Habitat selection of breeding birds in relation to forest succession in Northeastern Finland

Pekka Helle

Helle, P. 1985: *Habitat selection of breeding birds in relation to forest succession in Northeastern Finland.* – Ornis Fennica 62:113–123.

Breeding birds were censused in five different stages of forest succession (2–150 years) in Northeastern Finland, in dry and moist forest sites separately. The one-visit census method was used. The total area of the 36 plots studied amounted to 1167 ha.

In the dry series one species (*Anthus trivialis*) was observed to breed in all the five stages; in the moist series there were three such species (*Turdus iliacus, Phylloscopus trochilus, Carduelis flammea*). The 'mid-point of density' was used to measure the optimum location of a species in the forest succession gradient. The mid-points of density weighted for species abundance were practically the same in the dry and moist series. The similarly weighted value for the average habitat amplitude of the species was clearly higher in moist than in dry sites, which was mainly due to *Phylloscopus trochilus.* A dendrogram based on the similarities in habitat selection of the species produced five species groups, which, however, to some extent was due to the five-stage sampling used in the study.

The habitat amplitude and abundance of the species were positively correlated. The rarefaction method was used to analyse this relationship in details. The average habitat amplitude of congeneric passerines exceeded that of noncongeneric passerine species. The average habitat overlaps of these two species groups were equal.

The densities of the most abundant species were compared with five characteristics of the vegetation. There were no significant correlations between the densities of the species and the proportion of hardwood in the total foliage volume. The densities of *Fringilla coelebs* and *montifringilla, Turdus iliacus* and *Muscicapa striata* were correlated significantly with the height of the vegetation, foliage height diversity, total vegetation cover and the number of tree and shrub species.

Pekka Helle, Oulanka Biological Station, University of Oulu, Linnanmaa, SF-90570 Oulu, Finland, and Department of Biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100 Jyväskylä, Finland

> "The study of ecological successions is one of the best ways to analyze the nature and dynamics of the relationship between birds and plants."
>
> Prodon & Lebredon 1981

Introduction

The structure of breeding bird communities in boreal forests has been studied extensively (e.g. Palmgren 1930, Soveri 1940, Merikallio 1946, Alatalo 1980, Järvinen 1980). Thanks to quantitative analyses and to detailed monographs on individual species, abundant (descriptive) information is available on the habitat selection of bird species (e.g. in handbooks). Gradient analyses, in which a series of habitats is censused, are especially useful in quantitative studies of the habitat selection of organisms (see e.g. Whittaker 1970). The gradient most widely used in forest bird studies is the productivity of the forest (e.g. Merikallio 1946); the age of the forest is used less often (e.g. Johnston & Odum 1956, Glowaciński 1975). Both of these gradients are considered in a few papers (Engström 1955, Haapanen 1965, 1966) and there are numerous studies on the effects of forest age on individual bird species (e.g. Lack & Lack 1951, Haapanen 1966, Ahlén 1975, Franzreb 1977).

Habitat selection is basically a behavioural process because the birds recognize their environment by signals or cues in the characteristics of the vegetation or of the habitat in general (for reviews see Hildén 1965, Partridge 1978). Although birds are relatively flexible in their habitat selection, a genetic component is also involved (e.g. Lack 1971). Both inter- and intraspecific competition are thought to be associated with habitat selection, the latter broadening the habitat amplitude of a species and the former reducing it (Svärdson 1949, Fretwell 1978). The habitat breadths of species in northern bird communities are narrowest during the breeding season, which may be a consequense of special habitat requirements rather than interspecific competition (Alatalo 1981). The importance of interspecific competition in structuring bird communities has recently been questioned (Wiens 1977, 1983), and it is difficult to imagine that it plays a major role in the often unsaturated breeding bird communities of boreal forests (Järvinen 1980).

In other articles I have described the effects of the successional status and size of a stand on bird community structure in northern Finland (Helle 1984, 1985). Here I will discuss the habitat selection of individual bird species and the reasons for the general patterns observed.

Material and methods

The data for this study were gathered in, and close to, the Oulanka National Park, in Northeastern Finland (ca. 66°N, 30°E), during the breeding seasons of 1980–82. The area was originally covered by virgin taiga forest, but nowadays it is heavily exploited by forestry, except in the National Park. Detailed descriptions of the study area and methods can be found elsewhere (Helle 1985).

Five successional stages were studied in both dry and moist forest types, the ages of the stands being about 2 (I), 10 (II), 25 (III), 75 (IV), and 150 years (V). The dry series comprises the forest types *Calluna–Cladina* and barren *Empetrum–Myrtillus,* the moist series the more productive *Emptrum–Myrtillus* and *Hylocomium–Myrtillus* (for the Finnish forest site type classification see Kalela 1961, and for the details of the study area, Söyrinki et al. 1977, and Helle 1985). The three youngest stages have originated from clear-felling, while the older stages have developed after slash-and-burn cultivation or forest fires. The total area of the 36 study plots amounts to 1167 ha, and the avian data relate to 522 breeding pairs belonging to 53 species. (The primary data are included in the Appendix.) Breeding birds were censused by one-visit censuses during 5 June–6 July in each season. In stages I–III the study plot method (see Palmgren 1930) was employed, and in stages IV–V the line transect method (Järvinen and Väisänen 1976, 1977), using only the main belt (breadth 50 m) data. It should be remembered that in both these methods one-sixth to one-half of all pairs are missed (Järvinen 1978, Järvinen & Väisänen 1980, and the references therein).

