Ann. Zool. Fennici 17:87-106. 1980

Habitat distribution and species associations of land bird populations on the Åland Islands, SW Finland

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Haila, Y., Järvinen, O. & Väisänen, R. A. 1980: Habitat distribution and species associations of land bird populations on the Åland Islands, SW Finland. — Ann. Zool. Fennici 17:87—106.

Line transect censuses of breeding land birds were made on the mainland of Åland (about 60°N, 20°E) in 1975. Over 3000 pairs were observed in a total area of about 8.5 km^2. Sixteen different habitats were distinguished in the field, and the census results are given. As a result of a cluster analysis, nine major communities emerged (six forest and three open habitats), with densities ranging from 124 pairs/km^2 (rocky pine forest) to 925 pairs/km^2 (deciduous grove). Habitat associations of different species were studied numerically, and four main groups were distinguished. These were the species favouring pine forests, spruce forests, luxuriant deciduous and mixed forests, and open habitats. In abundant species habitat amplitude tended to be wide, though a number of rather scarce species also had wide habitat amplitudes. Species favouring spruce forests were generally habitat specialists. Bird species diversity was correlated with vegetation structure (vertical foliage structure and vegetation cover), but lack of a predictive theory makes it difficult to interpret this correlation in causal terms, and it is equally difficult to find causal explanations for certain discrepancies from previous values for the proportions of different taxa as a function of community density.

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1. Introduction

Finnish ornithologists (e.g. P. Palmgren 1930 and Merikallio 1946, 1958) have been pioneers in quantitative bird census work, but few studies have as yet covered all the major habitats of a certain region. Such studies are greatly needed, for only extensive and systematically collected data can give us sufficient information on the habitats used by different species; quantitative data are required for adequate testing of many hypotheses on population changes, for an understanding of patterns of habitat selection, and for many other purposes. In this paper we present census results of our studies of the land bird fauna of the Åland Islands. We also discuss the habitat distribution and species associations of the land bird populations, as these aspects throw light on community structure. Three other papers (Haila et al. 1979a, b, 1980) analyse long-term changes in the bird populations of the Åland Islands during the recent decades, comparing modern data with those presented by P. Palmgren (1930, 1935).

2. Study area

The Åland Islands lie in the northern Baltic between the south-western part of the Finnish mainland and the county of Uppland in Sweden, about 60°N and 20°E (Fig. 1). The archipelago consists of four adjacent islands of large size, known as the mainland of Åland, with a total area of about 970 km^2, and several thousand small islands (6654, according to Meinander 1961), which connect Åland with the archipelago of south-western Finland. The mainland of Åland is separated from the Finnish mainland by about 70 km, and from the Swedish mainland by about 40 km. Åland archipelago emerged from the sea a few thousand years ago, the present rate of land uplift being about 40 cm a century.

The islands lie in the most maritime climatic zone of Finland. The growing season is somewhat longer than in southern Finland, but mean summer temperatures are 1—2 degrees lower than on the mainland (Kolkki 1966).

The bedrock of the mainland of Åland consists mainly of weathered rock (Atlas över Skärgårds-Finland 1960), which is very poor in nutrients. Surface deposits consist of moraine (more than half the area), clay soils and sandy soils. These deposits contain lime, and as a result the soils in several regions support a rich vegetation (Kalliola 1973).

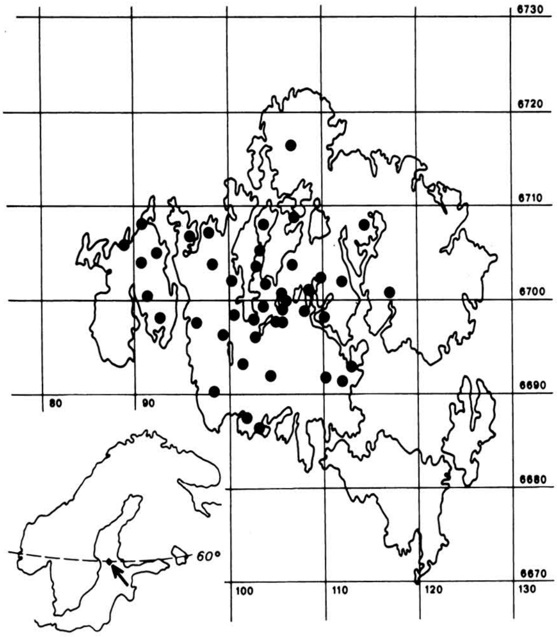


Fig. 1. The distribution of our line transects on the mainland of Åland. The coordinates indicate the Finnish uniform gird (27°E); the geographical coordinates of Åland are about 60°N and 20°E.

Because open bedrock abounds, forest habitats cover relatively small areas on small islands. On the mainland of Åland forests cover 60—70 % of the land area, but about 1/3 grow poorly (Kuusela & Salovaara 1974), fields cover 14 % of the mainland (Suomi-Käsikirja 1968), and shore meadows cover modest areas. Peatlands are scarce, covering less than 10 % of the land area, and open peatland habitats are almost absent.

Forest stands on Åland are poorer than in corresponding forest types on the Finnish mainland, mostly because the trees are, on average, shorter on Åland; Högnäs (1966) attributes this difference to climatic factors and to the thinness of the soil on Åland. On the other hand, the herb and bush layers are well developed (Högnäs 1966).

Coniferous forests dominate. According to the National Forest Survey, pine is the dominant tree species in 62 %, and spruce in 19 % of the forest area (Kuusela & Salovaara 1974). Deciduous forests make up 15 % of the forest area. The most common forest type is *Myrtillus* Type (MT, about 40 % of the forest area), *Oxalis-Myrtillus* Type (OMT) covering about 35 %. Different forest types will be described in Sect. 3.

A conspicuous feature of the forests is their patchiness, which is caused by irregular topography and abundant outcrops of bare rock. Height differences in the archipelago are not striking, for the highest hilltops rise to little more than 100 m. Fields tend to be small, often covering only a few hectares, or at most some tens of hectares; they increase the mosaic-like patchiness of the landscape.

Luxuriant forests, about one third of the forest area, are mostly scattered among more barren forests and along field edges. The climax community of the luxuriant forests on the mainland is the luxuriant spruce forest (A. Palmgren 1922). Luxuriant deciduous forests, especially grove meadows maintained by continuous cultural intervention, are a special feature of the mainland and large islands in the archipelago (see A. Palmgren 1915—17). In the beginning of the century grove meadows were mostly scattered in the western and southern parts of the mainland, but because these habitats are no longer used for grazing and growing hay, they are rapidly disappearing. Forest succession is transforming them into mixed forests and even luxuriant spruce forests (Hæggström 1970, Haila et al. 1980).

Phytogeographically, the Åland Islands are near the northern margin of the hemiboreal zone (Ahti et al. 1968). Patches of luxuriant deciduous woodland represent typical hemiboreal forests with southern deciduous trees and bushes. Extensive botanical data on the archipelago can be found in the studies of A. Palmgren (e.g. 1915—17, 1922, 1946) and Högnäs (1966).

3. Material and methods

The field-work was carried out using the line transect method (Järvinen & Väisänen 1976a). In total, 172.9 km of normal transects were censused between 26 May and 26 June, 1975 (for the effect of annual fluctuations, see Järvinen et al. 1977). Most censuses were made by Y. Haila and J. Markkola, but O. Järvinen, S. Kuusela, K. Vepsäläinen and R. A. Väisänen also participated. When pooling the data collected by different observers (cf. Enemar 1962, Hogstad 1967, Enemar et al. 1978), we noted that different observers reported similar densities from similar habitats. The data analysed here are based on the main belt of the transects (the main belt extends 25 m on each side of the observer). Theoretically, 172.9 km transects would yield over 8.6 km^2 for the main belt, but a small proportion of the data were not used (unclassified habitats, or habitats covering areas so small that only a few birds per habitat were observed). Our normal transects were supplemented by main belt censuses made mostly in rocky pine forest (habitat 1), but these censuses account for less than 10 % of the present data. These supplementary censuses were partly made in late morning, though always before 10 a.m. Censuses in late morning give poorer results than those made in early morning, but this effect was small for the main belt (Järvinen et al. 1977), and we believe that it was totally compensated for by the fact that the observer was able to make a highly concentrated effort, as only the main belt was censused (cf. Järvinen & Väisänen 1975).

