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Patterns and variations in the structure of forest bird communities in southern Finland

Tapio Solonen

Solonen, T., Department of Ecology and Systematics, Division of Population Biology, P.O.Box 17, FIN–00014 University of Helsinki, Finland; Present address: Solonen, Neitsytsaarentie 7 b B, FIN-00960 Helsinki, Finland

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Species richness and density of forest birds in relation to habitat area and characteristics were studied on the basis of census data from various localities in southern Finland. The number of species increased with increasing size of the study area, firstly steeply up to a plot size of about 10 ha, and then progressively more gently sloping. The number of species increased significantly with increasing bird density as well. The expected number of species per ha averaged 7.0±0.4 (SE) and ranged from 3 to 12. In the standardized sample size of 50 pairs, the number of species averaged 20.7±0.3 (SE) (range 16–26). Species richness had a significant positive relationship with the amount of edges. There was a significant dependence between the number of species and forest productivity in larger (5.0–55.0 ha) study plots, but not in a set of smaller (0.2–10.0 ha) ones. The number of species had a significant positive relationship both with the age and amount of trees, and it also coincided with the intensity of thinning of forests. The bird density decreased with increasing study area. The relative but not absolute amount of edges showed a highly significant positive relationship with bird density. Densities of birds were, in general, higher in the more productive study sites. The average bird densities of the main forest types ranged from about 440 to 1060 pairs/km^2. The general average bird density in forests was 668.8±57.2 (SE) pairs/km^2. Bird densities varied significantly between forest types, coniferous forests differingnsignificantly from mixed and deciduous forests. Forests that were relatively light (open) due to a moderate amount of trees seemed to be most attractive for birds. The evenness of communities decreased significantly with increasing productivity of habitat. Species abundance distributions, in general, approximately fitted to the lognormal distribution. Two dominant species of the total data set together comprised a third of the total number of pairs. Some general features of habitat (such as patch size, amount of edges and productivity) explained part of the variation in the structure of forest bird communities. This proportion was not very high, however, particularly at larger geographical scales.

1. Introduction

The availability of essential resources for individual birds is evidently the limiting component on the structure of a bird community (Wiens 1989). Variations in the structure of bird communities can largely be assigned to spatial and temporal environmental variations. Forest habitats are characterized

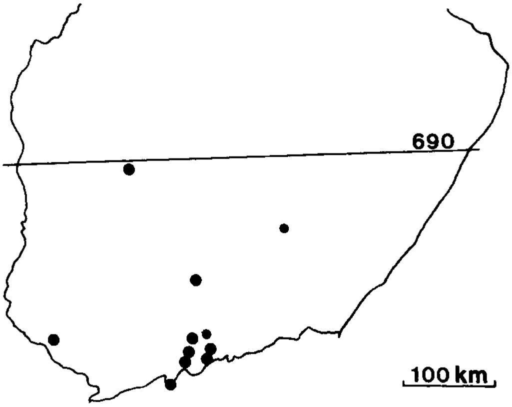

Fig. 1. Distribution of the study areas in southern Finland, south of the uniform grid coordinate 690 (62°N). Small dots denote single study plots, large dots groups of study plots (cf. Table 1).

by a high degree of heterogeneity at scales that are likely to be important for birds (Shugart 1990). Variations in spatial configuration, productivity, and vegetational diversity of habitats, for instance, can be expected to affect the species richness and abundance of forest birds. Even some general features of habitat that are more easily characterized than the availability of the resources itself might explain variation in the structure of forest bird assemblages (cf. MacArthur 1972, Willson 1974, Nilsson 1979, James & Warner 1982, Helle 1986, Haila & Järvinen 1990, Holmes 1990, Tomiałojć & Wesołowski 1990, Solonen 1994c).

In many studies of forest bird communities, forest area has been found to explain a high proportion of the variation in species numbers (Opdam et al. 1985, Ford 1987, Hinsley et al. 1995). Because of stochasticity and different spatial and habitat requirements of species, species richness should increase with increasing area (cf. MacArthur & Wilson 1967, May 1975, Haila 1983, Helle 1984, Wiens 1989). The number and abundances of species have been found to increase with increasing heterogeneity and fragmentation of habitat (e.g., Järvinen et al. 1977, Hansson 1983, Helle & Järvinen 1986, Haila et al. 1987, Haila & Järvinen 1990). Increasing productivity and ecological succession (increasing availability of bushes) generally affect birds in the same direction (see Palmgren 1930, Merikallio 1946, MacArthur & MacArthur 1961, Haapanen 1965, Odum 1969, Järvinen & Väisänen 1973, 1980, Røv 1975, Nilsson 1979, Cody 1985, Helle 1985, Raivio & Haila 1990, Helle & Mönkkönen 1990). These effects are probably due to an increase in the availability of niches and other resources.

The evenness of communities also seems to vary with the amount of resources provided by the environment and thus also with sample size, i.e., the size of the study area or density of birds (cf. Tramer 1969, Alatalo & Alatalo 1980, Alatalo 1981). Species abundance distributions commonly coincide with the canonical lognormal distribution (Preston 1948, 1962, Sugihara 1980), especially if the community contains many species (Wiens 1989, Solonen 1994b). A close fit to some other models, such as the geometric series or the broken stick distributions, has seldom been met (Wiens 1989).

This paper is an attempt to describe patterns and assess the degree of variations in southern Finnish forest bird communities. A forest bird is defined here as a species that is restricted to forest, is dependent on it, or whose centre of distribution is forest, including scrubby habitats of forest edges (cf. Keast 1990, Tomiałojć & Wesołowski 1990). A primary goal of the present study is to demonstrate what kinds and how many species and individuals occur in various forest areas, particularly in order to elucidate the range of variation in species richness and bird density, and the implications of some general measures of habitat. Another general aspect of the study is to evaluate how well the present data fit to the general features of forest bird assemblages described above.

2. Material and methods

The study areas were situated in the hemiboreal and south–boreal zoogeographical zones (Järvinen & Väisänen 1980) in southern Finland (60–62°N, 22–27°E) (Fig. 1). The data used included results of my own bird censuses and census interpretations as well as appropriate information from other sources, totalling 125 census plots (Table 1). To improve the generality of results, the spatial scale of investigation included both a local level of neighbouring study plots and a regional level covering southern

Finland (cf. Wiens et al. 1986, 1987, Wiens 1989, Virkkala 1991). To cover the whole forest bird fauna of the region, including sparse and restricted species, as comprehensively as possible and for environmental analysis, study areas of various size and habitats were investigated. Thus, they included small, more or less homogeneous habitat patches (averaging 1.5±0.3 (SE) ha, $n = 51$), regular mapping plots (of more than three surveys, averaging 13.8±1.6 (SE) ha, $n = 68$), and six larger study areas monitored by the mapping method or by a combination of the territory mapping and line transect methods. There was no correlation ($r_S = 0.20$, $n = 48$, ns) between the number of visits and bird density in the mapping plots, suggesting that the results of different censuses were in this respect comparable. The number of visits was also taken into consideration in interpreting the mapping data (for details of the census methods, see Koskimies & Väisänen 1991). To minimize the risk of unrealistically high estimates, densities for single species in each sample were calculated only if the species were repre-

Table 1. Sources of the data used. Data included both mapping plots of various size and larger study areas monitored by a combination of the mapping and line transect methods. The number of different plots in parentheses. The area covered by the censuses (km^2), census years, and the number of visits in each census are given.