At a representative point in every study plot and transect, five features of the vegetation were determined or estimated (see Helle 1985 for details):

(1) Height of vegetation in metres (HEI),
(2) Total vegetation cover (TVC),
(3) Proposition of hardwood in total foliage volume (HW),
(4) Foliage height diversity (FHD),
(5) Number of dominant tree and shrub species within a radius of 25 m (NUM).

The similarity of habitat selection of two species was measured using the percentage similarity index (Renkonen 1938) $PS_{ij} = \Sigma \min (p_{ih}, p_{jh})$, where p is the proportion of pairs of species i and j in stage h. A dendrogram based on the similarities in habitat selection of the species was then constructed with the simple algorithm described by, for example, Cody (1974). The habitat amplitude of a species was measured by the inverse of the Simpson index, or $HA_i = 1/\Sigma p_{ih}^2$, where p is the frequency of species in stage h.

The stage where a species reaches its highest density may be considered to be its optimum stage (e.g. Wasilewski 1961), though this assumption is not fully correct (Tomiałojć et al. 1977, Nilsson & Ebenman 1981). In order to have a measure of where the 'average' pair of species is situated in the forest regeneration gradient, a median was calculated from the densities of a species in the different stages of succession. Instead of the true ages of the stands, relative figures were used ranging from one to five. This median will be termed the 'mid-point of density'.

Results and discussion

Habitat occupancy. The bulk of the species were observed in only a few succession stages: the proportion of the species breeding in one or two stages amounts to 78 % in the dry and 82 % in the moist series (Table 1). In the dry sites only one species out of 36 (the Tree Pipit *Anthus trivialis*) occupied all five stages and in the moist sites three species out of 44 (the Redwing *Turdus iliacus,* the Willow Warbler *Phylloscopus trochilus,* and the Redpoll *Carduelis flammea;* see Appendix). The most abundant species use the habitat spectrum widely, so that the species inhabiting four or five stages of a series make up 46 % of the total number of pairs and the species breeding in one or two stages 37 % (dry and moist sites combined, Table 1).

The most common species in each succession stage and their proportions in both site type series are presented in the following table:

		Dry series	Moist series
Stage I:	*Motacilla alba*	33.3 %	20.7 %
	Oenanthe oenanthe	20.0	17.2
Stage II:	*Phylloscopus trochilus*	40.5	23.7
	Saxicola rubetra	9.5	–
	Motacilla flava	9.5	–
	Anthus trivialis	–	18.4

Table 1. Numbers and percentages of species and of pairs belonging to these species in five forest succession stages i Northeastern Finland. See text for the definition of dry and moist series and for the ages of the stages.

	Number of succession stages occupied														
	Dry series					Moist series					Total				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Number of species	18	10	4	3	1	22	14	4	1	3	25	14	9	1	4
% of species	50	28	11	8	3	50	32	9	2	7	47	26	17	2	8
Numbers of pairs	29	36	36	71	19	41	89	53	26	122	55	87	92	74	216
% of pairs	15	19	19	37	10	12	27	16	8	37	11	16	18	14	41

Stage III:	*Phylloscopus trochilus*	40.0	52.4
	Anthus trivialis	11.4	–
	Turdus iliacus	–	14.3
Stage IV:	*Fringilla montifringilla*	20.0	–
	Anthus trivialis	15.6	–
	Phylloscopus trochilus	–	21.5
	Fringilla coelebs	–	14.0
Stage V:	*Fringilla montifringilla*	14.8	16.7
	Muscicapa striata	11.1	–
	Phylloscopus trochilus	–	16.7

See Appendix for the abundance of all species.

Differences between dry and moist series. Statistically significant preferences for the moist forest series can be observed in *T. iliacus* and *C. flammea* ($P<0.05$) and in *Ph. trochilus* ($P<0.01$); no species shows a preference for the dry series. Of the species common to dry and moist forests (27 species), 10 have a higher population density in the dry than in moist series, and in the other 17 species the result is the opposite; this distribution does not deviate significantly ($P<0.1$) from that expected. In addition to differences in densities between the series, the distribution of the pairs among the different stages of succession may be dissimilar; significant differences were found in *Ph. trochilus* ($P<0.01$) and nearly significant ones in *T. iliacus* and *M. alba* ($P<0.1$). See the Appendix for the numbers, which were standardized for and equal area in the above tests.