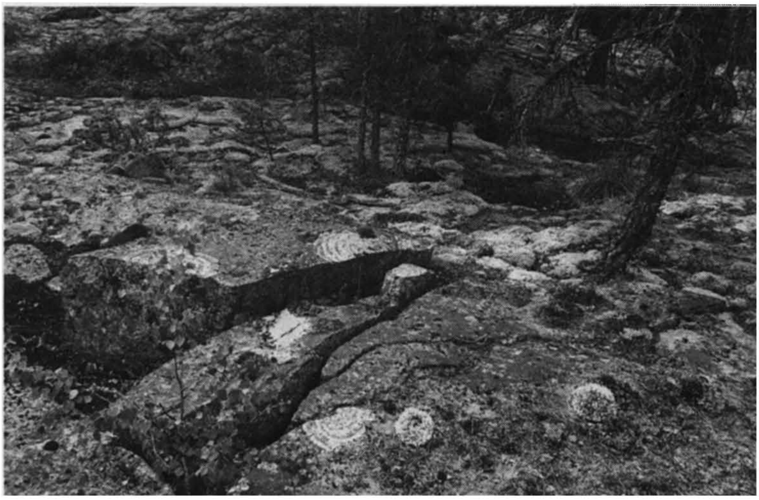
We classified the habitats of the main belt in the field, following as closely as possible the scheme of P. Palmgren (1930), whose classification was based on Cajander's forest type system. The habitats distinguished are described in Table 1 and Fig. 2.

The habitats sampled by P. Palmgren (1930) did not include our forest habitats 2, 7 or 10 or man-made habitats 13—16. The difference in forest habitats is probably mainly due to the fact that he sampled only pure stands, whereas our sample areas accumulated along transects (cf. also Haila et al. 1980). Table 2 A gives sample sizes and areas censused for our 16 habitats

Table 1. Characteristics of the habitats studied (the German names of the equivalent habitats of Palmgren (1930) are given, when appropriate). *Betula* = *Betula* spp., *Picea* =*P. abies*, *Pinus* = *P. silvestris*.

Habitat	Tree layer	Bush layer	Field layer	Special features
1. Rocky pine forest (Felsenkiefernwald) Fig. 2A	*Pinus*, seldom *Picea* or *Betula* in depressions	Saplings (sparsely)	Lichens on bare bedrock, elsewhere *Calluna vulgaris* and grasses	Coverage of bare bedrock up to 50 %, trees low; sparse pine forest on barren rocky ground
2. Moderately barren pine forest, Fig. 2B	Almost closed stands of *Pinus*; *Picea* and *Betula* in wet depressions	Saplings (sparsely)	As in VT (e.g. Kalliola 1973)	Growth of trees impaired, occasional patches of bare bedrock; tree layer more continuous and field layer richer than in rocky pine forest
3. Mixed coniferous forest (Nadelmischwald) Fig. 2C	Closed stands of *Picea* and *Pinus*; *Betula* sparse	Saplings	Relatively poor, as in MT (e.g. Kalliola 1973)	A typical heath forest dominated by spruce and pine; more barren than spruce forests, distinguished from the others by the composition of the tree layer
4. Spruce forest (Fichtenwald) Fig. 2D	Closed stands of *Picea*; *Betula* and *Pinus* sparse	Rather sparse (mostly saplings), scattered bushes of luxuriant forests	As in OMT (e.g. Kalliola 1973)	A typical moist heath forest dominated by spruce; herb vegetation present; cf. luxuriant spruce forest
5. Thinned forest (Hiebsfläche) Fig. 2E	Mainly *Picea*, but also *Pinus* and *Betula*	Sapling stands (*Picea*, *Betula*, *Sorbus aucuparia*) often dense	Patchy; tall grasses dominate	Relatively recently thinned; semi-open coniferous forest
6. Marsh grove (Hainbruch) Fig. 2F	Typically *Picea*, *Betula* and *Alnus glutinosa*	*Rhamnus frangula* typical, saplings of *Picea* and *Betula* abundant	Shady; typical herbs and ferns of luxuriant forests, but also species of luxuriant marshes	Growth of trees impaired by wet soil; species composition of plants characteristic; luxuriant marsh type
7. Luxuriant spruce forest, Fig. 2G	A dense, closed stand of *Picea* dominates; some deciduous trees (*Betula*, *Populus tremula*)	Very dense compared with other coniferous forests in Finland; bushes of luxuriant forests (e.g. *Corylus avellana*)	Dense, but shady; herbs dominate	Distinguished from other spruce forests by the bush and field layers, which are typical of luxuriant forests
8. Luxuriant mixed forest (Laubmischwald) Fig. 2H	All deciduous species and frequently *Picea*, occasionally *Pinus*	Dense, rich in species (e.g. *Corylus avellana*, *Lonicera xylosteum*)	Shady, small herbs typical (*Anemone nemorosa* and *A. hepatica*, *Oxalis acetosella*, *Maianthemum bifolium*)	A successional stage, spruce increasing; distinguished from other luxuriant forests by the tree layer
9. Luxuriant deciduous forest (Haine) Fig. 2I	Deciduous (incl. *Quercus robur* and *Fraxinus excelsior*)	Dense, mainly bushes of luxuriant forests	Shady, but rich, dominated by herbs	Dense growth, often recently abandoned grove meadows; horizontal heterogeneity slight, more closed than grove meadows or wooded pastures
10. Alder grove, Fig. 2J	Almost exclusively *Alnus glutinosa*	Fairly dense in many places, including *Juniperus communis* and saplings of *Picea*	Dense coverage, tall; dominant herb *Filipendula ulmaria*	Usually as narrow zones near shores; dominant tree *Alnus glutinosa*
11. Grove meadow (Laubhaine) Fig. 2K	Deciduous (*Betula*, *Fraxinus excelsior*, *Populus tremula*, *Prunus padus*, *Alnus glutinosa*)	Numerous bushes and deciduous saplings (*Rosa* spp., *Viburnum opulus*, *Lonicera xylosteum*), but also *Juniperus communis*	Patches of extremely species-rich meadow	Horizontal structure mosaic-like: patches of open meadow and clumps of trees; produced by man (trees cut in order to increase the coverage of meadow patches, hay-making, light grazing, pollarding)
12. Wooded pasture (Hage) Fig. 2L	Deciduous (see grove meadow), but sparse	Sparse (especially *Juniperus communis*, some *Corylus avellana*)	Small herbs and grasses	A park-like habitat; similar to grove meadows, but heavily grazed and therefore shows vegetational differences
13. Sapling stand Fig. 2M	*Betula* and *Sorbus aucuparia* (1—3 m)	Dense sapling stand (*Betula*, *Sorbus aucuparia*)	Tall grasses in open patches	Structurally diffuse, forest cut 5—20 years ago, rapidly changing with age
14. Village pasture Fig. 2N	Scattered (all species)	Garden bushes	Grasses dominate, but also meadow herbs	Open habitat; farm houses with surroundings (gardens, pastures and meadows)
15. Field, Fig. 2O	None	Deciduous bushes in edges, but ± absent	Cereals	Occasional stone heaps and hillocks of bare bedrock and bushes (e.g. *Juniperus communis*, *Betula*, *Sorbus aucuparia*, *Rosa* spp.)
16. Shore meadow	None	Occasional bushes (e.g. *Salix* spp.)	Grasses if grazed; dense *Phragmites communis* if not grazed	At shores

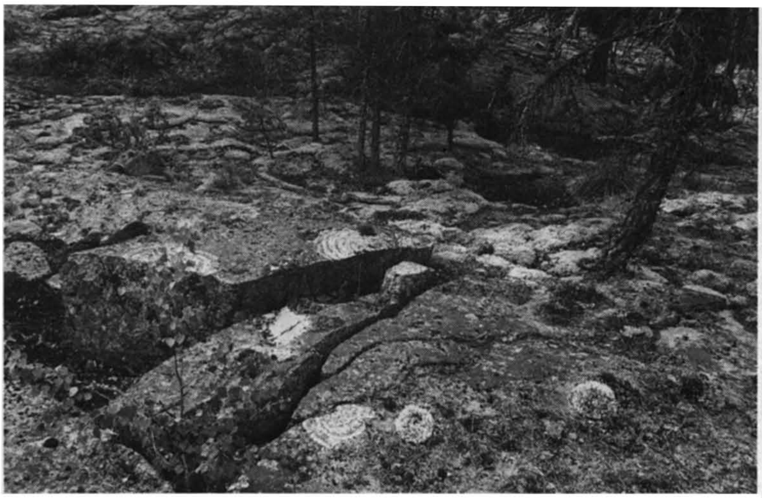
Fig. 2. Photographs of the habitats 1—15 distinguished in the field (cf. Table 1). Al photos L. Saraste.



2A. Rocky pine forest (Finström, Bjärström 24.VI.1975). Exposed bedrock with lichens, *Calluna vulgaris* and grasses. Poorly growing *Pinus* dominates the tree layer.

2B. Moderately barren pine forest (Finström, Bjärström 8.VI.1975). The thin soil supports a poor field layer. Closed stands of *Pinus*.

2C. Mixed coniferous forest (Finström, Bjärström 24.VI.1975). In the field layer, *Vaccinium myrtillus* is abundant; *Carex* spp. grow in moist depressions. Closed stands of *Picea* and *Pinus*.



2D. Spruce forest (Finström, Bjärström 2.IX.1975). The field layer is dominated by *Vaccinium myrtillus* and some grasses and herbs (*Oxalis acetosella, Maianthemum bifolium*), the tree layer by *Picea*.

