaluations, which are based only on a description of the individual's immediate habitat, are questionable.

From the conservation point of view, our results supported the idea that "no park is an island" (Janzen 1983), since the surrounding matrix affected so many bird species. In our case, the landscape was quite fine-grained as the average patch size was about 20 ha. Even quite large virgin forest patches (see e.g. Väisänen et al. 1986 (1 km^2), Helle 1986b (70 km^2)) surrounded by managed forests may not maintain their original bird community structure in the long run. Very large virgin forest areas, perhaps several hundreds of square kilometres, are needed for the conservation of virgin forest bird species (Virkkala 1987a, 1991a). However, because the proportion of protected areas is under 5% of the total land area of Finland (Anon. 1988), it is especially important how the surroundings of those areas are managed.

4.2.1. Effects of fragmentation

Large-scale fragmentation positively affected the abundance of managed forest species, habitat generalists and edge species. Positive impacts of forest fragmentation may be related to increased heterogeneity of landscapes (Roth 1976, Strelke & Dickson 1980, Hansson 1983, McGarical & McComb 1995). However, hole-nesters suffered from small-scale fragmentation. Our results agree with the observation that fragmentation favours widespread generalist species (Terborgh 1976, Whitcomb et al. 1976, Haila et al. 1994). This may have important consequences for the whole community structure. It is possible that habitat generalists or edge species may exclude species with higher conservation values, like forest-interior species with large home ranges, from the area (see e.g. Ambuel & Temple 1985, Askins & Philbrick 1987).

Fragmentation had a negative impact on the Redstart, whereas the Willow Warbler and the Song Thrush benefited from it. Since the Redstart is a mature forest specialist and the Willow Warbler a mosaic generalist (Raivio & Haila 1990), responses of those species to fragmentation are easy to understand. Song Thrushes breed mainly in mature forest, but frequently use other parts of mosaics (Raivio & Haila 1990). Therefore, increased mosaics of habitat may be advantageous for Song Thrushes. These observations coincide with the overall long-term population changes of those species. Redstarts have decreased, whereas Willow Warblers have increased in numbers along with fragmentation during the past few decades in Finland (Järvinen et al. 1977, Järvinen & Väisänen 1979).

4.2.2. Edge effect

We did not observe any edge effect at the large-scale matrix level. However, the amount of edges was one of the most important factors affecting birds at the small-scale matrix level. Helle (1983) and Virkkala (1987a) have shown that the amount of edges positively affected habitat generalists, edge birds and managed forest species, but negatively affected virgin forest species, hole-nesters and Redstarts. Our results agreed well with their observations. In our study area, the total amount of birds was positively related to the amount of edges at the small-scale matrix level. Higher bird densities near the edge may be due to the higher diversity of foliage layers or the presence of more than one habitat type (Strelke & Dickson 1980), denser shrub layers (Helle 1983) or richer invertebrate food supplies (Hansson 1983, Helle & Muona 1985) near the edges than in the forest interior. All these characteristics are found in edges in our study area (Jokimäki et al., unpublished). These positive features of edges may attract many birds, despite the fact that nesting near the edge may be dangerous due to increased nest predation (Gates & Gysel 1978). In our study area, one possible predator species, the Hooded Crow, had a positive association with fragmentation and areas with a high proportion of fields (see also Andrén 1992, Hinsley et al. 1995). However, in forest dominated landscapes, distance to the edge may not have an effect on predation rate (Rudnicky & Hunter 1993, Huhta 1995). The amount of edge had a negative impact on the Redstart, but a positive impact on the Willow Warbler (see also Helle 1983, Virkkala 1987a). We suppose that ground-nesting Willow Warblers benefit from increased field and shrub layer cover near the edges, providing shelter for their nests (see also Hinsley et al. 1995). However, hole-nesting Redstarts get little added protection against predators.

4.3. Importance of habitat structure

Within a habitat, both the vegetation structure (e.g. MacArthur & MacArthur 1961) and the floristic composition of habitat (e.g. Rotenberry 1985) may influence bird community composition. In our study, structural components explained 0–14% and floristic composition explained 3–35% of the variation in the abundance of individual bird species or groups of birds when the habitat components were entered into the models. The importance of structural and floristic composition for the birds differed between groups of birds or species. Hence, birds responded in an individualistic way to variations in habitat structure. Tree species diversity and foliage height diversity had only low loadings in principal component analysis. Therefore, they were not entered into any bird-habitat relationship models. Overall, floristic composition seems to be more important for birds than structural variables at the forest stand level (see also Rotenberry 1985).