Data	Area	Years	Visits	Sources
Local habitat patches				
Vantaa, Ojanko (51)	0.770	1989–91	5	1,2
Regular mapping plots				
Vantaa, Ojanko (10)	1.311	1989–91	5	1, 2
Vantaa, Mustavuori (2)	0.520	1985–87	5	3, 4
Vantaa, western (5)	1.170	1987–88	4–8	5, 6, 7
Kauniainen (6)	0.863	1989–90	4–5	8, 9
Sipoo, Hindsby (2)	0.360	1990	4–5	10
Nurmijärvi, Myllykoski (1)	0.087	1987	8	11
Tuusula, Harminsuo (1)	0.200	1988	4	12
Järvenpää, Lemmenlaakso (1)	0.200	1991	4	13
Kirkkonummi, Hirsala (5)	0.300	1980	14	14
Lammi, Pappila (4)	1.638	1980–83	13	15
Lammi, biol. station (1)	0.250	1982	4	16
Lammi, Kaurastensuo (2)	0.735	1975–76	7	16
Turku, Ruissalo (12)	1.278	1971–81	8	17
Kuru, Seitseminen (15)	0.313	1985	4	18
Mäntyharju, Mäkelä (1)	0.140	1981	>20	19
Larger mapping plots				
Kirkkonummi (1)	1.64	1980	14	14
Helsinki (1)	0.84	1990	4	16
Kauniainen (1)	0.82	1988	4	22
Other larger census areas				
Vantaa (1)	90	1987–91	..	20, 21
Sipoo (1)	6	1990	..	10
Turku (1)	5	1971–81	..	17

Sources: 1. Solonen 1991a, 2. Solonen 1992a, 3. Solonen & Saarikko 1987, 4. Solonen 1988b, 5. Rajasärkkä & Virolainen 1987, 6. Rajasärkkä & Virolainen 1988, 7. Solonen 1988c, 8. Solonen & Simula 1989, 9. Solonen & Simula 1990, 10. Solonen 1991b, 11. J. Laaksonen & T. Solonen, unpubl., 12. A. Aaltonen & S. Niiranen, unpubl., 13. Lavinto & Niiranen 1992, 14. Tiainen et al. 1984, 15. Virolainen 1988, 16. T. Solonen, unpubl., 17. Gustafsson et al. 1982, 18. Haila et al. 1987, 19. Palmgren 1987, 20. Rajasärkkä & Virolainen 1989, 21. Solonen 1992b, 22. Solonen 1988a.

sented by more than one pair, because territory sizes were not measured. In the case of the small local habitat patches, the territories were divided between the neighbouring plots on the basis of their centres of gravity. In fact then, the total bird density, especially in the smallest patches, was composed of parts of often overlapping territories of different species.

Out of 109 terrestrial bird species characteristically breeding in real forests or in scrubby habitats of early stages of forest succession in Finland (Solonen 1994a), the present census data included 84 species occurring more or less regularly and commonly in southern Finland (Appendix). The distributional data of the total number of forest bird species occurring in the geographical range of the study in southern Finland (south of the national grid coordinate 690; Fig. 1) (107) were from the first Finnish bird atlas (Hyytiä et al. 1983).

In order to characterize some factors possibly affecting the structure of the bird communities considered, I studied relationships between species richness and bird density as well as habitat area and various habitat variables. For environmental analyses, forest habitats were characterized, if possible, by dominant trees (pine, spruce, deciduous) and also by the abundance of edges (km), the relative amount of edges (km/ha), productivity as indicated by forest type (Cajander 1949), amount of trees (m^3/ha) (Forestry management plan, Vantaa 1989), successional stage (age of trees in yrs), density of holes (nest-boxes), and intensity of management (thinning) (Table 2). The indices of productivity and management were considered to be of the ordinal scale of measurement. If forest types could not be considered as pure (or homogeneous), especially in the case of larger study plots, they were characterized by the dominant forest type. In southern Finland, in general, pine, spruce, mixed and deciduous forests largely correspond, with increasing productivity, to the forest types VT, MT, OMT and OMaT, respectively.

To study the variation in species numbers, the samples were standardized by area, and, if the data were large enough for the procedure, also to a common sample size of 50 pairs, by rarefraction (Ludwig & Reynolds 1988; usually spelt rarefaction, e.g., James & Rathbun 1981, Wiens 1989). In general, log-transformation was used to normalize the data. Significance of differences between means was established by the analysis of variance, and pairwise multiple comparisons were evaluated with the Tukey–Kramer test (Sokal & Rohlf 1981). In the case of heteroscedasticity (revealed by Bartlett's test), unplanned comparisons among pairs of means were done using the Games–Howell method (Sokal & Rohlf 1981). The evenness of communities was measured by the modified Hill's ratio (Alatalo 1981, Ludwig & Reynolds 1988). The approximate goodness of fit of the species abundance distributions to the

Table 2. Characterization of habitats and measurements or indices used in the analyses. Forest types (Cajander 1949) corresponding to the productivity gradient are coded as follows: VT = *Vaccinium*, MT = *Myrtillus*, OMT = *Oxalis-Myrtillus*, and OMaT = *Oxalis-Maianthemum* type. Successional stages follow the scheme by Haapanen (1965).

Characteristic of habitat	Measurements or indices
Amount of edges	Measured (km), or 1 = scanty, 2 = moderate, 3 = abundant
Productivity	1 = VT, 2 = VT/MT, 3 = MT, 4 = MT/OMT, 5 = OMT, 6 = OMaT
Amount of trees	Estimated (m^3/ha)
Age of trees (successional stage)	5 yrs = open brush, 10 yrs = closed brush, 20 yrs = thicket, 50 yrs = young stand, 75 yrs = old stand
Density of holes	Number of nest–boxes/ha
Management (thinning)	0 = no management, 1 = slightly, 2 = moderately, and 3 = heavily thinned

lognormal distribution was estimated with chi-square statistics (Ludwig & Reynolds 1988) and by Kolmogorov–Smirnov tests (Sokal & Rohlf 1981).

Correlation and regression analyses (Sokal & Rohlf 1981) were used for the general environmental interpretation of the community data. To elucidate further those environmental factors that might be important in determining the structure of the communities from which the study plot samples were drawn, sampling units were also arranged within synthetic axes, based on their dissimilarities in occurrence and abundance of species, by the principal components analysis (PCA) (Ludwig & Reynolds 1988).

3. Results

3.1. Number of species

The number of species increased with increasing size of the study area ($y = 7.89*x^{0.38}$; $r = 0.76$, df = 123, $P < 0.001$), firstly steeply ($b = 0.67$) up to a plot size of about 10 ha, and then progressively more gently sloping ($b = 0.18$) (Fig. 2). The expected number of species per ha (by rarefraction) averaged 7.0±0.4 (SE) and ranged from 3 to 12 (n = 44). The atlas grid data from the same general area, from 12 100*100 km squares, showed on average 96.3±0.6 (SE) (range 92–99) of the total of 107 species. In the local set of 51 small (0.2–10.0 ha) neighbouring habitat patches, the slope varied between 0.51 and 0.65 in three years, being 0.45 if the data over the years were combined. In the total data set, the number of species increased significantly with increasing bird density as well ($y = 0.83*x^{0.42}$; $r = 0.32$, df = 123, $P < 0.001$) (Fig. 3). In the small, local habitat patches this relationship was even steeper ($b = 0.73$).