2E. Thinned forest (Finström, Bjärström 24.VI.1975). Different grasses and herbs dominate open patches between saplings (*Betula*). At the site shown the tree layer consists of *Pinus*; however, the species depends on the original forest.

2F. Marsh grove (Finström, Emkarby 12.VI.1975). Dense vegetation of grasses and herbs (at the site shown even *Phragmites communis*); the tree (and bush) layer consists of a thicket of *Betula, Picea* and *Rhamnus frangula.*

2G. Luxuriant spruce forest (Finström, Emkarby 5.VI.1975). Herbs of luxuriant forests in the field layer. Bushes abundant (at the site shown mostly *Sorbus aucuparia*). A dense, closed stand of *Picea.*

2H. Luxuriant mixed forest (Finström, Bjärström 20.VI.1975). Herbs of luxuriant forests in the field layer. Deciduous trees and bushes abundant. A successional stage. (Notice the fallen wattle fence.)

2I. Luxuriant deciduous forest Jomala, Ramsholmen 23.VI.1975). The luxuriant field layer is dominated by herbs. Southern deciduous trees and bushes (*Quercus robur, Fraxinus excelsior, Corylus avellana*) are abundant.

2J. Alder grove (Finström, Bjärström 24.VI.1975). *Filipendula ulmaria* dominates the field layer, *Alnus glutinosa* the tree layer.

2K. Grove meadow (Finström, Åttböle 27.V.1975). A moderately grazed habitat, with numerous grasses and herbs in the field layer and clumps of bushes and trees (*Betula, Sorbus* spp., *Juniperus, Fraxinus excelsior*).

2L. Wooded pasture (Finström, Emkarby 23.VI.1975). Grazed; the field layer is dominated by grasses, with a few scattered bushes. The dominant tree is *Betula*.

2M. Sapling stand (Finström, Emkarby 2.IX.1975). Forest cut about 10 years ago, a mosaic of saplings (*Betula, Sorbus* spp.) and patches dominated by tall grasses.

2N. Village pasture (Finström, Bjärström 20.VI.1975). A man-made habitat complex comprising farmhouses, gardens and paddocks.

2O. Field (Finström, Bjärström 22.VI.1975). Dense grass, herb and bush (*Rosa* spp., *Juniperus*) vegetation along the edge of a field.

distinguished in the field. The proportional coverage of our habitats is in fairly good agreement with that given by the National Forest Survey for 1971—72 (Kuusela & Salovaara 1974). The main difference can be found in coniferous forests: Kuusela & Salovaara (1974) give a higher percentage for pine forests than our data suggest. Most of this difference is due to the fact that our censuses in 1975 were made on the mainland of Åland, except for 2 km on Kökar, and pine is more characteristic elsewhere in the archipelago. Our censuses were also slightly concentrated in the southern parts of the mainland of Åland, where spruce forests are more abundant than in the north. Finally, ornithologists tend to classify a forest as a spruce forest more readily than foresters do.

In estimating densities we did not apply any corrections due to census efficiency, but it is likely that for most species the densities obtained lie somewhere between 50 and 80 % of the actual breeding populations (Järvinen et al. 1978a, b, J. Tiainen pers. comm.). Järvinen (1978) has suggested an approach for correcting the bias caused by the variable efficiencies of different species but, as he stressed, the application of his method is as yet premature. Other definitions of the basic concepts can be found for example in Järvinen & Väisänen (1977) or Järvinen et al. (1978b), or in the text in the pertinent contexts.

4. Major bird communities

The results of our censuses are given in Table 2A and the Appendix. The 16 communities, named after their habitats, were compared numerically with the index *Ddiff*, ranging from 0 (communities identical) to 1 (communities very different). This index (for an exact definition, see Järvinen & Väisänen 1977) takes into account both the identity and the frequencies of the species in the communities compared. As a result of this comparison (Fig. 3A), we combined the communities into nine major communities (shore meadows were excluded from further analyses owing to scarcity of data). The relations between the major communities are shown in Fig. 3B.

The rules for combining communities are, of course, relative. As a limit we chose 0.09 *Ddiff* units between the communities in Fig. 3A. The forest communities were divided into three main branches: pine forests, spruce forests and deciduous forests (Fig. 3B). Each of these branches includes two major communities. The forest communities (altogether 6) differ greatly from the other three communities, which basically inhabit man-made habitats and form a heterogeneous group.

Table 3 shows the densities and frequencies of the 53 most numerous species (5 pairs or more observed in the major communities). Table 4 lists the habitat distribution of the 30 most numerous

Table 2. A. Basic statistics for the 16 communities in habitats distinguished in the field. B. Basic statistics for the nine major communities formed on the basis of a numerical comparison of the original communities (see Fig. 3A).

	Area (km^2)	Species	Pairs	Density (pairs/km^2)	Assigned to MC
A. Original communities					
1. Rocky pine forest	1.01	22	125	124	1
2. Moderately barren pine forest	0.86	33	166	193	2
3. Mixed coniferous forest	0.55	31	183	333	3
4. Spruce forest	0.98	39	382	390	3
5. Thinned forest	0.52	29	139	267	3
6. Marsh grove	0.21	28	116	552	4
7. Luxuriant spruce forest	0.52	39	329	633	4
8. Luxuriant mixed forest	0.46	45	300	652	5
9. Luxuriant deciduous forest	0.52	43	430	827	5
10. Alder grove	0.25	37	195	780	5
11. Grove meadow	0.24	37	191	796	6
12. Wooded pasture	0.27	32	171	633	6
13. Sapling stand	0.52	23	107	206	7
14. Village pasture	0.28	23	95	339	8
15. Field	1.32	28	169	128	9
16. Shore meadow	0.26	18	36	139	—
					Original communities
B. Major communities					
MC 1. Rocky pine forest	1.01	22	125	124	1
MC 2. Moderately barren pine forest	0.86	33	166	193	2
MC 3. Spruce forest	2.05	49	704	343	3—5
MC 4. Luxuriant spruce forest	0.73	45	445	610	6—7
MC 5. Grove	1.23	54	925	752	8—10
MC 6. Grove meadow	0.51	42	362	710	11—12
MC 7. Sapling stand	0.52	23	107	206	13
MC 8. Village pasture	0.28	23	95	339	14
MC 9. Field	1.32	28	169	128	15

species. Eastimates of habitat distribution (Fretwell 1972, Järvinen & Väisänen 1978) are given as percentages of the total population of each species in the different habitats. As additional habitats (cf. Appendix) were included in the calculations, sums are sometimes less than 100 %. The bird communities can be characterized as follows:

The habitats of major communities (MC) 1 and 2 (rocky pine forest and moderately barren pine forest) are dominated by pine. These two communities differ greatly from the others, but are relatively similar to each other. The main difference between MC 1 and 2 is that density is higher and species richness is greater in MC 2. *Cuculus canorus, Anthus trivialis* and *Parus cristatus* reach their highest densities in MC 1, *Phoenicurus phoenicurus* and *Parus montanus* in MC 2. Species typical of more luxuriant forest types, e.g. *Phylloscopus trochilus* and *Regulus regulus,* are clearly more important in MC 2. Tits *Parus* spp. and certain species typical of open habitats, such as *Anthus trivialis* and *Motacilla alba,* are abundant in both MC 1 and 2.

MC 3, the spruce forest community, consists of three communities distinguished in the field (Table 2); notice that mixed coniferous forests were also closely connected with spruce forests (cf. also Palmgren 1930). Species richness is high, being second only to that of deciduous forests, but not more than 4 rather scarce species attain their highest densities in this habitat (*Bonasa bonasia, Tetrao tetrix, Troglodytes troglodytes* and *Garrulus glandarius*). However, this is the most important habitat for many populations which attain their highest densities in MC 4, luxuriant spruce forests (e.g. *Erithacus rubecula, Turdus philomelos*) or in MC 1—2, pine forests (e.g. *Anthus trivialis, Parus cristatus, Parus montanus*). The importance of spruce forests for *Anthus trivialis* is due, however, to the presence of forest clearings (in thinned forests).

MC 4, the community of luxuriant spruce forest, consists of two communities in habitats distinguished in the field (Table 2). Total bird density is markedly higher than in MC 3. Ten species attain their maximum densities in MC 4 (see Table 3), and luxuriant spruce forests provide the most important habitat for two species (*Phylloscopus sibilatrix* and *Pyrrhula pyrrhula*). A few species typical of deciduous forest also attain relatively high densities in MC 4, e.g. *Sylvia atricapilla* and *Phylloscopus trochilus.*

The communities of deciduous forests were divided into two major communities, MC 5 (grove) and MC 6 (grove meadow), the former consisting of three communities in habitats distinguished in the field, the latter of two. Total bird density is highest in MC 5, but the difference between MC 5 and MC 6 is small. As seen in Table 3, thirteen species reach their highest densities in MC 5 (e.g. *Turdus pilaris, T. iliacus, Phylloscopus trochilus, Parus caeruleus, P. major*), and seven species in MC 6 (e.g. *Sylvia borin, Fringilla coelebs, Emberiza citrinella*). Edge species are clearly more numerous in MC 6 than in MC 5, no doubt because of the open patches in grove meadows. The effect of spruce is clearly seen in the species list of MC 5 (which includes luxuriant mixed forests, see Table 2), for *Erithacus rubecula, Turdus merula* and *Regulus regulus* are abundant. Thrushes are fairly frequent in MC 5. Many scarce species, not included in Table 3, occur strikingly often in MC 5 (cf. Appendix), in which species richness reaches the maximum in our data.