Our results support the idea that at the small-scale birds may use floristic variables for territory selection (Hildén 1965, Bersier & Meyer 1994). In particular, the tree species composition had a great impact on birds. Mixed-tree species composition was beneficial for virgin forest birds, whereas managed forest species, habitat generalists and edge species preferred deciduous tree species composition. A high proportion of deciduous trees may be an indicator of a high quality breeding habitat for some species, since the insect fauna, which is an important food resource for birds, is richer in birch branches than in coniferous trees (Palmgren 1932). The importance of deciduous trees for the Willow Warbler may be related to its feeding behaviour. The Willow Warbler is a microhabitat specialist that mainly forages in birches (Virkkala 1988). However, Helle (1985a) did not find any importance of deciduous trees for individual bird species in Kuusamo, NE-Finland. One reason for the differing results may be that Helle used complicated habitat indices, such as foliage height diversity, which may have masked the importance of deciduous trees. Selection of different tree species in forest management may play an important role in bird conservation. From the viewpoint of conservation, mixed-tree species composition may be the best solution. However, too many deciduous trees may have a negative effect on sedentary bird species. For example, the Siberian Jay and Siberian Tit are specialists of coniferous forests, and the Siberian Tit prefers coniferous over deciduous trees both during nesting and fledgling periods (Virkkala 1988).

The stand age was one of the most important structural components for birds. Bird species richness, total amount of birds and hole-nesters were positively associated with stand age. Helle (1985b) and Virkkala (1987b) have reported a positive relationship between bird density and timber volume in northern coniferous forests. Our results agree with that since the stand age correlated positively with the tree volume ($r_S = 0.62$, $P < 0.001$). The high timber volume may indicate high overall productivity of those forest areas. In harsh northern conditions, the productivity of habitat is especially important for the survival and successful reproduction of birds. Migratory birds may use sedentary birds as indicators of the high quality habitats as both of these bird groups had a positive association with stand age in our study area. If this is true, heterospecific attraction may be an important factor affecting bird community structure in northern areas with overall low densities (Mönkkönen et al. 1990). The importance of old forests for sedentary birds has been demonstrated in many earlier studies (e.g. Järvinen et al. 1977, Helle 1985b). Moreover, old forests may be more favourable for sedentary species in winter time since they contain many more invertebrates than do managed forests (Pettersen et al. 1995).

Occurrence of snags was important for many bird species, especially for the virgin forest species and hole-nesters. Many studies have reported the decrease of hole-nesting birds due to forest management practices (Haapanen 1965, Helle 1985b, Virkkala 1987a, Virkkala et al. 1994). The obvious reason for that is the lack of suitable nesting trees in managed forests.

4.4. Management implications

The impacts of landscape matrix and habitat structure on birds were complex and species-specific. We suggest that consideration of both the landscape level and stand characteristics is necessary when forest management or reserve establishment plans are made. For example, landscape-level planning is needed to meet the area requirements of birds with large home ranges, while stand level planning can be used to ensure enough nesting places for hole-nesting birds. Although management practices increase overall habitat complexity, managing landscapes too heavily may result in an overall trivialization of bird communities and extinctions of local area-sensitive bird populations.

Fragmentation may increase the total amount of birds and already abundant bird species, but many conservationally valuable species, such as hole-nesters and virgin forest bird species, suffer from increased subdivision of habitats and creation of edges. The importance of old forests for many different kinds of birds was clear. It must be assured that enough old forests are left in the managed landscapes. The reduction of the deciduous component of forests may cause severe problems for many birds. Deciduous trees contain rich insect fauna for the food of breeding birds and old deciduous trees contain many suitable nesting places for many hole-nesting birds. However, too high a proportion of young-aged deciduous forests in the landscape may simplify the overall structure of bird assemblages since many habitat generalists and edge species benefit from deciduous shrubs. These habitat generalists are already very abundant and need no special assistance from man. Many reduced populations of sedentary bird species (e.g. Siberian Jay, Siberian Tit) feed mainly in conifers in winter time and a high proportion of young-aged deciduous forests in the landscape may reduce the food supply for wintering birds. Without sufficient knowledge of the importance of matrix structure, evaluation of bird-habitat relationships may be misleading.