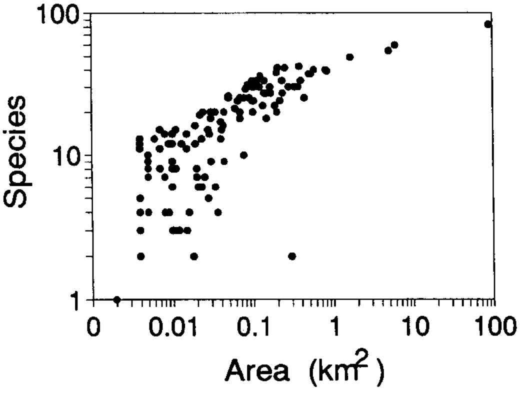

Fig. 2. The relationship between the number of species of forest birds and the size of the study area (km^2) (n = 125) in various forest habitats in southern Finland.

The increase in the number of species with increasing sample size seemed to be largely due to an increase in the size of the study area ($r^2 = 0.58$), and less due to an increase in bird density ($r^2 = 0.10$) (cf. above). When the data (that were large enough

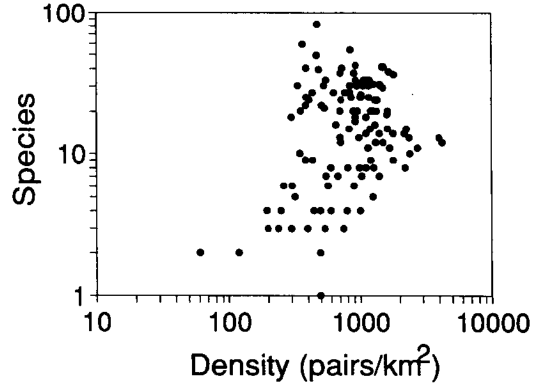

Fig. 3. The relationship between the number of species of forest birds and total bird density (pairs/km^2) (n = 125) in southern Finland.

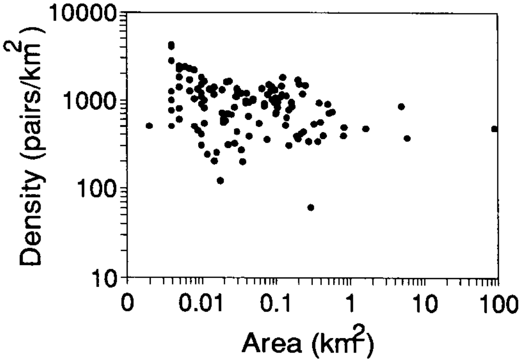

Fig. 4. The relationship between the density of breeding forest birds (pairs/km^2) and the size of the study area (km^2) (n = 125) in southern Finland.

for the procedure) were standardized (by rarefraction) to a common sample size of 50 pairs, the number of species varied relatively little (averaging 20.7±0.3 (SE); range 16–26) and independently of the size of the study area ($r = -0.10$, df = 46, ns) and the density of birds ($r = 0.19$, ns).

There were many significant relationships between the number of species and various environmental variables (Table 3). The number of species was, in general, significantly related to the abundance of edges. In small habitat patches, however, there was no such relationship with the relative amount of edges. There was a significant dependence between the number of species and productivity in the regional set of larger study plots, but not in the local set of small habitat patches. The number of species had a significant positive relationship with the amount and age of trees in the local habitat patches. It also coincided, however, positively with the intensity of management (thinning) of forests.

3.2. Bird density

The bird density decreased gently with increasing study area ($y = 567.69*x^{-0.11}$; $r = -0.29$, df = 123, $P < 0.01$) (Fig. 4). The highest densities were found in small island-like patches. Densities varied greatly, however, especially between the smallest patches, which also exhibited diverse habitats.

The bird density showed a highly significant positive relationship with the relative (but not absolute) amount of edges in the small patches, contrary to the situation with the number of species (Table 3). Densities of birds were, in general, higher in the more productive study sites. They also showed positive relationships with the age of trees and density of nest-boxes.

The average bird densities of the main forest types ranged from about 440 to 1060 pairs/km^2 in the relatively heterogeneous habitats of the largish regular mapping plots (Table 4). The general average density in this sample was 668.8±57.2 (SE) pairs/km^2. Bird densities varied significantly between forest types ($F = 12.52$, df = 2, 42, $P < 0.001$), coniferous forests (VT, MT) differing significantly from mixed and deciduous forests (OMT, OMaT) (Tukey–Kramer test, $P < 0.05$).

A more detailed description of the relationships between the bird density and various habitat characteristics was provided by the data from the most homogeneous habitat patches studied (Table 4). In these small plots, the average bird density was at its lowest(6.6 pairs/ha) in pine-dominated VT-forests and at its highest (15.8 pairs/ha) in mixed or deciduous OMT-forests, corresponding to the assumed productivity gradient of the forest types. The average bird densities for the forest types considered differed significantly from each other (Games–Howell test, $P < 0.05$). The differences were largely similar also when the categorization was based on the

Table 3. Relationships (correlation coefficients r or r_S) of the number of species (S) and bird density (D) with some environmental variables (Table 2) in a regional set of study areas (5.0–55.0 ha; n = 44) and in a local set of smaller habitat patches (0.2–10.0 ha; n = 51) in southern Finland. SP denotes the number of species standardized by the number of pairs, SA the number of species standardized by area. Significance of the relationships is given as follows: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Environmental variable	rr_S	Study plots				Habitat patches	
		S	SP	SA	D	S	D
Amount of edges	r	–	–	–	–	0.63 ***	0.05
Edges per area	rr_S/r	0.28 *	0.02	0.48 **	0.45 **	–0.14	0.48 ***
Productivity	r_S	0.48 **	0.18	0.61 **	0.62 **	0.19	0.24 *
Amount of trees	r_S	–	–	–	–	0.66 **	0.34 *
Age of trees	r_S	–0.09	0.01	0.09	0.08	0.43 **	0.28 *
Density of holes	r_S	0.03	–0.02	0.31 *	0.32 *	–	–
Management	r_S	–	–	–	–	0.34 *	–0.01

dominant tree type.

Forests that were relatively light (open) due to a moderate amount of trees seemed to be most attractive for birds (Table 4), the difference being significant between each of the three categories (Games–Howell test, $P < 0.05$). The average bird density in young and older forests (14.6 pairs/ha) was about two-fold compared to that of brush habitats (7.1 pairs/ha) (Table 4). The average bird densities differed, in general, significantly between the age classes of forests (Games–Howell test, $P < 0.05$). There was, however, considerable variation due to forest type. In the spruce-dominated MT-forests the main difference was between young and old stands, while in the largely deciduous OMT-forests the difference was between brush and older stands.

3.3. Patterns of species abundance

The evenness of communities (modified Hill's ratio between 0.51 and 0.94) decreased significantly with increasing size of the study area ($r = -0.49$, $df = 42$, $P < 0.001$) and with increasing productivity of habitat ($r_S = -0.42$, $n = 44$, $P < 0.01$). In the study areas where the number of species was relatively low, abundance distributions were relatively even, while in areas where the number of species was relatively high, there were large differences in abundance between species ($r = -0.50$, $P < 0.001$). There was, however, no correlation either between evenness and the number of species standardized by area ($r = 0.03$, ns) or between evenness and density ($r = -0.09$, ns).