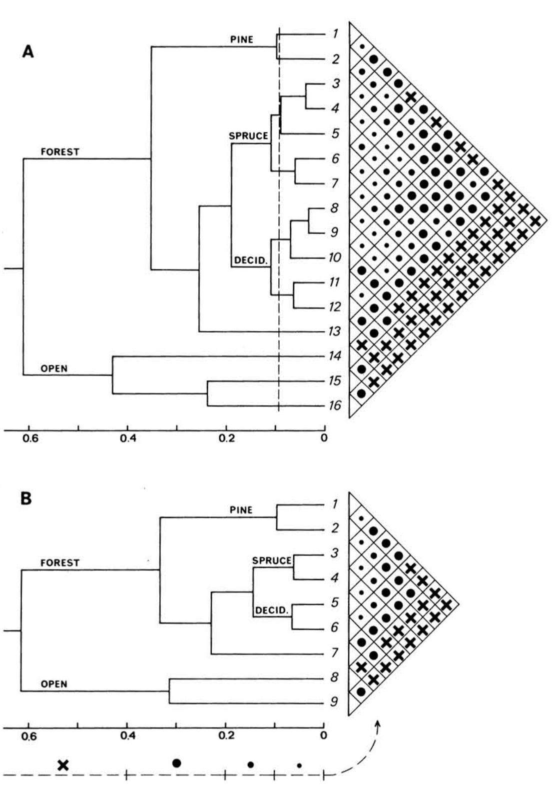


Fig. 3. A. A dendrogram showing the similarity of the communities in the 16 habitats distinguished in the field. On the right, the pairwise comparisons between the communities. — B. A dendrogram showing the similarity of the nine major communities.

Table 3. Densities (pairs/km²) and frequencies (%, in parentheses) of birds in different main communities. Total number of observations in these communities is given in parentheses after the species name. All species observed less than five times in these communities were omitted. For complete data with exact numbers of observations, see the Appendix.

	MC 1 Rocky pine forest (1.01 km²)	MC 2 Moder. barren pine forest (0.86 km²)	MC 3 Spruce forest (2.05 km²)	MC 4 Luxuriant spruce forest (0.73 km²)	MC 5 Grove (1.23 km²)	MC 6 Grove meadow (0.51 km²)	MC 7 Sapling stand (0.52 km²)	MC 8 Village pasture (0.28 km²)	MC 9 Field (1.32 km²)
Bonasa bonasia (5)	—	—	2.0 (0.6)	—	0.8 (0.1)	—	—	—	—
Tetrao tetrix (5)	—	3.5 (1.8)	1.0 (0.3)	—	—	—	—	—	—
Vanellus vanellus (9)	1.0 (0.8)	—	—	—	—	—	—	—	6.1 (4.7)
Scolopax rusticola (7)	—	—	1.0 (0.3)	2.7 (0.4)	1.6 (0.2)	—	1.9 (0.9)	—	—
Columba palumbus (18)	—	—	1.0 (0.3)	6.8 (1.1)	7.3 (1.0)	2.0 (0.3)	1.9 (0.9)	—	—
Cuculus canorus (5)	3.0 (2.4)	—	0.5 (0.1)	—	0.8 (0.1)	—	—	—	—
Jynx torquilla (5)	—	—	—	1.4 (0.2)	0.8 (0.1)	—	1.9 (0.9)	7.1 (2.1)	—
Dendrocopos major (14)	1.0 (0.8)	2.3 (1.2)	1.5 (0.4)	1.4 (0.2)	3.3 (0.4)	5.9 (0.8)	—	—	—
Alauda arvensis (62)	—	—	—	—	—	2.0 (0.3)	—	10.7 (3.2)	43.9(34.3)
Anthus trivialis (85)	20.8(16.8)	16.3 (8.4)	14.1 (4.1)	6.8 (1.1)	6.5 (0.9)	5.9 (0.8)	9.6 (4.7)	—	—
Motacilla alba (36)	5.9 (4.8)	4.7 (2.4)	0.5 (0.1)	2.7 (0.4)	4.1 (0.5)	7.8 (1.1)	—	21.4 (6.3)	6.1 (4.7)
Troglodytes troglodytes (6)	—	—	2.4 (0.7)	1.4 (0.2)	—	—	—	—	—
Prunella modularis (23)	—	1.2 (0.6)	4.4 (1.3)	8.2 (1.3)	4.1 (0.5)	3.9 (0.6)	—	—	—
Erithacus rubecula (80)	—	2.3 (1.2)	15.6 (4.5)	27.4 (4.5)	17.1 (2.3)	3.9 (0.6)	5.8 (2.8)	—	—
Phoenicurus phoenicurus (8)	4.0 (3.2)	4.7 (2.4)	—	—	—	—	—	—	—
Saxicola rubetra (9)	—	—	—	—	—	—	3.8 (1.9)	3.6 (1.1)	4.5 (3.6)
Oenanthe oenanthe (9)	1.0 (0.8)	—	—	—	—	3.9 (0.6)	—	7.1 (2.1)	3.0 (2.4)
Turdus merula (107)	1.0 (0.8)	2.3 (1.2)	10.7 (3.1)	42.5 (7.0)	31.7 (4.2)	17.6 (2.5)	5.8 (2.8)	—	—
T. pilaris (115)	1.0 (0.8)	—	6.8 (2.0)	12.3 (2.0)	52.8 (7.0)	37.3 (5.2)	—	14.3 (4.2)	2.3 (1.8)
T. philomelos (84)	3.0 (2.4)	5.8 (3.0)	14.6 (4.3)	30.1 (4.9)	13.8 (1.8)	5.9 (0.8)	7.7 (3.7)	—	—
T. iliacus (143)	—	2.3 (1.2)	13.7 (4.0)	41.1 (6.7)	43.9 (5.8)	37.3 (5.2)	13.5 (6.5)	7.1 (2.1)	0.8 (0.6)
Hippolais icterina (21)	—	1.2 (0.6)	1.0 (0.3)	4.1 (0.7)	8.9 (1.2)	7.8 (1.1)	—	—	—
Sylvia curruca (16)	—	—	3.4 (1.0)	1.4 (0.2)	5.7 (0.8)	2.0 (0.3)	—	—	—
S. communis (34)	—	—	—	1.4 (0.2)	2.4 (0.3)	7.8 (1.1)	1.9 (0.9)	14.3 (4.2)	15.9(12.4)
S. borin (109)	—	1.2 (0.6)	3.9 (1.1)	13.7 (2.2)	43.9 (5.8)	56.9 (8.0)	7.7 (3.7)	—	2.3 (1.8)
S. atricapilla (48)	—	—	0.5 (0.1)	13.7 (2.2)	26.0 (3.5)	3.9 (0.6)	5.8 (2.8)	—	—
Phylloscopus sibilatrix (23)	—	—	1.5 (0.4)	19.2 (3.1)	4.9 (0.6)	—	—	—	—
Ph. collybita (39)	—	—	6.8 (2.0)	12.3 (2.0)	11.4 (1.5)	3.9 (0.6)	—	—	—
Ph. trochilus (208)	—	7.0 (3.6)	27.8 (8.1)	42.5 (7.0)	52.0 (6.9)	49.0 (6.9)	42.3(20.6)	7.1 (2.1)	0.8 (0.6)
Regulus regulus (112)	1.0 (0.8)	5.8 (3.0)	27.8 (8.1)	32.9 (5.4)	15.4 (2.1)	11.8 (1.7)	—	—	—
Muscicapa striata (109)	11.9 (9.6)	10.5 (5.4)	15.1 (4.4)	17.8 (2.9)	25.2 (3.4)	19.6 (2.8)	3.8 (1.9)	—	0.8 (0.6)
Ficedula hypoleuca (35)	4.0 (3.2)	5.8 (3.0)	2.4 (0.7)	4.1 (0.7)	12.8 (1.6)	2.0 (0.3)	—	7.1 (2.1)	—
Parus montanus (78)	11.9 (9.6)	15.1 (7.8)	12.2 (3.6)	11.0 (1.8)	10.6 (1.4)	5.9 (0.8)	7.7 (3.7)	—	—
P. cristatus (36)	10.9 (8.8)	8.1 (4.2)	7.3 (2.1)	—	1.6 (0.2)	—	—	3.6 (1.1)	—
P. ater (81)	5.0 (4.0)	12.8 (6.6)	17.6 (5.1)	19.2 (3.1)	5.7 (0.8)	9.8 (1.4)	1.9 (0.9)	7.1 (2.1)	—
P. caeruleus (52)	—	1.2 (0.6)	0.5 (0.1)	5.5 (0.9)	27.6 (3.7)	21.6 (3.0)	1.9 (0.9)	—	—
P. major (89)	5.9 (4.8)	4.7 (2.4)	6.3 (1.8)	16.4 (2.7)	28.5 (3.8)	21.6 (3.0)	1.9 (0.9)	14.3 (4.2)	2.3 (1.8)
Certhia familiaris (30)	1.0 (0.8)	1.2 (0.6)	4.4 (1.3)	4.1 (0.7)	10.6 (1.4)	3.9 (0.6)	1.9 (0.9)	—	—
Lanius collurio (16)	—	1.2 (0.6)	0.5 (0.1)	1.4 (0.2)	1.6 (0.2)	11.8 (1.7)	7.7 (3.7)	—	0.8 (0.6)
Garrulus glandarius (9)	—	1.2 (0.6)	2.4 (0.7)	1.4 (0.2)	1.6 (0.2)	—	—	—	—
Pica pica (7)	—	—	—	—	—	5.9 (0.8)	—	7.1 (2.1)	1.5 (1.2)
Corvus monedula (10)	—	—	—	—	4.9 (0.6)	3.9 (0.6)	—	7.1 (2.1)	—
C. corone (13)	1.0 (0.8)	1.2 (0.6)	0.5 (0.1)	1.4 (0.2)	5.7 (0.8)	—	—	7.1 (2.1)	—
Sturnus vulgaris (63)	—	1.2 (0.6)	0.5 (0.1)	—	17.9 (2.4)	15.7 (2.2)	—	82.1(24.2)	6.1 (4.7)
Passer domesticus (5)	—	—	—	—	—	—	—	14.3 (4.2)	0.8 (0.6)
Fringilla coelebs (730)	25.7(20.8)	48.8(25.3)	95.1(27.7)	160.3(26.3)	182.1(24.2)	196.1(27.6)	26.9(13.1)	35.7(10.5)	1.5 (1.2)
Carduelis chloris (22)	—	—	—	—	2.4 (0.3)	23.5 (3.3)	—	14.3 (4.2)	2.3 (1.8)
C. spinus (17)	1.0 (0.8)	1.2 (0.6)	2.9 (0.9)	4.1 (0.7)	3.3 (0.4)	3.9 (0.6)	—	—	—
C. cannabina (9)	—	—	—	—	0.8 (0.1)	3.9 (0.6)	—	7.1 (2.1)	3.0 (2.4)
Carpodacus erythrinus (18)	—	—	—	1.4 (0.2)	8.9 (1.2)	11.8 (1.7)	—	—	—
Pyrrhula pyrrhula (21)	—	2.3 (1.2)	1.5 (0.4)	13.7 (2.2)	0.8 (0.1)	9.8 (1.4)	—	—	—
Emberiza citrinella (136)	3.0 (2.4)	11.6 (6.0)	6.3 (1.8)	11.0 (1.8)	21.1 (2.8)	51.0 (7.2)	38.5(18.7)	32.1 (9.5)	15.9(12.4)
E. schoeniclus (6)	—	—	—	—	3.3 (0.4)	2.0 (0.3)	—	—	0.8 (0.6)