The mid-points of the densities, weighted for species abundance, are 3.35 in dry and 3.39 in moist forests. The similarly weighted values for the average habitat amplitudes are 2.37 and 2.63 for dry and moist forest, respectively (the difference is highly significant, $P<0.001$). The difference in the average habitat amplitudes is due to 1) differences in the abundances of narrow- and wide-amplitude species between the two series and/or 2) differences in the amplitudes of the same species between the series. In order to assess the latter explanation, I checked the habitat amplitudes of the 10 most abundant species in the data. All these species were observed in the two series (see Appendix). The mean amplitudes (weighted for the abundance) for these species are 2.73 and 3.11 for dry and moist forest, respectively. Since the difference observed here is practically the same as that calculated from the total data (2.38 vs. 2.63), the difference between the dry and moist series is due to the abundant species. *Ph. trochilus*, with its fairly high relative frequency, has the greatest effect on the figures: the contribution of this species to the difference is 0.38 units, which means that without it the mean habitat amplitudes in dry and moist sites are equal. There are certain differences in the other abundant species, but they tend to compensate each other.

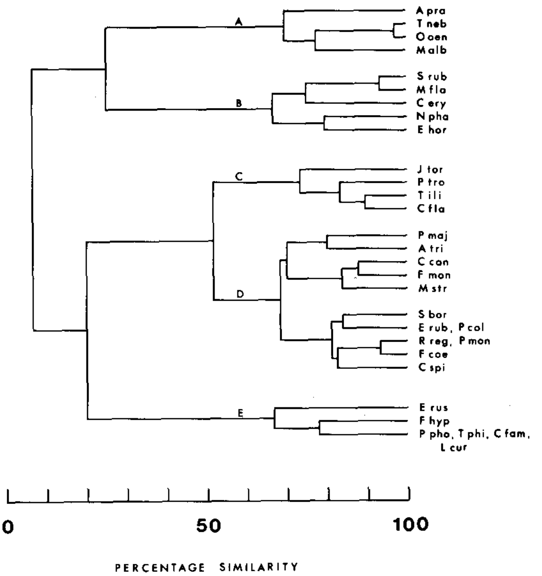

Fig. 1. A dendrogram of similarities in habitat selection among the most frequent species in the material. For species abbrevations see Appendix. Species groups: A) species of clear-felled areas, B) older clear-felled areas, C) young forest, D) young and mature forest and E) climax forest.

Species associations. A dendrogram based on the similarities in habitat selection reveals five different groups of species (Fig. 1). The picture is generalized because the dry and moist site data are combined. For this reason, for example, the Chaffinch *F. coelebs* and the Siberian Tit *Parus cinctus* are close to each other, although the former prefers moist forests and the latter drier ones. It should be noted here, however, that dry and moist forests are not two distinct categories but rather two ends of the moisture gradient with all kinds of intermediate types. One may ask whether the five groups of species merely result from the fact that the data originate from five stages of forest succession. This property of the material has indeed an influence on the five-group pattern. If five groups of species were formed according to the successional stages in which the species reach their maximum density, they would be nearly identical to those in Fig. 1, with only some minor exceptions. *C. flammea* would be in group 4 instead of group 3 (when the groups in Fig. 1 are numbered from the top to bottom), and *A. trivialis* and *M. striata* in group 4. The densities of the five groups of species formed by the latter method in the different stages of forest regeneration are presented in Fig. 2. The species belonging to group 1 (maximum density in stage I) are concentrated in the initial stage. The same is true of group 2, while the three other species groups show more diversified patterns in their habitat utilization.