Species abundance distributions, in general (Appendix), approximately fitted to the lognormal distribution (based on chi-square statistics and Kolmogorov–Smirnov tests). The dominant species of the total data set, *Fringilla coelebs* (25.0%) and *Phylloscopus trochilus* (11.5%), together comprised a third of the total number of pairs. Other most abundant species, in order of their numerical importance, included *Erithacus rubecula* (5.0%), *Parus major* (5.0%), *Muscicapa striata* (4.9%), *Anthus trivialis* (4.3%), *Ph. sibilatrix* (3.7%), *Regulus regulus* (3.7%), *Turdus merula* (3.6%), and *T. iliacus* (3.5%).

In a PCA of the regional set of bird communities (plot size between 5.0 and 55.0 ha), the first three principal components (PC I, PC II and PC III,

Table 4. Average bird densities (pairs/ha) in different forest types in relation to some other characteristics of forest habitats (dominant tree, age of trees, amount of trees) in small local study plots (Vantaa, Ojanko 1989–91, total area 77.7 ha). For comparisons, also the regional average bird densities of corresponding forest types in a set of regular mapping plots (total area 508.4 ha, not including nest-box areas) in southern Finland are given. The number of plots monitored in parentheses.

	Main forest type			
Local plots	VT	MT	OMT/OMaT	Average
Dominant tree				
Pine	6.6 (5)	8.6 (3)	–	7.4 (8)
Spruce	–	12.4 (13)	11.9 (2)	12.3 (15)
Deciduous	–	18.7 (12)	19.5 (16)	15.8 (28)
Amount of trees (m^3/ha)				
< 100	6.6 (5)	8.2 (6)	13.1 (8)	9.8 (19)
100–200	–	17.5 (10)	18.6 (9)	18.0 (19)
> 200	–	12.1 (12)	12.3 (1)	12.1 (13)
Age of trees				
Brush	–	7.3 (4)	6.8 (4)	7.1 (8)
Young	–	8.9 (3)	18.7 (7)	15.8 (10)
Old	6.6 (5)	14.9 (21)	18.0 (7)	14.3 (33)
Local averages	6.6 (5)	13.2 (28)	15.8 (18)	13.5 (51)
Regional averages	4.4 (17)	6.6 (18)	10.6 (8)	6.7 (45)

respectively) accounted for 17.6%, 12.0% and 9.2%, in total 38.8% of the variation. PC I was negatively correlated in particular with the abundance of species preferring rich deciduous forests (such as *Luscinia luscinia, T. iliacus, Ph. trochilus, P. caeruleus, P. major*). PC II was negatively correlated especially with the abundance of species preferring spruce forests (such as *E. rubecula, T. philomelos, Ph. sibilatrix, R. regulus, P. ater*). PC III was positively correlated particularly with the abundance of hole-nesting species preferring rich habitats (such as *Columba oenas, Dendrocopos minor, P. caeruleus, Corvus monedula, Sturnus vulgaris*).

The features of community structure characterized by the PCA coordinates of the species abundance distributions of the regional set of bird communities were significantly correlated with various environmental factors (Table 5). The correlation was positive between PC I and the size of the study area, but negative between PC I and the amount of edges, productivity, and the abundance of nest-boxes. PC II was negatively correlated with productivity but showed no significant relationships with the other variables studied. PC III was negatively correlated with the amount of edges and positively correlated with productivity. At its best, the size of the study area alone explained only 10.3% of the variation on PC I.

In a PCA ordination of the species abundance distributions of the 51 local habitat patches, the first three components accounted for 26.2%, 9.4% and 6.4%, in total 42.0% of the variation. PC I was positively correlated with the abundance of a great number of species (such as *A. trivialis, E. rubecula, T. merula, R. regulus, F. coelebs*) many of them preferring spruce forests. PC II was positively correlated especially with the abundance of species preferring deciduous forests and edges (such as *L. luscinia, T. pilaris, Sylvia borin, S. atricapilla, Emberiza citrinella*). PC III was positively correlated with the abundance of some secondary hole-nesters (*C. oenas, P. caeruleus, C. monedula*) and negatively correlated with that of two open-nesters (*S. borin, Carpodacus erythrinus*), all these species preferring edges and rich habitats.

The PCA revealed significant relationships between the bird assemblages of the habitat patches and the environmental factors studied (Table 6). PC I was significantly correlated with all the variables studied except productivity. PC II was positively correlated with the amount of edges and productivity. At its best, the size of the study area alone explained 79.4% of the variation.

4. Discussion

4.1. Species richness

The number of species increased, following the general rule, with increasing sample size. Large study areas included more species that were wide-ranging and, accordingly, sparse and less common. Such species were excluded from the data of small plots. The general slope of the relationship (0.42) was somewhat higher than theoretical expectations (0.20–0.35; MacArthur & Wilson 1967, May 1975). Much higher values than expected might be due to incomplete censuses (Helle 1984). Differences in habitats have also caused variation in the patterns of the present data as well as in other studies (cf., e.g., MacArthur & Wilson 1967, Johnson 1975, Helle & Helle 1982, Ambuel & Temple 1983, Järvinen & Haila 1984). The nonlinearity in the

Table 5. Relationships between the PCA coordinates (PC I, PC II and PC III) of a regional set of forest bird communities (n = 42, S = 56) and certain environmental variables (Table 2). Correlation coefficients (r or r_S) and their significance (* = $P < 0.05$, ** = $P < 0.01$) are given.

Environmental variable	r/r_S	PC I	PC II	PC III
Size of the study area	r	0.321 *	0.221	–0.167
Amount of edges per area	r_S	–0.597 **	–0.109	–0.550 **
Productivity	r_S	–0.332 *	–0.401 **	0.291 *
Successional stage	r_S	–0.015	–0.077	0.211
Density of holes	r_S	–0.476 **	–0.136	–0.008

species-area relationship of the present data was pronounced when compared with data from islands (Rusterholz & Howe 1979, Haila 1983) and from isolated forest fragments (Howe 1984). However, species-area relationships seem to be nonlinear commonly and at various spatial scales (Wiens 1989).

Stochastic effects are more pronounced in small than in larger areas. It can be expected that with an increase in size of the study area, the heterogeneity of habitats also increases. Species richness increases with increasing area due to the logical increase in the sample size, but evidently at the same time the heterogeneity or diversity of habitats also increases, providing niches for new species. Correspondingly, the number of species coincided with the intensity of management (thinning) of forests, probably due to the increase of niches provided by the enhanced bush layer. For species richness, the heterogeneity of habitats seemed to be a more important characteristic than their productivity.

In standard sample size, the high expected number of species in less densely populated habitats may primarily be due to a larger area needed for a similar-sized sample, and thus possibly caused by higher heterogeneity of habitats (cf. MacArthur & Wilson 1967, Haila 1983). Variation in the number of species was at a similar order of magnitude in a wide range of habitats (cf. Preston 1960, Haila 1983, Haila & Järvinen 1990). In a longer time scale, the local differences were even less than suggested by single-year data.

4.2. Factors affecting bird densities

Relationships of bird densities with certain environmental factors largely followed the patterns expected. In Finland, bird densities in forests are, in general, clearly higher than in other habitats (e.g., Solonen 1994b), and they increase with increasing site productivity (see also Palmgren 1930, Haapanen 1965). In southern Finland, poor forests are more common than rich forests and most forests are intermediate in productivity (Uusitalo 1989). Thus, on average, the forest bird density should decrease with increasing size of a study area, because probably progressively more poor than rich habitats would be included in a sample (cf. Ambuel & Temple 1983, Rafe et al. 1985, Haila et al. 1987). In addition, in small plots the relative amount of edge zones, which usually include attractive habitats for birds (cf. Helle & Helle 1982, Haila et al. 1983, 1987, Hansson 1983, Rosenberg & Raphael 1986, Wiens 1989), is often higher than in larger homogeneous areas.