The community of sapling stand forms MC 7. The community differs greatly from those of the forest habitats. A few species dominate the community (*Phylloscopus trochilus, Emberiza citrinella, Fringilla coelebs, Turdus iliacus*). The habitat is a rapidly changing successional stage of various forest types, and the birds breeding there are a collection of species characteristic of other habitats, especially deciduous forests. MC 8, the community of village pasture, deviates clearly from the other communities. Several species attain their highest densities in this man-made habitat complex, e.g. *Motacilla alba, Oenanthe oenanthe, Corvus corone, Corvus monedula, Pica pica, Sturnus vulgaris* and *Passer domesticus*. MC 9, the community of open field, also occupies a man-made habitat. A few species attain their highest densities in fields: *Vanellus vanellus, Alauda arvensis, Saxicola rubetra* and *Sylvia communis*, the last of these because bushes along ditches were also included in the censuses. Bird communities breeding in open habitats on the Åland Islands are generally poor compared with the Finnish mainland: *Motacilla flava* is absent (see P.Palmgren 1935), *Emberiza hortulana* has almost totally disappeared during recent decades (Haila et al. 1979b), and *Anthus pratensis* is scarce (cf. Appendix). A clear difference between farmlands in Åland and adjacent parts of the Swedish mainland is the absence of *Corvus frugilegus* from Åland, though the species is abundant in Sweden.

5. Patterns of habitat selection

Clearly, a distinction must often be made between the optimal habitat (where a species attains its maximal density), and the most important habitat, where the highest proportion of the population breeds (Järvinen & Väisänen 1978). The difference can be seen by comparing Tables 3 and 4. It is due, of course, to the uneven distribution of the major habitats and variations in the densities of different species in different habitats on Åland. Assuming that our censuses sampled different habitats in fairly correct proportions (see Sect. 3), several clear patterns emerge:

Table 4. Habitat distribution of all species observed at least 20 times in the major communities. Habitat distribution gives the percentages of the population of each species breeding in different habitats; for the less common species, see Table 3 and Appendix. The total number of observations in these communities is given in parentheses after the species name. If this number is given as a sum (a+b), b observations were made in habitats not shown in the Table, but they were included in the calculations (see Appendix).

	MC 1	MC 2	MC 3	MC 4	MC 5	MC 6	MC 7	MC 8	MC 9
Alauda arvensis (62+5)	—	—	—	—	—	1	—	4	87
Anthus trivialis (85+4)	24	16	33	6	9	3	6	—	—
Motacilla alba (36+5)	15	10	2	5	12	10	—	15	20
Prunella modularis (23+1)	—	4	38	25	21	8	—	—	—
Erithacus rubecula (80+2)	—	2	39	24	26	2	4	—	—
Turdus merula (107)	1	2	21	29	36	8	3	—	—
T. pilaris (115)	1	—	12	8	57	17	—	3	3
T. philomelos (84+1)	4	6	35	26	20	4	5	—	—
T. iliacus (143+1)	—	1	19	21	38	13	5	1	1
Hippolais icterina (21)	—	5	10	14	52	19	—	—	—
Sylvia communis (34+2)	—	—	—	3	8	11	3	11	58
S. borin (109)	—	1	7	9	50	27	4	—	3
S. atricapilla (48)	—	—	2	21	67	4	6	—	—
Phylloscopus sibilatrix (23)	—	—	13	61	26	—	—	—	—
Ph. collybita (39+1)	—	—	35	22	35	5	—	—	—
Ph. trochilus (208+2)	—	3	27	15	30	12	10	1	0
Regulus regulus (112+2)	1	4	50	21	17	5	—	—	—
Muscicapa striata (109+3)	11	8	28	12	28	9	2	—	1
Ficedula hypoleuca (35)	11	14	14	9	43	3	—	6	—
Parus montanus (78+2)	15	16	31	10	16	4	5	—	—
P. cristatus (36+1)	30	19	41	—	5	—	—	3	—
P. ater (81+1)	6	13	44	17	8	6	1	2	—
P. caeruleus (52)	—	2	2	8	65	21	2	—	—
P. major (89+2)	7	4	14	13	38	12	1	4	3
Certhia familiaris (30)	3	3	30	10	43	7	3	—	—
Sturnus vulgaris (63)	—	2	2	—	35	13	—	37	13
Fringilla coelebs (730+6)	4	6	26	16	30	14	2	1	0
Carduelis chloris (22)	—	—	—	—	14	55	—	18	14
Pyrrhula pyrrhula (21)	—	10	14	48	5	24	—	—	—
Emberiza citrinella (136+4)	2	7	9	6	19	19	14	6	15

1. Spruce forest (bird community MC 3) is the most important habitat for three species with optima in pine forests (MC 1 and MC 2) and for six species, including those most clearly favouring spruce, with optima in luxuriant spruce forest (MC 4). *Phylloscopus collybita* is interesting, for it makes equal use of spruce forests (MC 3) and groves (MC 5). In Finland the species is a typical inhabitant of spruce forests (von Haartman et al. 1963—72), but in Central Europe (Lack 1971) and even in Sweden (Rudebeck 1962—64) it is common in deciduous woods.

2. Grove (MC 5) is the most important habitat for *Turdus merula* which has its optimum in luxuriant spruce forest (MC 4) and for four species (*Dendrocopos major, Sylvia borin, Fringilla coelebs* and *Carpodacus erythrinus*) with optima in grove meadow (MC 6).

3. Most of the species whose optimum is in village pasture (MC 8) have the bulk of their population either in MC 9 (*Motacilla alba, Oenanthe oenanthe, Carduelis cannabina*) or in MC 5 and MC 6 (corvids).