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Selostus: **Habitaatin laadun ja ympäröivien alueiden vaikutukset pohjoiseen metsälintuyhteisöön: monimittakaavainen tarkastelu**

Lintujen elinympäristön valintaan liittyviä kysymyksiä tutkittiin pistelaskentamenetelmällä Rovaniemen maalaiskunnan metsäalueilla vuosina 1990–95 kolmella eri mittakaavatasolla; laajassa metsämaisemassa (4 km^2), suppeassa metsämaisemassa (4 ha) ja habitaatin sisäisessä (< 0.78 ha) tasossa. Habitaatti-tasolta mitattiin metsätieteellisin menetelmin elinympäristön rakennetta ja kasvillisuuden koostumusta kuvaavia muuttujia. Laskentapisteiden lähiympäristössä (4 ha) tehtiin metsäkuviokartoitus. Laaja-alaiset maisemapiirteet kartoitettiin ilmakuvien ja peruskarttojen avulla. Maisema- ja habitaattiaineistojen muuttujien määrää vähennettiin pääkomponenttianalyysin avulla. Muodostettujen pääkomponenttien ja lintujen välisiä suhteita tutkittiin askeltavan regressioanalyysin avulla. Tutkimuksemme kaksi pääkysymystä olivat: reagoivatko linnut samoihin ympäristötekijöihin eri mittakaavatasoilla ja mikä on habitaattilaikun laadun sekä niitä ympäröivien alueiden merkitys linnustolle? Aikaisemmissa tutkimuksissa on todettu sekä kasvillisuuden koostumuksen että rakenteen vaikuttavan lintujen esiintymiseen. Monissa tutkimuksissa ei kuitenkaan ole huomioitu riittävästi tutkimusalueita ympäröivien alueiden mahdollisia vaikutuksia paikallisen lintuyhteisön rakenteeseen. Lintujen esiintymistä ja runsautta selittävät ympäristötekijät ovat usein riippuvaisia tutkimuksessa käytetystä mittakaavasta. Tulostemme mukaan eri lajien ja lajiryhmien esiintyminen korreloi eri ympäristömuuttujiin eri mittakaavatasoilla. Esimerkiksi reunavaikutusta ei ollut havaittavissa laajan mittakaavan tarkastelussa, kun taas pienemmän mittakaavan tasolla reunojen määrä oli yksi keskeisimmistä lintuihin vaikuttavista ympäristötekijöistä. Havainto ei tue hierarkiateorian pääoletuksia, joiden mukaan samat ympäristötekijät vaikuttaisivat eliöihin eri mittakaavatasoilla. Tuloksemme korostavat monimittakaavaisen lähestymistavan merkitystä lintujen elinympäristövalinnan ja -käytön tutkimuksissa. Tulostemme mukaan laaja-alaiset maisematekijät olivat tärkeitä talousmetsien linnuille ja habitaattigeneralisteille, kun taas lähiympäristön rakennepiirteet olivat oleellisimpia vanhojen metsien linnuille. Maisematekijät selittivät jopa 40% lajiryhmien ja yksittäisten lajien tiheysvaihtelusta. Tärkeimmät maisematekijät linnuston kannalta olivat metsien pirstoutuminen ja reunavaikutus. Talousmetsien linnut, habitaattigeneralistit, reunalajit ja pajulintu hyötyivät, kun taas vanhojen metsien lajit, kololinnut ja leppälintu kärsivät metsäalueiden pirstoutumisesta sekä lisääntyneestä reuna-alueiden määrästä. Habitaatti-tasolla kasvillisuuden koostumus oli yleensä linnuille tärkeämpää kuin metsän rakenteelliset piirteet. Monipuolisesta puulajistosta oli hyötyä vanhojen metsien lintulajeille, kun taas habitaattigeneralistit ja reunalajit hyötyivät lehtipuiden suuresta määrästä. Metsien ikä oli tärkein rakenteellinen muuttuja. Lintujen lajimäärä, kokonaisparimäärä, kolopesijöiden sekä vanhojen metsien lintujen määrä korreloi positiivisesti metsikön iän kanssa. Tutkimuksemme perusteella näyttää siltä, että pienipiirteiset habitaatin laatuun liittyvät tekijät voivat olla keskeisiä joillekin lajeille, kun taas laaja-alaisemmat metsämaiseman rakennepiirteet voivat olla oleellisempia toisille lajeille.