The major increase in total bird density during the early stages of succession was in accordance with earlier findings. During the later stages, however, various alternative patterns have been demonstrated (see, e.g., Haapanen 1965, Odum 1969, Helle 1986, Helle & Mönkkönen 1990). The overall proportion of tropical migrants is found to be highest in the early phases of forest succession, while overall density of migrants peaks in the intermediate stages (Mönkkönen 1991).

4.3. Species abundance distributions

Following the increasing total density with increasing productivity, the evenness of communities decreased largely due to an increase in density of the most abundant species. This shift in the structure of communities can be described by a change in a

Table 6. Relationships between the PCA coordinates (PC I, PC II and PC III) of bird assemblages (S = 45) of 51 local forest patches (0.2–10.0 ha) and certain environmental variables (cf. Tables 2 and 5). Correlation coefficients (r or r^S) and their significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) are given.

Environmental variable	r/r^S	PC I	PC II	PC III
Size of the study area	r	0.891 ***	0.172	–0.080
Amount of edges	r	0.582 ***	0.587 ***	–0.174
Edges per area	r	–0.292 *	0.232	–0.139
Productivity	r^S	0.018	0.366 **	–0.039
Amount of trees	r^S	0.757 **	–0.076	–0.026
Age of trees	r^S	0.562 **	–0.111	0.125

lognormal distribution to a steeper shape (cf. May 1975, Røv 1975, Pielou 1977, Svensson et al. 1984, Wiens 1989). The biological interpretations of lognormal species abundance distributions have, however, been controversial (e.g., May 1975, 1984, Sugihara 1980, 1989, Harvey & Godfray 1987, Wiens 1989, Pagel et al. 1991, Solonen 1994b).

The original derivation of the lognormal model (Preston 1948, 1962) was based on the assumption that the community is at equilibrium. It has been found that data from disturbed, nonequilibrial communities do not fit the lognormal distribution (Ugland & Gray 1982). This suggests that some of the scatter of data sets about a lognormal distribution may reflect varying degrees of departure from equilibrium (Wiens 1989). However, it does not warrant the conclusion that a close fit of observations to the model certifies that the community is in equilibrium.

The relationships between the PCA coordinates of the species abundance distributions and environmental variables suggest, that some general features of habitat patches such as area and productivity explain a part of the variation in the structure of forest bird communities. This proportion is not very high, however, particularly at larger geographical scales. The proportional contribution of many environmental factors to the variation in the community structure decreases with increasing size of study areas probably because of the simultaneously increasing array of contributory factors.

4.4. Methodological aspects

The mapping method using four visits can be considered adequate for detecting breeding bird species (cf. Haila & Hanski 1984, Hinsley et al. 1995). However, the census efficiency always varies for several reasons, causing some variation in density estimates. This variation is partly due to the effect of differences in habitats, and to species-specific differences in the detectability of birds at the community level and in groups of species. To make estimates between censuses and between species as comparable as possible, observations of various species cannot be considered by strictly similar standards, but different features of species have to be taken into account when choosing methodology (cf., e.g., Ralph & Scott 1981, Järvinen & Väisänen 1983, Koskimies & Väisänen 1991). The interpersonal variation in density estimates may, however, be considerable (Svensson 1974, Ralph & Scott 1981, Morozov 1994).

Methodological variations probably have not affected seriously the results of the present study — density estimates of different sources for same species and similar habitats seemed to be comparable. Categorization of larger study areas by dominant tree and forest type was somewhat arbitrary, however, due to known or probable variation of these characteristics within the areas. The present data were somewhat concentrated in richer habitats. Thus, the general average densities given are not quite representative for generalizations, but they are probably somewhat higher than the real average forest bird densities of the region.

In this study, the rarest species were not included in estimating local densities of individual species but the range of variation in estimates was still wide, when the sample size was small. Thus, estimates based on small number of pairs must, in general, be considered more uncertain than those based on larger samples. Accordingly, the larger the area, the less the number of pairs affects density estimates (cf. also van Horne 1983). On the other hand, simultaneously the census efficiency diminishes.

Density calculated per habitat patch may be misleading in cases where birds include several patches of different habitats in their territories (Haila et al. 1987, 1989). So, it may be difficult to conclude the importance of different habitats for a species, and this concerns also the proportion of the area of a territory that should be included in data in border cases. Average densities per patch type may be unrealistic and unreliable in mosaic-like habitats (see also Scherner 1981, Haila 1988). In addition, there seems to be an unknown amount of stochasticity inherent in year-to-year site selection patterns of birds. Thus, a picture of how breeding pairs are distributed in a single year over a habitat mosaic may be misleading.

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Selostus: **Etelä–Suomen metsälinnuston rakenne**

Metsälintujen lajirunsauden, tiheyden ja linnuston kokonaisrakenteen suhdetta ympäristön yleisiin piirteisiin tarkasteltiin eri puolilta Etelä-Suomea kartoitusmenetelmällä koottujen lintulaskenta-aineistojen valossa. Lajimäärä kasvoi tutkimusalueen koon kasvaessa aluksi jyrkästi, sitten yhä loivemmin. Lajimäärä kasvoi myös lintutiheyden kasvaessa. Odotettu lajimäärä hehtaaria kohti oli keskimäärin 7 (vaihteluväli 3–12). Vakioidussa 50 parin näytteessä oli keskimäärin 21 (16–26) lajia. Lajimäärä oli sitä suurempi, mitä enemmän tutkimusalueella oli metsänreunaa. Metsän tuottavuudella näytti olevan lajimäärää kohottava vaikutus suurehkoilla (5–55 ha) tutkimusalueilla, mutta ei pienillä (0.2–10 ha), toisiaan lähellä olevilla ympäristölaikuilla. Lajimäärä kasvoi sekä puuston iän ja määrän että metsän valoisuuden kasvaessa.

Lintutiheys laski tutkimusalueen koon kasvaessa, mutta se kasvoi sitä mukaa, mitä enemmän alueella oli metsänreunaa pinta-alaa kohti. Lintutiheydet olivat yleensä sitä suurempia, mitä tuottavampia metsät olivat. Keskimääräiset lintutiheydet tärkeimmissä metsätyypeissä vaihtelivat 440 parista 1 060 pariin/km^2 yleisen metsälintutiheyden ollessa keskimäärin 669 paria/km^2. Havumetsissä lintutiheys oli merkitsevästi pienempi kuin seka- ja lehtimetsissä. Valoisat, kohtalaisen harvat metsät näyttivät olevan lintujen suosiossa.

Lajien runsausjakauman tasaisuus väheni metsätyypin tuottavuuden kasvaessa. Kaksi valtalajia (peippo ja pajulintu) muodostivat kolmanneksen kokonaisparimäärästä. Ympäristön yleiset piirteet, kuten alueen koko, reunojen määrä ja tuottavuus, selittivät osan metsälinnuston rakenteen vaihtelusta. Etenkin laajemmassa maantieteellisessä mittakaavassa selitysosuus oli kuitenkin verraten pieni. Tämä johtunee paljolti vaikuttavien tekijöiden määrän kasvusta alueen koon kasvaessa.