Patterns of habitat selection were further studied by measuring the degree of association between different species. As a result, groups of species with similar habitat requirements could be identified. For this purpose we applied an index introduced by Hurlbert (1978):

$$L = (A/XY)\ \Sigma\ (x_i y_i / a_i)$$

which measures the similarity of habitat selection of two species. X and Y are the total numbers of pairs of the two species, x_i and y_i being the respective numbers of pairs in habitat i, A the total area censused and a_i the area of habitat i. The index is based on the concept of interspecific encounter: L expresses the probability of interspecific encounter between the two species compared with the probability of encounter if both species were uniformly distributed over the habitats. The index value is 1 if both species are uniformly distributed, and $L = 0$ if the species have no habitat in common. Values greater than 1 indicate that the probability of encounter is relatively high (i.e. that the high and the low densities of the species tend to coincide). Notice that the formula takes into account the areas of the habitats, and so two species which are numerous in the same scarce habitat get a high value of association. Of course, high L should not be interpreted as similarity of niches, for L indicates only similarity of habitat requirements in relation to the habitats (or habitat complexes) here analysed.

To facilitate comparisons between all species pairs, an UPGMA dendrogram (Sneath & Sokal 1973) was computed (Fig. 4), including the 30 most numerous species in our data (at least 20 pairs observed). The most important secondary connections are also indicated. The species were divided into four groups according to their relative association in habitat selection. *Muscicapa striata* was not closely associated with any of the groups. On the basis of the dendrogram, this species can be classified as a forest generalist; suitable open foraging areas are more important to it than the actual forest type.

1. The first group comprises four pine forest species, but the association is interestingly low. Each of the species has strong secondary connections with other groups, especially with group 2 (spruce forests). *Parus ater* belongs to group 1, even though it has a higher degree of association with each of the eight species in group 2. This curious result is due to the compactness of group 2 and the fact that the species of group 2 (but not *P. ater*) tend to be associated with group 3. So *P. ater* is best regarded as intermediate between groups 1 and 2. The most typical representatives of group 1 are *Anthus trivialis* and *Parus cristatus*.

2. The second group is formed by the species of spruce forests. *Phylloscopus sibilatrix* and *Pyrrhula pyrrhula* are very closely associated, and six other species are grouped with this nucleus. *Phylloscopus sibilatrix* and *Turdus merula* have some associations with group 3, *Pyrrhula pyrrhula* with group 4 (*Carduelis chloris*). Otherwise group 2 is clear-cut.

3. The third group can be interpreted as species of luxuriant deciduous (or mixed) forests. Five species form the kernel (*Sylvia atricapilla, Parus caeruleus, Turdus pilaris, Hippolais icterina, Sylvia borin*) and six others, including the two most abundant of our species, *Fringilla coelebs* and *Phylloscopus trochilus*, are associated with them, though with relatively low index values. The group is quite distinct, however, for secondary connections with other groups tend to be weak. Most important of them are with *Carduelis chloris* and with some species of spruce forests (*Sylvia atricapilla*, $L = 2.69$ and *Turdus iliacus*, $L = 2.28$).

4. The fourth group comprises the species of open habitats. The two characteristic species of fields, *Alauda arvensis* and *Sylvia communis*, show the highest association in our data, and four other species favouring open habitats are connected with the same branch. One of these, *Carduelis chloris*, has fairly strong connections with some

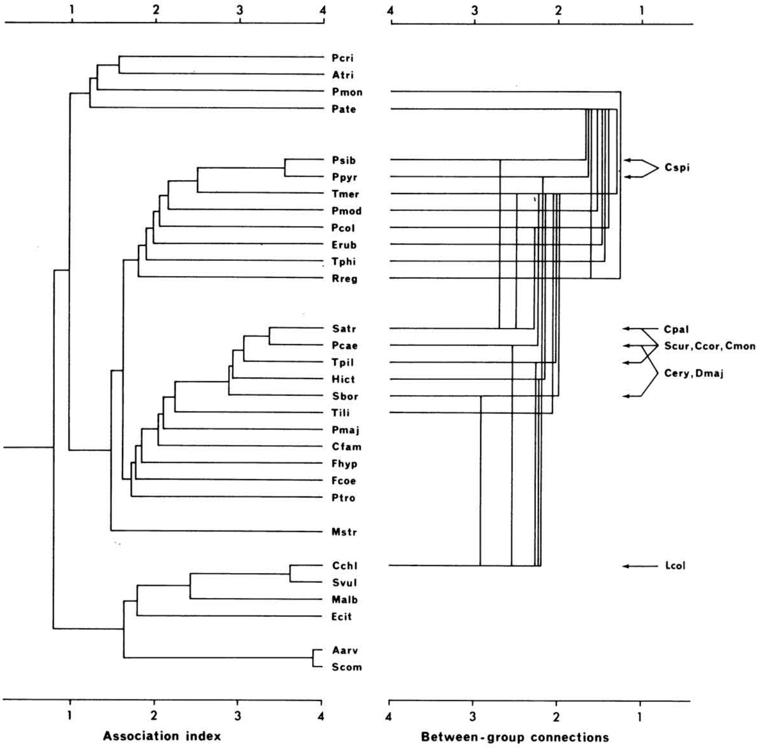


Fig. 4. Habitat associations of the 30 most numerous species in our data (at least 20 pairs observed). Left: an UPGMA dendrogram showing the main clusters. Right: the most important connections between the groups. Note that between-group connections are often absent or very few, but numerous in *Parus ater, Turdus merula, Sylvia atricapilla* and *Carduelis choris*. The closest associations of the eight species with 10—19 observations in our data are shown on the extreme right. For the species codes, see the Appendix.

species of luxuriant forests (especially *Sylvia borin*, $L = 2.91$).

A similar association matrix was also computed for all the 53 species included in Table 3. The general pattern was similar to that depicted in Fig. 4, but — as was to be expected — the structure of the groups was greatly affected by the rare species, and groups were often formed round less numerous species pairs, which is a consequence of the logic of the index. This dendrogram (not shown) was therefore less informative than Fig. 4, but we have indicated the closest associations of the eight species which were observed 10—19 times in the main communities.

The habitat amplitude of a species was measured from the equation:

$$A_h = \exp H',$$

where H' is the Shannon diversity based on the frequencies of the species in the different habitats. A_h increases with the number of habitats occupied, and with the similarity of the frequency values of the species in the different habitats. A_h is thus dependent on the number of communities studied and distinguished by the observers; in this study, the possible range is 1—9. Of course, the absolute value of A_h is not important; the interesting point to study is the interspecific differences. Corrections for sample size were computed from the numbers of pairs observed. Calculations were based on frequencies, as they express the ecological significance of the species in relation to the bird community as a whole better than do densities, for example. Indeed, the logic used here is the same as in Hanski's (1978) idea that in measuring niche breadth allowance must be made for the variable magnitudes of different resources. Measurements of habitat amplitude and niche breadth have features in common, although habitat and niche are different categories (Whittaker et al. 1973). Other measures of habitat amplitude, proposed by Simpson (1949) and Hurlbert (1978), were also tried, but they were much more sensitive to differences in sample size (as observed for Simpson's measure by Järvinen & Sammalisto 1973 and Järvinen & Lokki 1978).

It seems reasonable to expect a correlation between habitat amplitude and abundance (e.g. Levins 1968). From the average densities presented by Haila et al. (1979a) the total numbers of pairs of each land bird species on Åland can be calculated. In Fig. 5, we assume that our censuses were representative of an area of 1000 km^2, which is about the size of the mainland of Åland. The figure includes all species for which at least 10 pairs were observed in the censuses. There is a positive correlation between habitat amplitude and total numbers ($r = 0.418$, $P < 0.01$), but the variables do not share more than about 17 % of their variance, and the correlation is greatly affected by *Fringilla coelebs*.

Special interest attaches to those species which deviate clearly from the general pattern. Those with a narrow amplitude but relatively high numbers belong to open or man-made habitats (*Alauda arvensis, Sylvia communis, Sturnus vulgaris*). *Regulus regulus* and *Phylloscopus trochilus* also have narrow amplitudes in relation to their total numbers, i.e., the proportion of these species was especially high in one or a few habitats. Many species have wide habitat amplitude but relatively few pairs, especially *Dendrocopos major, Carduelis spinus, Certhia familiaris* and *Parus major*. Relatively many of the species observed 10—40 times in the censuses have comparatively wide amplitudes, perhaps partly owing to the effects of chance on small samples.

6. Concluding remarks

In his pioneering census studies of the Åland Islands P.Palmgren (1928, 1930, 1935) observed a correlation between habitat productivity and bird density. He also investigated the relations between species richness and area, and between species richness and sample size. He found, for example that in coniferous forests (OMT), a sample of about 100 pairs included about 20 bird species but in luxuriant deciduous and mixed forests about 25 species (see P.Palmgren 1930:140). In modern terms, species diversity was higher in luxuriant than in coniferous forests.