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Appendices

Appendix 1. Ecological grouping of species and total amount of data. The five letters or – indicate from left to right: migratory habit (M = migratory, S = sedentary or partly migratory), prefered habitat type (V = virgin forest, M = managed forest or forest mosaics), habitat generalist (G), edge species (E) and holenesters (H). SUM is total number of pairs in the whole data 1990–1995.

	GROUPS	SUM
Accipiter gentilis (Goshawk)	SV – – –	3
Accipiter nisus (Sparrowhawk)	SV – – –	1
Bonasa bonasia (Hazel Grouse)	SV – – –	9
Lagopus lagopus (Willow Grouse)	SM – – –	4
Tetrao tetrix (Black Grouse)	SM – – –	28
Tetrao urogallus (Capercaillie)	SV – – –	7
Pluvialis apricaria (Gold Plover)	M – – – –	1
Vanellus vanellus (Lapwing)	M – – – –	1
Lymnocryptes minimus (Jack Snipe)	M – – – –	3
Gallinago gallinago (Common Snipe)	M – – – –	52
Scolopax rusticola (Woodcock)	M – – – –	1
Numenius phaeopus (Whimbrel)	M – – – –	49
Numenius arquata (Curlew)	M – – – –	61
Tringa nebularia (Greenshank)	M – – – –	54
Tringa ochropus (Green Sandpiper)	M – – – –	3
Tringa glareola (Wood Sandpiper)	M – – – –	92
Columba palumbus (Woodpigeon)	MM – – –	17
Cuculus canorus (Cuckoo)	MM – – –	680
Apus apus (Swift)	MV – – H	11
Dryocopus martius (Black Woodpecker)	SV – – H	18
Dendrocopus major (Great Spotted Woodpecker)	SV – – H	14
Picoides tridactylus (Three-toed Woodpecker)	SV – – H	4
Riparia riparia (Sand Martin)	M – – –	4
Hirundo rustica (Swallow)	M – – –	1
Delichon urbica (House Martin)	M – – –	1
Anthus trivialis (Tree Pipit)	MMGE –	653
Anthus pratensis (Meadow Pipit)	MM – E –	11
Motacilla flava (Yellow Wagtail)	MM – – –	5
Motacilla alba (Pied Wagtail)	MM – – –	1
Bombycilla garrulus (Waxwing)	SV – – –	13
Prunella modularis (Dunnock)	MM – E –	1
Erithacus rubecula (Robin)	MV – E –	91
Phoenicurus phoenicurus (Redstart)	MV – – H	640
Saxicola rubetra (Whinchat)	MM – E –	3
Oenanthe oenanthe (Northern Wheatear)	MM – – –	2
Turdus pilaris (Fieldfare)	MM – E –	7
Turdus philomelos (Song Thrush)	MV – – –	164
Turdus iliacus (Redwing)	MMGE –	207
Turdus viscivorus (Mistle Thrush)	MV – – –	93
Acrocephalus schoenobaenus (Sedge Warbler)	MM – – –	1
Sylvia curruca (Lesser Whitethroat)	MM – E –	1
Phylloscopus borealis (Arctic Warbler)	MV – – –	2
Phylloscopus trochilus (Willow Warbler)	MMGE –	2245
Regulus regulus (Goldcrest)	MV – – –	36
Muscicapa striata (Spotted Flycatcher)	MVGE –	71
Ficedula hypoleuca (Pied Flycatcher)	MV – – H	180
Parus montanus (Willow Tit)	SV – – H	89
Parus cinctus (Siberian Tit)	SV – – H	10
Parus cristatus (Crested Tit)	SV – – H	1
Parus major (Great Tit)	SV – – H	33
Certhia familiaris (Treecreeper)	SV – – H	1
Garrulus glandarius (Jay)	SM – – –	1
Perisoreus infaustus (Siberian Jay)	SV – – –	14
Pica pica (Magpie)	SM – – –	20
Corvus corone cornix (Hooded Crow)	SM – – –	123
Corvus corax (Raven)	SV – – –	59
Fringilla coelebs (Chaffinch)	MV – E –	202
Fringilla montifringilla (Brambling)	MVG – – –	1244
Carduelis chloris (Greenfinch)	SM – – –	7
Carduelis spinus (Siskin)	MV – – –	221
Carduelis flammea (Redpoll)	SMGE –	188
Loxia curvirostra (Crossbill)	SV – – –	110
Loxia pytyopsittacus (Parrot Crossbill)	SV – – –	27
Carpodacus erythrinus (Scarlet Rosenfinch)	MM – E –	1
Pyrrhula pyrrhula (Bullfinch)	SV – – –	31
Emberiza citrinella (Yellowhammer)	SM – E –	12
Emberiza rustica (Rustic Bunting)	MV – E –	26
Emberiza schoeniclus (Reed Bunting)	MM – – –	8