References

Alatalo, R. V. 1981: Problems in the measurement of evenness in ecology. — Oikos 37:199–204.

Alatalo, R. V. & Alatalo, R. H. 1980: Seasonal variation in evenness of forest bird communities. — Ornis Scand. 11:217–222.

Ambuel, B. & Temple, S. A. 1983: Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. — Ecology 64:1057–1068.

Cajander, A. K. 1949: Forest types and their significance. — Acta Forest. Fennica 56:1–71.

Cody, M. L. 1985: An introduction to habitat selection in birds. — In: Cody, M. L. (ed.), Habitat selection in birds: 3–56. Academic Press, Orlando.

Ford, H. A. 1987: Bird communities on habitat islands in England. — Bird Study 34:205–218.

Gustafsson, E., Lehikoinen, E. & Mäntylä, K. 1982: Ruissalon linturetkeilyopas. — Turun Lintutiet. Yhdistys & Turun Luonnonsuojeluyhdistys, Turku.

Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — Ann. Zool. Fennici 2:153–196.

Haila, Y. 1983: Land birds on northern islands: a sampling metaphor for insular colonization. — Oikos 41:334–351.

— 1988: Calculating and miscalculating density: the role of habitat geometry. — Ornis Scand. 19:88–92.

Haila, Y. & Hanski, I. K. 1984: Methodology for studying the effects of habitat fragmentation on land birds. — Ann. Zool. Fennici 21:393–397.

Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga in southern Finland. — Ornis Fennica 64:90–106.

— 1989: Methodology for studying the minimum habitat requirements of forest birds. — Ann. Zool. Fennici 26:173–180.

Haila, Y. & Järvinen, O. 1990: Northern conifer forests and their bird assemblages. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 61–85. SPB Academic Publishing, The Hague.

Haila, Y., Järvinen, O. & Kuusela, S. 1983: Colonization of islands by land birds: prevalence functions in a Finnish archipelago. — J. Biogeogr. 10:499–531.

Hansson, L. 1983: Bird numbers across edges between mature conifer forest and clearcuts in Central Sweden. — Ornis Scand. 14:97–103.

Harvey, P. H. & Godfray, H. C. J. 1987: How species divide resources? — Am. Nat. 129:318–320.

Helle, E. & Helle, P. 1982: Edge effect on forest bird densities on offshore islands in the northern Gulf of Bothnia. — Ann. Zool. Fennici 19:165–169.

Helle, P. 1984: Effects of habitat area on breeding bird communities in northeastern Finland. — Ann. Zool. Fennici 21:421–425.

— 1985: Effects of forest regeneration on the structure of bird communities in northern Finland. — Holarct. Ecol. 8:120–132.

— 1986: Effects of forest succession and fragmentation on bird communities and invertebrates in boreal forests. — Acta Univ. Ouluensis A 178.

Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — Oikos 46:107–115.

Helle, P. & Mönkkönen, M. 1990: Forest successions and bird communities: theoretical aspects and practical implications. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 299–318. SPB Academic Publishing, The Hague.

Hinsley, S. A., Bellamy, P. E., Newton, I. & Sparks, T. H. 1995: Habitat and landscape factors influencing the precence of individual breeding bird species in woodland fragments. — J. Avian Biol. 26:94–104.

Holmes, R. T. 1990: The structure of a temperate deciduous forest bird community: variability in time and space. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 121–139. SPB Academic Publishing, The Hague.

van Horne, B. 1983: Density as a misleading indicator of habitat quality. — J. Wildl. Manage. 47:893-901.

Howe, R. W. 1984: Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. — Ecology 56:1585–1601.

Hyytiä, K., Kellomäki, E. & Koistinen, J. (eds.) 1983: Suomen lintuatlas. — Lintutieto, Helsinki.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98:785–800.

James, F. C. & Wamer, N. O. 1982: Relationships between temperate forest bird communities and vegetation structure. — Ecology 63:159–171.

Järvinen, O. & Haila, Y. 1984: Assembly of land bird communities on northern islands: a quantitative analysis of insular impoverishment. — In: Strong, D. R. Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. (eds.), Ecological communities. Conceptual issues and the evidence: 138–147. Princeton Univ. Press, Princeton.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. (In Finnish with summary in English) — Silva Fennica 11:284–294.

Järvinen, O. & Väisänen, R. A. 1973: Species diversity of Finnish birds, I: Zoogeographical zonation based on land birds. — Ornis Fennica 50:93–125.

— 1980: Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. — Ann. Zool. Fennici 17:67–85.

— 1983: Correction coefficients for line transect censuses of breeding birds. — Ornis Fennica 60:97–104.

Johnson, N. K. 1975: Controls of number of bird species on montane islands in the Great Basin. — Evolution 29:545–567.

Keast, A. 1990: Distribution and origins of forest birds. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 45–59. SPB Academic Publishing, The Hague.

Koskimies, P. & Väisänen, R. A. 1991: Monitoring bird populations. — Zoological Museum, Finnish Museum of Natural History, Helsinki.

Lavinto, A. & Niiranen, S. 1992: Järvenpään arvokkaat lintukohteet. Perusselvitys 1991. — Järvenpään ympäristölautakunta, Järvenpää.

Ludwig, J. A. & Reynolds, J. F. 1988: Statistical ecology. — Wiley, New York.

MacArthur, R. H. 1972: Geographical ecology. — Harper & Row, New York.

MacArthur, R. H. & MacArthur, J. W. 1961: On bird species diversity. — Ecology 42:594–598.

MacArthur, R. H. & Wilson, E. O. 1967: The theory of island biogeography. — Princeton Univ. Press, Princeton.

May, R. M. 1975: Patterns of species abundance and diversity. — In: Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 81–120. Belknap Press, Cambridge, Mass.

— 1984: An overview: real and apparent patterns in community structure. — In: Strong, D. R. Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. (eds.), Ecological communities. Conceptual issues and the evidence: 3–16. Princeton Univ. Press, Princeton.

Merikallio, E. 1946: Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. — Ann. Zool. Soc. Vanamo 12:1/1–143, 2/1–120.

Morozov, N. S. 1994: Inter–analyst variation in the combined version of the mapping method: the role of experience. — Acta Orn. 29:89–99.

Mönkkönen, M. 1991: Geographical patterns and local processes in holarctic breeding bird communities. — Acta Univ. Ouluensis A 223.

Nilsson, S. G. 1979: Density and species richness of some forest bird communities in south Sweden. — Oikos 33:392–401.

Odum, E. P. 1969: The strategy of ecosystem development. — Science 164:262–270.

Opdam, P., Rijsdijk, G. & Hustings, F. 1985: Bird communities in small woods in an agricultural landscape: effects of area and isolation. — Biol. Conserv. 34:333–352.

Pagel, M. D., Harvey, P. H. & Godfray, H. C. J. 1991: Species–abundance, biomass, and resource–use distributions. — Am. Nat. 138:836–850.

Palmgren, P. 1930: Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands. — Acta Zool. Fennica 7:1–218.

— 1987: On the constancy of annually repeated bird censuses. — Ornis Fennica 64:85–89.

Pielou, E. C. 1977: Mathematical ecology. — Wiley, New York.

Preston, F. W. 1948: The commonness and rarity of species. — Ecology 29:254–283.

— 1960: Time and space and the variation of species. — Ecology 41:611–627.