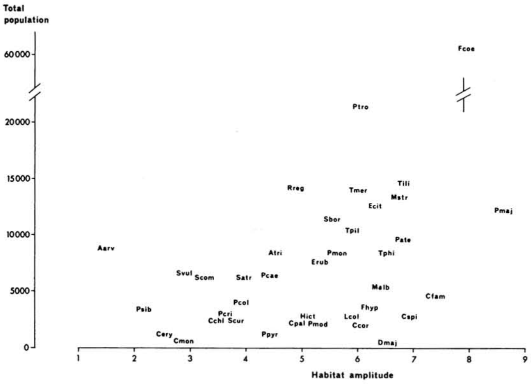


Fig. 5. The relation between habitat ampilitude and total breeding population on Åland for the 38 species observed most often in our censuses. For the species codes, see the Appendix.

Following MacArthur (e.g. 1964, 1971), it has been customary to correlate bird species diversity with vegetation structure. We did not make systematic measurements of habitat variables on Åland, but foliage height diversity (*FHD*) and percent vegetation cover (*PVC*, see e.g. Blondel et al. 1973 and Willson 1974) were estimated by eye in representative habitats. Of course, such estimates are imprecise, but the error is small compared with the total range of *FHD* and *PVC* in our data. *FHD* was defined as the natural logarithm of the numbers of "equally common" vegetation layers estimated in the field (we used an accuracy of 0.5 layers, the range being 1—3). If, for example, the tree, bush and field layers were all abundant, $FHD = \ln 3 = 1.1$. *PVC* was estimated with an accuracy of 50 %, each of the three layers contributing 0—100 % to *PVC* (range 0—300 %). For a description of the vegetation layers, see Table 1 (see also Fig. 2). Fig. 6 shows the correlations between bird species diversity and *FHD* and *PVC*. Both correlations were highly significant ($r = 0.94$, $P < 0.001$, for *FHD* and $r = 0.84$, $P < 0.001$, for *PVC*). Though based on approximate values of *FHD* and *PVC*, the trends are abundantly clear.

Nilsson (1979) has recently suggested that, ultimately, the factor determining variations in the local species richness and community density of birds is availability of food; correlations between diversity and vertical foliage structure (*FHD*) may be due to correlations between vertical foliage structure and ecosystem productivity. Unfortunately, accurate measurements of the productivity available to birds would be prohibitively laborious. Indeed, Nilsson (1979) found that bird species diversity was correlated with the proportion of the basal tree and shrub area standing dead in his plots, but the relations of this index to productivity are obscure. The data from Åland support the idea that productivity plays an important role in determining vegetation structure and diversity, as the trend in bird species diversity is similar to the trend in productivity, as judged from Högnäs (1966).

Nilsson (1979) also studied the relationship between total bird density and the proportions of

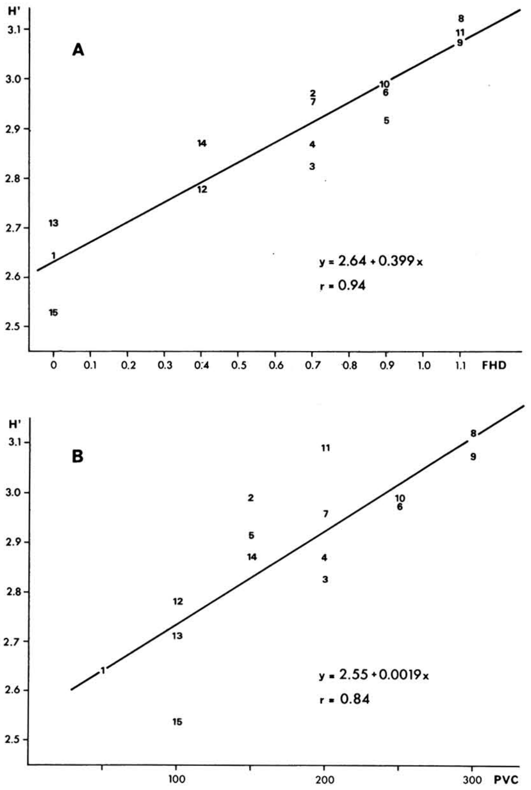


Fig. 6. The relation between bird species diversity and foliage height diversity in the habitats 1—15 distinguished in the field. — B. The same for bird species diversity and percentage of vegetation cover.

four bird (sub)families in eight forest communities. In his forest plots Turdinae showed a negative correlation and Sylvidae a positive correlation, while Paridae and Muscicapidae did not show any trend. We used our data for an identical analysis, including the 12 forest habitats distinguished in the field (habitats 1—12 in the Appendix). The results are shown in Fig. 7. The proportions are much the same in all habitats, except that the points for the habitats with the lowest bird densities deviated somewhat. We have not given any significances to the correlations shown in Fig. 7, as they are heavily affected by the two habitats with the lowest densities (pine forests), which are marginal for most of the species. It is obvious, however, that the trends in our data differ from those obtained by Nilsson for Turdinae (upward trend), and Paridae and Muscicapidae (downward trend). Sylvidae shows an upward trend in both sets of data. The discrepancies suggest that variations in the proportions of the different taxa are probably not causally related to community density. It is of wider significance, however, that we lack a theory predicting how our bird communities are basically assembled.

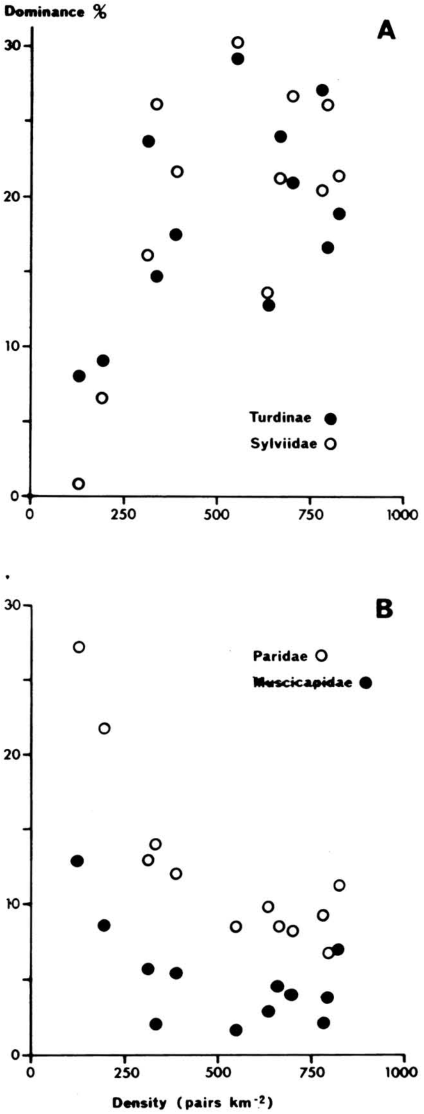


Fig. 7. A. Proportion of all pairs belonging to Turdinae and Sylviidae in the habitats 1—12 distinguished in the field. — B. The same for Paridae and Muscicapidae.

Community structure is the outcome of the habitat selection of different species. Habitat selection may be studied behaviourally, but is ultimately based on adaptive processes leading to variation in breeding success in different habitats. Immelmann (1973) concluded that, from the adaptive point of view, the most important single aspect of the habitat is probably the quantity and quality of available food resources; however, adaptive patterns may be difficult to demonstrate adequately (Partridge 1978). Adaptation to different habitats is complicated by the fact that the bulk of the population may breed in, and so become adapted to suboptimal habitats (Järvinen & Väisänen 1978). Our present data also show the importance for many species of suboptimal habitats.

Let us finally examine Fig. 5, as it throws some light on habitat selection. The median of habitat amplitude is about 5.3. The group of spruce forest species (see Fig. 4) tends to show a generally narrower habitat amplitude than the species of luxuriant forests (6/8 and 3/12 below the median, respectively). Pine forest species are also often habitat specialists. These conclusions are strengthened by the fact that two species of coniferous forests, *Parus ater* and *Regulus regulus*, had a peak year in 1975 (for data and references, see Järvinen et al. 1977 and Haila et al. 1980), and their habitat amplitudes may be narrower in average years. Annual population fluctuations have not been considered in this paper, as we have studied general trends. Furthermore, Nilsson (1979) observed that annual fluctuations in density within habitats did not affect *differences* in density between habitats, though, of course, this is not true of single populations (see also Fretwell 1972; Ch. 5). As a consequence of the habitat specialist strategy of spruce forest species, we shall expect that in northern Finland, where spruce is absent, between-habitat diversity of forests will be slight. This is true (Järvinen & Väisänen 1976b). The exceptional shape of spruce trees (they do not have a distinct canopy layer, but branches from top to base) probably requires a special feeding technique and, perhaps, morphological adaptations.