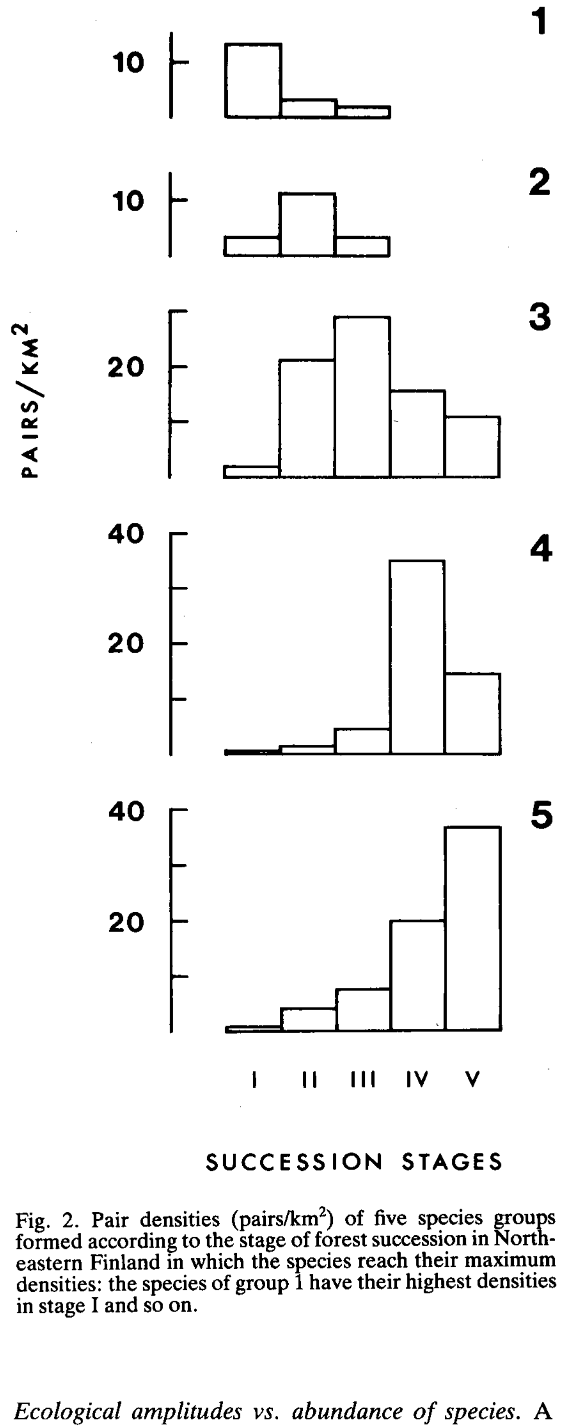

Fig. 2. Pair densities (pairs/km^2) of five species groups formed according to the stage of forest succession in North-eastern Finland in which the species reach their maximum densities: the species of group 1 have their highest densities in stage I and so on.

Ecological amplitudes vs. abundance of species. A positive correlation can be expected between the habitat amplitude and the abundance of species, since intraspecific competition will presumably oblige individuals of an abundant species to use less suitable habitats as well (Brown 1969). The correlation between the habitat amplitude and the relative abundance of the species is significant ($r=+0.47$, $P<0.05$; Fig. 3). Those species that do not follow the general trend are most interesting (see Haila et al. 1980). There are no abundant habitat specialists in the present material: they would be situated in the upper left corner of Fig. 3. Further, there are no habitat generalists, which would be concentrated in any habitat. The Cuckoo *Cuculus canorus,* the Wryneck *Jynx torquilla* and the Great Tit *Parus major* are the most promising candidates for the latter classification; the data base is, however, very restricted as regards to these species.

As the values for habitat amplitude, or habitat breadth, depend decisively on the number and quality of habitat categories, quantitative comparisons between the present results and earlier studies are not meaningful. Moreover, corresponding analyses have concentrated mainly on mature forests (Haila et al. 1980, Alatalo 1981, Tiainen 1981). In their study area in the Åland archipelago Haila et al. (1980) found that open-habitat species tended to have a narrow habitat amplitude but relatively high abundance (position in the upper left corner in Fig. 3). Most of these species bred in fields, and this is probably the reason for the different result obtained with the present data. In some species the habitat amplitude differs clearly between the south and north of the range (e.g. *Fringilla coelebs*). In southern Finland the Chaffinch has been generally considered a genuine habitat generalist, whereas in northern Finland it breeds only in the most productive habitats (Merikallio 1951, Järvinen & Väisänen 1979). The southern and northern forests differ in many respects, the latter being less productive and having a small proportion of hardwoods. Consequently, most of the forests of "northern" quality would presumably be avoided by the Chaffinch in southern Finland as well (see Mikkonen 1983).

Haila et al. (1980) considered that the Great Spotted Woodpecker *Dendrocopus major,* the Treecreeper *Certhia familiaris* and the Siskin *Carduelis spinus* (wide amplitude but relatively few pairs) were species supporting the hypothesis of Cody (1974) that food or feeding specialists are habitat generalists, and *vice versa.* In Kuusamo these species do not behave in accordance with the hypothesis. Two reservations must be made: 1) the present material represents only four mature stages, which is a small sample of the total spectrum of forested habitats in the study area; 2) all the species named above have southern distributions and Kuusamo is fairly near the limit of their regular breeding. Although there are some difficulties with the definitions of 'food and habitat specialist/generalist', we can see that the most abundant species in the present material (*A. trivialis, T. iliacus, Ph. trochilus* and *C. flammea* all with broad habitat amplitudes) are not food or feeding specialists (except *C. flammea* in winter).

The relationship between the habitat amplitude and the abundance of a species might be interpreted in another way: is it only a consequence of sample size that, say, a species with 100 pairs observed in seven habitats is supposed to be more generalist in habitat selection tha species with 20 pairs observed in four habitats? I analysed the amplitude-abundance data by the statistical 'rarefaction' method (Heck et al. 1975), which makes it possible to compare the numbers of occupied habitats after standardizing the sample sizes. The expected number of occupied habitats in a random sample of 10 pairs is presented below for the 10 most numerous species:

	Number of pairs	Number of habitats occupied	Expected number of habitats (±SD) in a random sample of 10 pairs	
Ph. trochilus	122	9	5.39 ±	1.183
Fr. montifringilla	55	7	4.77	1.012
Anthus trivialis	45	9	5.63	1.224
Fringilla coelebs	33	5	3.88	0.696
Turdus iliacus	29	8	4.94	1.166
Carduelis flammea	20	7	4.82	1.032
Motacilla alba	19	6	4.41	0.881
Muscicapa striata	17	5	4.20	0.741
Motacilla flava	14	6	4.55	0.905
Carduelis spinus	13	4	3.59	0.559

The observed number of pairs and the expected number of habitats in a sample of 10 pairs are positively correlated ($r_s = +0.66$ $P<0.05$). Although the habitat amplitudes of the 10 species are much narrower in the smaller samples, the order of the species is the same for the observed and sample size-corrected habitat amplitudes. This is due to the rather similar habitat-abundance distributions of the species. There are no statistically significant differences among the expected numbers of habitats of the 10 species.