— 1962: The canonical distribution of commonness and rarity. — Ecology 43:185–215, 410–432.

Rafe, R. W., Usher, M. B. & Jefferson, R. G. 1985: Birds on reserves: the influence of area and habitat on species richness. — J. Appl. Ecol. 22:327–335.

Raivio, S. & Haila, Y. 1990: Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season. — Ornis Fennica 67:73–83.

Rajasärkkä, A. & Virolainen, E. 1987: Hämeenkylän ja Sotungin metsäalueiden sekä Pitkäkosken ja Tammiston luonnonsuojelualueiden linnustot. — Vantaan ympäristönsuojelulautakunnan julkaisu 1/1987.

— 1988: Vantaan metsäalueiden linnustot. — Vantaan ympäristönsuojelulautakunnan julkaisu 5/1988.

— 1989: Vantaan metsälinnusto. — Vantaan ympäristölautakunnan julkaisu 6/1989.

Ralph, C. J. & Scott, J. M. (eds.) 1981: Estimating numbers of terrestrial birds. — Stud. Avian Biol. 6:1–630.

Rosenberg, K. V. & Raphael, M. G. 1986: Effects of forest fragmentation on vertebrates in Douglas–fir forests. — In: Verner, J., Morrison, M. L. & Ralph, C. J. (eds.), Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates: 263–272. Univ. Wisconsin Press, Madison.

Røv, N. 1975: Breeding bird community structure and species diversity along an ecological gradient in deciduous forest in western Norway. — Ornis Scand. 6:1–14.

Rusterholz, K. A. & Howe, R. W. 1979: Species-area relation of birds on small islands in a Minnesota lake. — Evolution 33:468–477.

Scherner, E. R. 1981: Die Flächengrösse als Fehlerquelle bei Brutvogel-Bestandsaufnahmen. — Ökol. Vögel 3:145–175.

Shugart, H. H. 1990: Patterns and ecology of forests. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 7–26. - SPB Academic Publishing, The Hague.

Sokal, R. R. & Rohlf, F. J. 1981: Biometry. — Freeman, New York.

Solonen, T. 1988a: Kauniaisten linnustoselvitykset 1988. — Kauniaisten ympäristönsuojelulautakunnan julkaisu, Kauniainen.

— 1988b: Eräiden luonnonsuojelullisesti arvokkaiden alueiden linnusto Vantaalla 1987. — Vantaan ympäristölautakunnan julkaisu 3/1988.

— 1988c: Vantaan uhanalaiset ja harvalukuiset lintulajit sekä Mustakosken, Herukkapuron, Ojangon, Pitkäjärven ja Pikkujärven alueiden linnusto 1988. — Vantaan ympäristölautakunnan julkaisu 7/1988.

— 1991a: Vantaan Ojangon alueen linnusto vuosina 1989–90. — Vantaan ympäristöasiainkeskuksen julkaisu C8:1991.

— 1991b: Hindsbyn metsän linnusto. — Sipoon ympäristönsuojelulautakunnan julkaisu 1/1991.

— 1992a: Vantaan Ojangon alueen linnusto vuosina 1989–91. — Vantaan ympäristöasiainkeskuksen julkaisu C8:1992.

— 1992b: Vantaan uhanalaiset lintulajit ja niiden elinympäristöt. — Vantaan ympäristöasiainkeskuksen julkaisu C9:1992.

— 1994a: Structure and dynamics of the Finnish avifauna. — Mem. Soc. Fauna Flora Fennica 70:1–22.

— 1994b: Finnish bird fauna - species dynamics and adaptive constraints. — Ornis Fennica 71:81–94.

— 1994c: Factors affecting the structure of Finnish birds of prey communities. — Ornis Fennica 71:156–169.

Solonen, T. & Saarikko, J. 1987: Vantaan Mustavuoren linnusto. — Tringa 14:110–111.

Solonen, T. & Simula, J. 1989: Kauniaisten pienalaisten puistometsien linnusto 1989. — Kauniaisten ympäristönsuojelulautakunnan julkaisu, Kauniainen.

— 1990: Kauniaisten Suursuon ympäristön linnusto 1990. — Kauniaisten ympäristönsuojelulautakunnan julkaisu, Kauniainen.

Sugihara, G. 1980: Minimal community structure: an explanation of species abundance patterns. — Am. Nat. 116:770–787.

— 1989: How do species divide resources? — Am. Nat. 133:458–463.

Svensson, S. 1974: Interpersonal variation in species map evaluation in bird census work with the mapping method. — Acta Orn. 14:322–338.

Svensson, S., Carlsson, U. T. & Liljedahl, G. 1984: Structure and dynamics of an alpine bird community, a 20–year study. — Ann. Zool. Fennici 21:339–350.

Tiainen, J., Pakkala, T., Vickholm, M. & Virolainen, E. 1984: The breeding bird community of a natural coniferous forest in southern Finland. (In Finnish with summary in English) — Tringa 11(5):22–35.

Tomiałojć, L. & Wesołowski, T. 1990: Bird communities of the primaeval temperate forest of Białowieza, Poland. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 141–165. SPB Academic Publishing, The Hague.

Tramer, E. J. 1969: Bird species diversity: components of Shannon's formula. — Ecology 50:927–929.

Ugland, K. I. & Gray, J. S. 1982: Lognormal distributions and the concepts of community equilibrium. — Oikos 39:171–178.

Uusitalo, M. (ed.) 1989: Yearbook of forest statistics 1988. Folia Forestalia 730. — The Finnish Forest Research Institute, Helsinki.

Virkkala, R. 1991: Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. — Oikos 62:59–66.

Virolainen, E. 1988: Metsälintuyhteisöjen riippuvuus kasvillisuuden rakenteesta kahdella eteläsuomalaisella tutkimusalueella. — M. Sc. thesis, Dept. Zoology, Univ. Helsinki.

Wiens, J. A. 1989: The ecology of bird communities. — Cambridge Univ. Press, Cambridge.

Wiens, J. A., Addicott, J., Case, T. & Diamond, J. 1986: The importance of spatial and temporal scale in ecological investigations. — In: Diamond, J. & Case, T. (eds.), Community ecology: 145–153. Harper & Row, New York.

Wiens, J. A., Rotenberry, J. T. & van Horne, B. 1987: Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. — Oikos 48:132–147.

Willson, M. F. 1974: Avian community organization and habitat structure. — Ecology 55:1017–1029.

Appendix. Average bird densities (pairs/km^2) in forests in general (for sources of data, see Table 1, larger census areas) and in main forest habitats, characterized by dominant trees and forest type (see Table 2; for sources of data, see Table 1, mapping plots) in southern Finland. Data for secondary hole-nesters (*) do not include areas, in which their numbers were considerably increased by the availability of nest-boxes.