On the basis of optimal foraging models, Cody (1974) predicts that food specialists should generally be habitat generalists. In Fig. 5, there is a group of scarce habitat generalists (lower right) which support this idea; *Certhia familiaris, Carduelis spinus* and *Dendrocopos major* are undoubtedly food or feeding specialists. However, not all habitat generalists are food specialists (*Parus major* is a case in point). Another food generalist, *Fringilla coelebs,* is an intriguing species. It is an obvious habitat generalist, being able to breed in amazingly high densities in most habitats. Though *F. coelebs* is generally considered an inhabitant of forests of high productivity, its densities were also very high in grove meadows (indeed, higher than in any other major habitat in our data). So the species is able to utilize very patchy habitats, as is also indicated by its high frequency in wooded pastures. It would certainly be worthwile to study the adaptations which have made it possible for *F. coelebs* to exploit such a high proportion of the available resources in this limited world.

Acknowledgements. We thank Messrs Seppo Kuusela and Juha Markkola and Doc. Kari Vepsäläinen for helping us in the field work, and Prof. Pontus Palmgren, Doc. Samuel Panelius and Lic. Esa Ranta for comments on the manuscript. The English text was kindly revised by Mrs. Jean Margaret Perttunen, B.Sc. (Hons). Most of the census work was supported by a grant from the Academy of Finland.

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Appendix

Census results (pairs observed) in the 16 habitats distinguished in the field (for code numbers, see Table 2A). Numbers of pairs observed in four additional habitats included though the data are scanty. Abbreviations of species names used in Figs. 4 and 5 are indicated.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
Accipiter nisus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Bonasa bonasia	—	—	2	2	—	—	—	1	—	—	—	—	—	—	—	—	5
Tetrao tetrix	—	3	1	—	1	—	—	—	—	—	—	—	—	—	—	1	6
Crex crex	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Charadrius dubius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Ch. hiaticula	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Vanellus vanellus	1	—	—	—	—	—	—	—	—	—	—	—	—	—	8	3	12
Gallinago gallinago	—	—	—	—	1	—	—	—	—	—	—	—	2	—	1	1	5
Scolopax rusticola (S rus)	—	—	—	1	1	1	1	—	2	—	—	—	1	—	—	—	7
Numenius arquata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3
Tringa totanus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
T. ochropus (T och)	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	2
Actitis hypoleucos	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	1	4
Columba oenas	—	—	1	1	—	—	—	—	—	—	1	—	—	—	—	—	3
C. palumbus (C pal)	—	—	1	1	—	—	5	4	4	1	1	—	1	—	—	—	18
Cuculus canorus	3	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	5
Jynx torquilla	—	—	—	—	—	—	1	1	—	—	—	—	1	2	—	—	5
Picus canus	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	2
Dryocopus martius	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2
Dendrocopos major (D maj)	1	2	—	1	2	—	1	1	1	2	1	2	—	—	—	—	14
D. minor	—	—	—	—	1	—	—	—	1	1	—	—	—	—	—	—	3
Alauda arvensis (A arv)	—	—	—	—	—	—	—	—	—	—	—	1	—	3	58	5	67
Hirundo rustica	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	3
Delichon urbica	—	—	—	—	—	—	—	1	—	—	3	—	—	—	—	—	4
Anthus trivialis (A tri)	21	14	8	12	9	—	5	3	5	—	—	3	5	—	—	—	85
A. pratensis (A pra)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	4
Motacilla alba (M alb)	6	4	—	1	—	—	2	2	3	—	1	3	—	6	8	3	39
Troglodytes troglodytes	—	—	—	5	—	—	1	—	—	—	—	—	—	—	—	—	6
Prunella modularis (P mod)	—	1	3	6	—	1	5	4	1	—	1	1	—	—	—	—	23
Erithacus rubecula (E rub)	—	2	8	18	6	7	13	10	7	4	2	—	3	—	—	—	80
Luscinia luscinia	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	—	4
Phoenicurus phoenicurus	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Saxicola rubetra	—	—	—	—	—	—	—	—	—	—	—	—	2	1	6	1	10
Oenanthe oenanthe	1	—	—	—	—	—	—	—	—	—	1	1	—	2	4	—	9
Turdus merula (T mer)	1	2	1	13	8	9	22	11	20	8	6	3	3	—	—	—	107
T. pilaris (T pil)	1	—	6	6	2	3	6	12	29	24	9	10	—	4	3	—	115
T. philomelos (T phi)	3	5	6	18	6	6	16	8	5	4	2	1	4	—	—	—	84
T. iliacus (T ili)	—	2	6	12	10	9	21	21	21	12	12	7	7	2	1	1	144
T. viscivorus	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Acrocephalus scheonobaenus	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	2
A. palustris	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
A. scirpaceus	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	4	6
Hippolais icterina (H ict)	—	1	1	1	—	2	1	2	6	3	2	2	—	—	—	—	21
Sylvia curruca (S cur)	—	—	1	4	2	—	1	3	2	2	1	—	—	—	—	—	16
S. communis (S com)	—	—	—	—	—	—	1	2	—	1	4	—	1	4	21	2	36
S. borin (S bor)	—	1	4	3	1	2	8	9	33	12	20	9	4	—	3	—	109
S. atricapilla (S atr)	—	—	—	1	—	4	6	8	14	10	2	—	3	—	—	—	48
Phylloscopus trochiloides	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	2
Ph. sibilatrix (P sib)	—	—	—	3	—	2	12	2	3	1	—	—	—	—	—	—	23
Ph. collybita (P col)	—	—	1	10	3	3	6	7	5	2	1	1	—	—	—	—	39
Ph. trochilus (P tro)	—	6	23	26	8	13	18	35	23	6	16	9	22	2	1	—	208
Regulus regulus (R reg)	1	5	18	34	5	7	17	11	7	1	4	2	—	—	—	—	112
Muscicapa striata (M str)	12	9	7	17	7	1	12	9	20	2	5	5	2	—	1	—	109
Ficedula parva	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	2
F. hypoleuca (F hyp)	4	5	—	4	1	1	2	3	10	2	1	—	—	2	—	—	35
Aegithalos caudatus	—	—	—	1	—	1	—	—	1	1	—	—	—	—	—	—	4
Parus montanus (P mon)	12	13	7	10	8	2	6	6	7	—	2	1	4	—	—	—	78
P. cristatus (P cri)	11	7	6	8	1	—	—	—	2	—	—	—	—	1	—	—	36
P. ater (P ate)	5	11	12	20	4	2	12	5	2	—	1	4	1	2	—	—	81
P. caeruleus (P cae)	—	1	—	1	—	—	4	5	17	12	4	7	1	—	—	—	52
P. major (P maj)	6	4	1	7	5	6	6	9	20	6	6	5	1	4	3	—	89
Certhia familiaris (C fam)	1	1	2	7	—	—	3	4	8	1	—	2	1	—	—	—	30
Oriolus oriolus	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Lanius collurio	—	1	—	—	1	—	1	—	2	—	4	2	4	—	1	1	17
Garrulus glandarius	—	1	1	4	—	1	—	2	—	—	—	—	—	—	—	—	9
Pica pica	—	—	—	—	—	—	—	—	—	—	2	1	—	2	2	—	7
Nucifraga caryocatactes	—	—	—	—	—	—	1	—	2	1	—	—	—	—	—	—	4
Corvus monedula (C mon)	—	—	—	—	—	—	—	2	4	—	1	1	—	2	—	—	10
C. corone (C cor)	1	1	1	—	—	1	—	2	5	—	—	—	—	2	—	—	13
Sturnus vulgaris (S vul)	—	1	—	—	1	—	—	4	9	9	4	4	—	23	8	—	63

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
Passer domesticus	—	—	—	—	—	—	—	—	—	—	—	—	—	4	1	—	5
Fringilla coelebs (F coe)	26	42	46	113	36	24	93	74	104	46	41	59	14	10	2	1	731
Carduelis chloris (C chl)	—	—	—	—	—	—	—	1	1	1	8	4	—	4	3	—	22
C. spinus (C spi)	1	1	1	4	1	—	3	1	2	1	1	1	—	—	—	—	17
C. cannabina	—	—	—	—	—	—	—	1	—	—	—	2	—	2	4	—	9
Loxia curvirostra	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2
L. pytyopsittacus	—	2	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3
Carpodacus erythrinus (C ery)	—	—	—	—	—	—	1	3	6	2	6	—	—	—	—	—	18
Pyrrhula pyrrhula (P pyr)	—	2	1	2	—	2	8	—	—	1	2	3	—	—	—	—	21
Emberiza citrinella (E cit)	3	10	5	2	6	3	5	5	12	9	12	14	20	9	21	3	139
E. hortulana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
E. schoeniclus	—	—	—	—	—	—	—	1	1	2	—	1	—	—	1	3	9

Additional habitats:
Spruce swamp (5 ha): *Tetrao urogallus* 1, S rus 1, C pal 1, A tri 1, P mod 1, E rub 2, P col 1, P tro 2, R reg 2, M str 1, P mon 1, P ate 1, P maj 1, F coe 5.
Pine bog (5 ha): A tri 3, M str 2, P mon 1, P cri 1, P maj 1.
Open peat bog (2 ha): A pra 2.
Forest clearing (6ha): T och 1, M alb 2, T phi 1, L col 1, E cit 1.

Received 14.I.1980
Printed 22. IX. 1980