This analysis only partly answers the question raised above. In another analysis the abundance-amplitude "locations" of the most abundant species were compared with the calculated rarefaction curves. The comparison was made for each species group (see Fig. 1) separately. The deviations of the individual species from the group curves showed a clear effect of abuncance on habitat amplitude only in group 2 (Fig. 4). In group 4 only *Anthus trivialis* and *Cuculus canorus* are above the curve while all the other species are fairly specialized when compared to the group as a whole. The results suggest that the abundance and habitat amplitude are not clearly correlated when the specialization of the species on the different stages of succession is taken into account.

The average habitat amplitude for congeneric passerines is 2.02±1.083 and that for passive species that are not congenenic is 1.41±0.535. The difference is statistically significant ($P<0.05$). The average habitat overlaps (or similarities in habitat selection) do not differ between congeneric and noncongeneric passerines (53.5±11.20 for the former and 56.1±13.25 for the latter). This disagrees with Alatalo's (1981) report that congeneric passerines have lower habitat amplitudes and overlaps than passerines that are not congeners. One possible explanation for this difference is the habitat spectrum studied. The present habitats (succession stages) differ more clearly from each other than do those studied by Alatalo (1981): the habitat or 'microhabitat' level patterns cannot be found by assessing 'macrohabitats' (this study). The reverse result of this study concerning the habitat amplitudes is most probably due to the greater abundances of the congeners (25 species, 407 pairs) compared with the noncongeners (15 species, 87 pairs). The results obtained earlier on the relationship between the abundance and the habitat amplitude of species support this explanation.

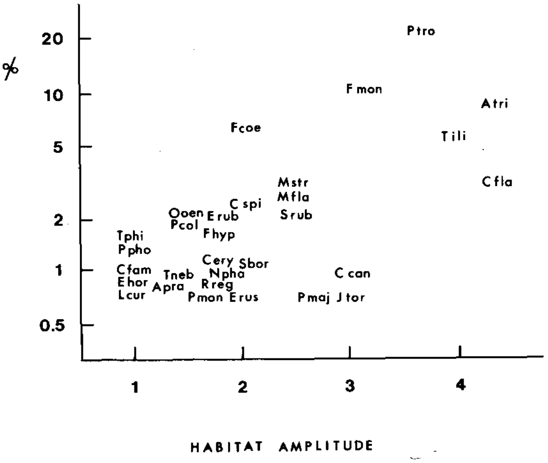

Fig. 3. Relationship between habitat amplitude and numerical dominance (%) among the most abundant species in the forest succession data in Northeastern Finland. For species abbreviations see Appendix.

Vegetation characteristics and densities of individual species. Correlations between the vegetation features studied and the densities of the 10 most numerous species are presented in Table 2. Linear correlations are given, because in the majority of cases they produced the best results.

There are no significant correlations for hardwood percentage. This is surprising, because Soveri's (1940) and several later studies have shown that an increase in the proportion of hardwood in the total foliage volume will cause an increase in bird density. In the present case, however, the effects of the hardwood proportion are most probably masked by the increase in vegetation height and other characteristics involved (foliage height diversity, amount of shrubs, among other things; Helle 1983, 1985). The four other vegetation features studied are positively correlated with the densities of *F. coelebs, F. monti-*