Species	Forests		Pine/ VT		Spruce/ MT–OMT		Deciduous/ OMaT	
	(104.3 km^2)		(2.6 km^2)		(4.5 km^2)		(2.3 km^2)	
	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%
Pernis apivorus	0.2	0.0	–		–		–	
Accipiter gentilis	0.1	0.0	–		0.2	0.0	–	
Accipiter nisus	0.2	0.0	0.4	0.1	–		–	
Buteo buteo	0.2	0.0	–		–		–	
Falco subbuteo	0.1	0.0	–		–		–	
Bonasa bonasia	2.3	0.5	3.1	0.7	10.2	1.3	3.0	0.3
Tetrao tetrix	0.8	0.2	0.4	0.1	0.2	0.0	–	
Tetrao urogallus	0.3	0.0	–		0.2	0.0	0.4	0.0
Scolopax rusticola	1.4	0.3	0.8	0.2	2.9	0.4	4.3	0.4
Tringa ochropus	0.6	0.1	1.2	0.3	0.9	0.1	0.9	0.1
Columba oenas *	1.2	0.2	0.6	0.1	0.4	0.1	12.7	1.3
Columba palumbus	3.0	0.6	4.6	1.0	12.9	1.7	9.6	1.0
Cuculus canorus	0.4	0.1	1.5	0.3	2.0	0.3	0.9	0.1
Bubo bubo	0.0	0.0	–		–		–	
Glaucidium passerinum *	0.0	0.0	–		–		–	
Strix aluco *	0.2	0.0	–		0.2	0.0	0.9	0.1
Strix uralensis *	0.0	0.0	–		–		–	
Asio otus	0.1	0.0	–		–		–	
Aegolius funereus *	0.1	0.0	–		–		–	
Caprimulgus europaeus	0.2	0.0	0.4	0.1	–		–	
Apus apus *	0.5	0.1	0.4	0.1	1.3	0.1	–	
Jynx torquilla *	0.6	0.1	0.6	0.1	0.9	0.1	0.9	0.1
Picus canus	0.1	0.0	–		–		0.4	0.0
Dryocopus martius	0.3	0.0	–		0.2	0.0	1.3	0.1
Dendrocopos major	3.0	0.6	2.3	0.5	6.4	0.8	8.3	0.9
Dendrocopos minor	0.1	0.0	–		–		1.7	0.2
Picoides tridactylus	0.1	0.0	–	0.2	0.0	–	–	
Lullula arborea	0.0	0.0	–		–		–	
Anthus trivialis	21.0	4.3	27.7	6.0	21.1	2.8	25.2	2.6
Troglodytes troglodytes	0.7	0.1	0.8	0.2	1.8	0.2	0.4	0.0
Prunella modularis	10.3	2.1	11.2	2.4	22.7	3.0	12.2	1.3
Erithacus rubecula	24.3	5.0	25.0	5.4	52.0	6.8	40.4	4.2
Luscinia luscinia	1.0	0.2	–		3.3	0.4	5.7	0.6
Phoenicurus phoenicurus *	0.6	0.1	3.8	0.8	1.3	0.2	0.4	0.0
Turdus merula	17.3	3.5	18.8	4.1	22.7	3.0	32.6	3.4
Turdus pilaris	5.0	1.0	9.6	2.1	21.7	2.9	25.2	2.6
Turdus philomelos	11.1	2.3	15.4	3.3	26.2	3.4	23.5	2.4
Turdus iliacus	17.0	3.5	14.6	3.2	46.2	6.1	50.0	5.1
Turdus viscivorus	0.3	0.1	0.8	0.2	–		0.4	0.0
Locustella naevia	0.0	0.0	–		0.9	0.1	–	
Locustella fluviatilis	0.0	0.0	–		–		–	
Acrocephalus dumetorum	0.1	0.0	–		–	0.4	0.0	
Acrocephalus palustris	0.3	0.1	–	0.4	0.1	–		
Hippolais icterina	0.8	0.2	0.8	0.2	3.3	0.4	5.7	0.6
Sylvia nisoria	0.1	0.0	–		–		–	
Sylvia curruca	3.3	0.7	3.1	0.7	5.8	0.8	3.9	0.4
Sylvia communis	3.8	0.8	2.7	0.6	6.2	0.8	6.1	0.6

Continued

Continued

Species	Forests (104.3 km^2)		Pine/ VT (2.6 km^2)		Spruce/ MT–OMT (4.5 km^2)		Deciduous/ OMaT (2.3 km^2)	
	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%
Sylvia borin	12.9	2.6	10.4	2.3	20.0	2.6	36.1	3.7
Sylvia atricapilla	3.1	0.6	2.7	0.6	8.7	1.1	20.0	2.1
Phylloscopus trochiloides	0.5	0.1	–		0.2	0.0	3.0	0.3
Phylloscopus sibilatrix	18.1	3.7	12.3	2.7	20.9	2.8	38.7	4.0
Phylloscopus collybita	3.3	0.7	1.9	0.4	8.4	1.1	3.9	0.4
Phylloscopus trochilus	56.1	11.5	62.7	13.6	59.3	7.8	87.4	9.0
Regulus regulus	18.0	3.7	17.7	3.8	33.3	4.4	23.5	2.4
Muscicapa striata	23.9	4.9	11.5	2.5	22.7	3.0	30.0	3.1
Ficedula parva	0.4	0.1	–		0.7	0.1	–	
Ficedula hypoleuca *	11.1	2.3	12.2	2.7	6.5	0.9	31.8	3.3
Parus montanus	6.7	1.4	8.1	1.8	17.1	2.3	11.3	1.2
Parus cristatus	2.5	0.5	5.4	1.2	5.8	0.8	1.3	0.1
Parus ater *	3.0	0.6	3.8	0.8	10.4	1.4	6.5	0.7
Parus caeruleus *	3.7	0.8	8.3	1.8	4.8	0.6	27.3	2.8
Parus major *	24.2	5.0	22.2	4.8	17.8	2.3	60.0	6.2
Certhia familiaris	1.7	0.3	1.5	0.3	7.1	0.9	9.1	0.9
Oriolus oriolus	0.1	0.0	–		–		–	
Lanius collurio	2.2	0.5	0.8	0.2	1.6	0.2	0.4	0.0
Garrulus glandarius	3.2	0.7	1.9	0.4	5.8	0.8	3.9	0.4
Pica pica	0.8	0.2	2.7	0.6	2.2	0.3	0.9	0.1
Nucifraga caryocatactes	0.1	0.0	–		0.2	0.0	–	
Corvus monedula *	0.5	0.1	–		1.6	0.2	13.0	1.3
Corvus corone	1.4	0.3	5.4	1.2	5.3	0.7	4.3	0.4
Corvus corax	0.0	0.0	–		–		–	
Sturnus vulgaris *	1.2	0.2	0.6	0.1	–		10.0	1.0
Fringilla coelebs	121.8	25.0	84.2	18.3	152.7	20.1	206.5	21.2
Fringilla montifringilla	0.1	0.0	0.4	0.1	0.2	0.0	0.4	0.0
Carduelis chloris	1.0	0.2	4.2	0.9	8.0	1.1	10.4	1.1
Carduelis spinus	13.4	2.7	14.2	3.1	29.1	3.8	15.7	1.6
Carduelis cannabina	0.1	0.0	–		–		0.4	0.0
Carduelis flammea	0.2	0.0	0.4	0.1	–		–	
Loxia curvirostra	5.0	1.0	1.9	0.4	1.8	0.2	0.9	0.1
Carpodacus erythrinus	3.1	0.6	1.5	0.3	6.2	0.8	19.6	2.0
Pyrrhula pyrrhula	1.2	0.2	2.7	0.6	10.9	1.4	4.3	0.4
Coccothraustes coccothraustes	0.2	0.0	–		0.2	0.0	–	
Emberiza citrinella	9.3	1.9	7.7	1.7	13.6	1.8	13.9	1.4
Emberiza rustica	0.2	0.0	–		0.4	0.1	–	
Total	487.5	100	459.9	100	759.9	100	971.9	100