Appendix 2. Descriptions of the principal components of the habitat structure (HF1–HF5, HS1–HS5) and matrix data (MS1–MS5, ML1–ML4). "HF" denotes a floristic component of the habitat; "HS" denotes a structural component of the habitat; "MS" denotes a small-scale matrix component and "ML" denotes a large-scale matrix component. Only the three highest loadings are shown for each component.

HABITAT	
HFspruce	Amount of spruce (spruce layer 1–3 m 0.85, total number of spruces within a circle of 3.3-m radius 0.78, spruce layer 3–5 m 0.78)
HFdecid.	Amount of deciduous trees (deciduous tree layer 1–3 m 0.91, deciduous tree layer 3–5 m 0.89, proportion of deciduous trees 0.85)
HFpseedl.	Amount of pine seedlings (pine layer 1–3 m – 0.84, total number of pines within a circle of 3.3-m radius – 0.79, pine layer 3 –5 m – 0.69)
HFmixed	Mixed tree species composition (pine layer 10–15 m – 0.73, deciduous tree layer > 15 m 0.60, spruce layer > 15 m 0.54)
HFlpines	Total number of large pines within a circle of 3.3-m radius (pine layer > 15 m – 0.72, total number of spruces within a circle of 3.3-m radius, – 0.74, pine layer 5–10 m 0.58)
HSshrubs	Shrub layer (proportion of tree layer 1–3 m 0.89, proportion of tree layer 10–15 m, total number of shrubs within a circle of 3.3-m radius 0.67)
HSage	Age (tree height 0.83, age 0.76, tree volume 0.76)
HSdensity	Tree density (proportion of tree layer > 15 m – 0.88, total number of stems within a circle of 3.3-m radius 0.86, proportion of tree layer 5–10 m 0.71)
HSsnags	Amount of dead trees (total number of hardwood snags within a circle of 3.3-m radius 0.85, total number of barkless trees within a circle of 3.3-m radius 0.80, foliage height diversity 0.53)
HSdwarfs	Dwarfs (proportion of dwarfs in field layer 0.81, tree species diversity 0.58, tree volume 0.29)
MATRIX	
MSedge	Amount of edges (proportion of forests – 0.85, proportion of pine swamps 0.80, total length of edges 0.79)
MSfrag.	Fragmentation (proportion of mixed forests 0.73, amount of standfigures 0.71, proportion of pine forests – 0.68)
MSseedl.	Proportion of seedling areas (proportion of seedling areas 0.80, proportion of spruce forests 0.51, proportion of pine forests – 0.46)
MSfields	Proportion of fields (proportion of fields 0.81, proportion of deciduous forests 0.47, proportion of open bogs – 0.38)
MSroads	Amount of roads (total length of roads 0.89, proportion of spruce swamps 0.78, amount of stand figures 0.33)
MLfrag.	Fragmentation (proportion of deciduous forest 0.78, proportion of pine forests – 0.78, amount of stand figures 0.74)
MLopen	Proportion of open areas (proportion of pine swamps 0.82, proportion of forests – 0.71, total length of roads 0.68)
MLspruce	Proportion of spruce forests (proportion of spruce forests 0.88, proportion of seedling areas – 0.54, proportion of deciduous forests 0.60)
MLedge	Amount of edges (total length of edges 0.83, proportion of spruceswamps 0.78, amount of stand figures 0.33)