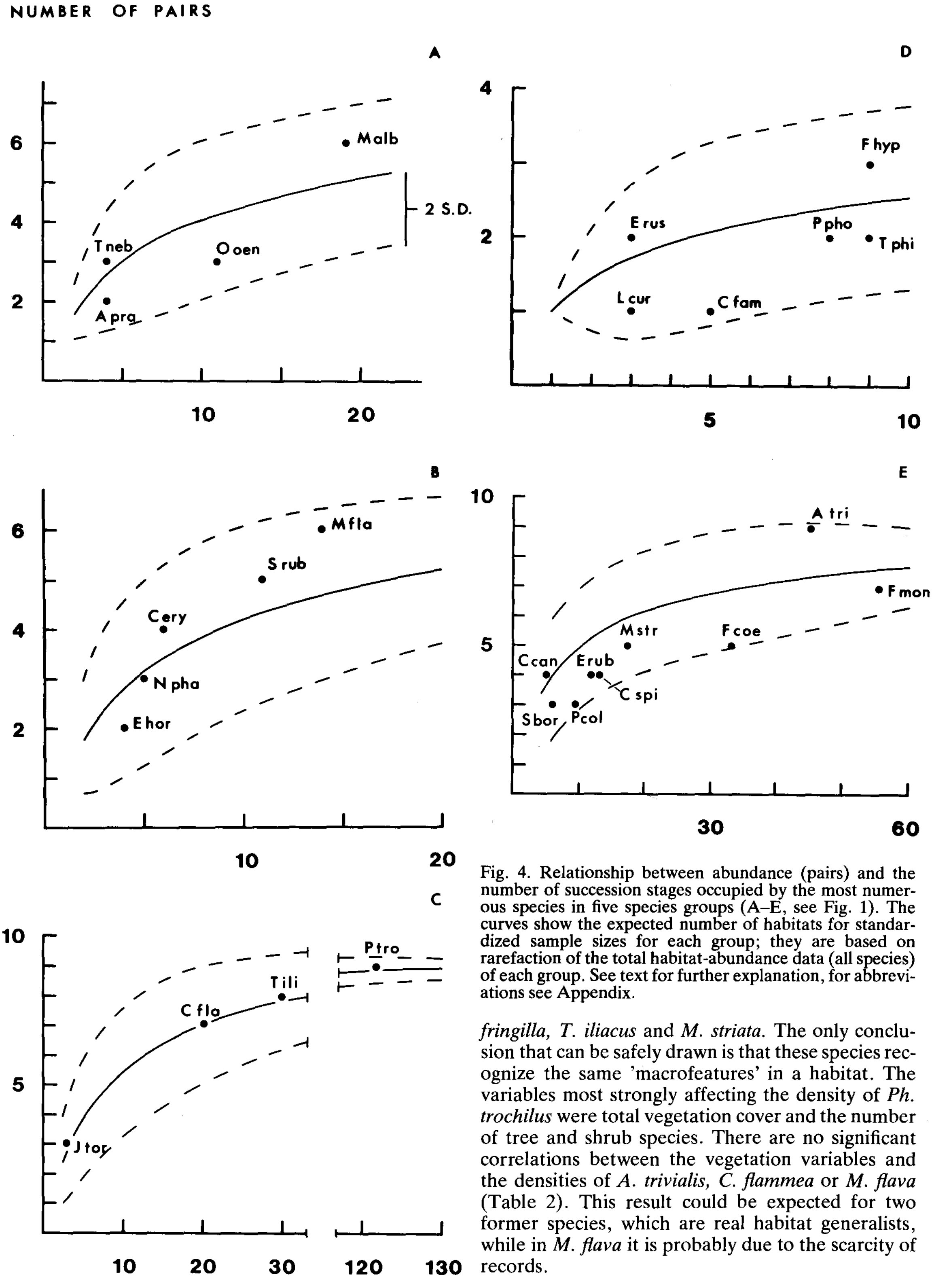

Fig. 4. Relationship between abundance (pairs) and the number of succession stages occupied by the most numerous species in five species groups (A–E, see Fig. 1). The curves show the expected number of habitats for standardized sample sizes for each group; they are based on rarefaction of the total habitat-abundance data (all species) of each group. See text for further explanation, for abbreviations see Appendix.

fringilla, T. iliacus and *M. striata.* The only conclusion that can be safely drawn is that these species recognize the same 'macrofeatures' in a habitat. The variables most strongly affecting the density of *Ph. trochilus* were total vegetation cover and the number of tree and shrub species. There are no significant correlations between the vegetation variables and the densities of *A. trivialis, C. flammea* or *M. flava* (Table 2). This result could be expected for two former species, which are real habitat generalists, while in *M. flava* it is probably due to the scarcity of records.

Specialization and succession. According to the general theory of succession (e.g. Odum 1969,Glowaciński 1979), the degree of 'specialization in communities' tends to increase in the course of succession. If this is correct, we can expect the average habitat amplitude of the species to decrease from initial stages to the climax. In order to test this I calculated the average habitat amplitudes of the species for the different succession stages (weighted for species abundance):

	I	II	III	IV	V
Dry series	1.8	2.4	2.7	2.6	2.4
Moist series	2.1	2.7	3.4	2.6	3.0

The average amplitude first increases and then slightly decreases in the dry sites; in moist series the trend is not so clear but the variation is great. The results thus do not support the prediction derived from the succession theory, but it must be kept in mind that the result obtained depends to some extent on the division of the succession gradient.

Specialization can also be examined by comparing the number of habitat (or stage) specialists among the stages studied. A specialist is taken here to be a species that is observed at only one stage, though this method is not entirely satisfacory, as rare species are too easily counted as specialists; on the other hand, habitat specialists may be expected to be rare. In the combined data (dry and moist sites) the numbers of one-stage species are: I 3, II 3, III 3, IV 5 and V 11. Since the sample sizes of the stages are not equal, these figures are not comparable. To eliminate the effect of the sample size, the following method was used. A random sample of 44 pairs was drawn from each of stages II–V (in stage I the sample size is 44 pairs), and the one-stage species were counted in these samples. In order to estimate the standard deviation, 50 such simulations were run; the results are as follows (number of one-stage species, x̄±SD):

Stage I	4.8 ± 0.89
Stage II	2.8 ± 0.91
Stage III	1.9 ± 0.97
Stage IV	4.8 ± 1.33
Stage V	6.9 ± 1.72

The result agrees to some extent with that obtained by the average habitat amplitude approach: these measures have a negative correlation (i.e. broad habitat amplitude of species – small number of habitat specialists, and *vice versa;* the correlation is, however, not significant, r=–0.40, P<0.1).

According to the previous results the initial stages of succession (I and II) do not agree with the succession theory: these stages are not occupied by generalists but rather specialized species. This conclusion is in accordance with that obtained by assessing the communities in the light of, for example, species diversity and average bird weight (Helle 1985). However, a problem of definition is involved here. If we restrict the analyses to the species of forest land proper, the patterns obtained are consistent with the succession theory (for details see Helle 1985). The deviations in the initial stages of succession are due to species of open bogs and shores, and whether these species belong to the *forest succession* or not is difficult to decide.

Table 2. Statistically significant (P<0.05) correlations between the densities of the 10 most numerous species (number of observations in parentheses) and the five vegetation characteristics estimated in the field. Abbreviations: HEI – Height of vegetation, TVC – Total vegetation coverage, HW – Hardwood percentage, FHD – Foliage height diversity, NUM – Number of tree and shrub species.

	HEI	TVC	HW	FHD	NUM
Ph. trochilus (122)		.40			.43
Fr. montifringilla (55)	.60	.54		.54	.71
Anthus trivialis (45)					
Fringilla coelebs (33)	.61	.51		.56	.66
Turdus iliacus (29)	.33	.40		.41	.40
Carduelis flammea (20)					
Motacilla alba (19)	–.38			–.39	
Muscicapa striata (17)	.54	.35		.45	.39
Motacilla flava (14)					
Carduelis spinus (13)	.53			.44	.55

General discussion

Methodology. The methods of this study and the representatives of the data are discussed elsewhere (Helle 1984, 1985). Some points are worth mentioning, however. The forest succession gradient studied is a mixed set of succession stages, because the first three are created by forestry whereas the two oldest stages are close to the natural condition. The brush phases (especially stage III) are the most problematic. One reason is that at his age stands are thinned, which has a pronounced effect on bird life. All the brush phases studied here had recently been thinned and this might be an explanation of the very low number of species and low species diversity observed in them (see also Helle 1985).

The numbers of both the succession stages and the vegetation features were too small for assessing phenomena at the species level;originally the study was planned to describe the main parameters of bird communities in different stages of forest succession. The measure 'mid-point of density' is less satisfactory for the present data, because hardly any species occurs only in forest habitats (i.e. in the gradient studied here), but many species breeding primarily in, for example, mature forests also breed in forested bogs, and several species observed in the early phases of forest succession also use many other kinds of open habitats.

Clear-felled areas. The clear-felled areas in Kainuu (64°N, 28°E; about 250 km south of Kuusamo) have a mean breeding bird density of 40 pairs/km^2 (Kaskinen 1976; the data correspond to those for stages I and II of the present study). *Anthus trivialis, Saxicola rubetra* and *Emberiza hortulana* are more abundant and *Motacilla alba* less abundant in Kainuu than in Kuusamo. In Kuusamo the clear-felled areas are characteristically inhabited by species originally breeding on open bogs (e.g. the Whimbrel *Numenius phaeopus,* the Wood Sandpiper *Tringa glareola,* the Whinchat *Saxicola rubetra,* the Meadow Pipit *Anthus pratensis* and the Yellow Wagtail *Motacilla flava*). Of the species, only *Saxicola rubetra* is typical breeder of clear-felled areas in Kainuu. The same difference exists between more northern (Forest Lapland, Haapanen et al. 1966) and more southern data (Central Finland, Mönkkönen 1984).

There are many reports of species of open bogs and shores occupying clear-felled areas (e.g. v. Haartman et al. 1963–72, Dement'ev & Gladkov 1966–70, Ahlén 1975, 1976), but quantitative information is scarce. In a geographical analysis of the breeding avifauna of Finnish bogs, Järvinen & Sammalisto (1976) reported 16 species breeding on open bogs in the province of 'Tornio-Kainuu', to which the present study area belongs (waterfowl species excluded). Eleven of these were observed in clear-felled areas in the present material. This is probably due to the similar physiognomy of clear-felled areas and open bogs: both are open and often large and bear low vegetation. Because the start of the vegetation succession is slow in the north, the clear-felled areas are suitable for birds breeding in open habitats for several years (see also Helle 1985).

The clear-felled areas are also inhabited by species originally breeding on open shores and similar habitats e.g. the Wagtail *Motacilla alba* and Wheatear *Oenanthe oenanthe.* These species seem to be especially abundant in areas that have been ploughed after clear-felling.

Forest regeneration after destruction by natural (e.g. forest fires) and anthropogenic events (e.g. clear-felling) is essentially the same. The boreal forests may have been burned down as often as once every hundred years on average (Zackrisson 1977, Huttunen 1980), and birds are assumed to have adapted to living in the resultant habitats (Stoddard 1963, Bendell 1974). During the last few decades forestry has created large open areas in Northern Finland (e.g. Järvinen et al. 1977). As birds are (in general) relatively flexible in their habitat selection (see e.g. Lack 1971), they can be expected to occupy clear-felled areas and hardwood brush, especially since these are very similar to some natural habitats. Ahlén (1976) has listed 17 species which have started breeding in these areas in Sweden. Eleven of these species breed in clear-felled sites in Northeastern Finland, too (the Willow Grouse *Lagopus lagopus, Numenius phaeopus, Saxicola rubetra, Oenanthe oenanthe,* the Great Grey Shrike *Lanius excubitor, Motacilla alba* and *flava, Anthus pratensis* and *trivialis,* the Ortolan Bunting *Emberiza hortulana* and the Yellowhammer *E. citrinella* (Helle et al. 1983, present study). From more northern localities in Finland (67°N) Ulmanen & Valste (1965) reported another of the species listed by Ahlén (1976), the Grey Plover *Pluvialis apricaria,* breeding in clear-felled areas. Species not reported to breed in clear-felled areas in Northern Finland, though listed by Ahlén, are the Red-backed Shrike *Lanius collurio,* the Tawny Pipit *Anthus campestris,* the Wood Lark *Lullula arborea,* the Sky Lark *Alauda arvensis* and the Three-toed Woodpecker *Picoides tridactylus.* Northern Finland lies outside the distribution areas of the three first species; *A. arvensis* is sparse there. *P. tridactylus* fairly often forages in clear-felled forest, but records during the breeding season are lacking (my own observation).

The number of bird species breeding in the brush stage is low, whereas the density is fairly high compared with that in the other young stages in the forest succession (see Haapanen 1965, Mönkkönen 1984, Helle 1985). Haapanen (1965) suggests that this habitat is transitory that birds are not well adapted to it. Support for this is provided by the fact that there are no strict habitat specialists in the brush phase (see also Helle 1984b), but the explanation is perhaps not so simple. In addition to the predictability of occurrence of the brush stage in time and space, one has to take into account the species involved and its ecology. For example the habitat of the crossbills *Loxia* spp. (mature conifer forest) is large in area and its distribution easily predicted, but since the species are extremely specialized in their feeding ecology, their occurrence is highly irruptive.

Dense scrub is unsuitable for many species: the field layer is too close for many species that feed on the ground, there is not enough space between the bushes for aerial feeding, and there are no suitable nest-sites for species that nest in/on the trunks or branches of trees. *Ph. trochilus* is not affected by these factors and is therefore the superdominant species in the brush stage.

Species of south boreal spruce forests. Erithacus rubecula, Turdus philomelos and *Carduelis spinus* – species of boreal spruce forests – have strongly increased in Southern Finland during the past few decades, the most probable reason being the increase of the spruce there (e.g. Järvinen & Väisänen 1978a). In Northern Finland these species have increased, too, although the area of spruce forests has diminished. It has been suggested that the population increases in the north are due to population pressure from southern Finland (Järvinen & Väisänen 1978b, Väisänen 1983). This explanation assumes that the species are specialists of spruce forests in Northern Finland as they are in Southern Finland, which is not wholly true. According to the present data the density of *Erithacus rubecula* in pine or pine-dominated forests (dry series, stages IV and V) amounts to 2.1 and in spruce or spruce-dominated forests (moist series, stages IV and V) to 3.2 pairs/km^2. The densities for *T. philomelos* and *C. spinus* are 0.9 and 3.2, and 1.7 and 4.1 pairs/km^2, respectively. The data are scanty, but these values are consistent with a larger material (P. Helle, unpubl.). Two-thirds of the coniferous forests in Northern Finland are pine or pine-dominated and one-third spruce-dominated. We can thus estimate that about one-third of the population of *Turdus philomelos* in the north breeds in pine forests and two thirds in spruce forests. The proportions for *Erithacus rubecula* are 55 and 45 % and for *Carduelis spinus* 45 and 55 %, respectively.

The habitat selection of *Phylloscopus collybita* resembles that of the previous species. Roughly two-thirds of the population of this species in Northern Finland breed in pine forests and one third in spruce forests (P. Helle, unpubl.). *P. collybita* has slightly decreased in Northern Finland in recent decades (e.g. Väisänen 1983).

Mela (1975) censused the birds of the forests of the Oulanka National Park in Kuusamo in 1970–73; exactly the same habitats were studied ten years later (1980–84; Helle & Mönkkönen 1985). The changes in the densities of the four species discussed above between the 1970s and 1980s are presented below for pine and spruce forests (+ increase, – decrease):

	pine	spruce
Erithacus rubecula	+	+
Turdus philomelos	+	–
Phylloscopus collybita	+	–
Carduelis spinus	+	–

The mean bird density in the National Park has slightly decreased between the census periods, which makes the observation that all the species concerned have increased in pine forests particularly interesting. The results suggests that the increase in the area of pine forests has been favourable for these species, since their density in this habitat has increased. The role played by population pressure in Southern Finland in the population changes taking place in Northern Finland is thus uncertain, or the effect is at least not simple.

Acknowledgements. I thank E. Helle, O. Järvinen, E. Pulliainen, S. Sulkava, J. Tiainen and T. Törmälä for their suggestions and criticisms of the manuscript. I am also indebted to Alan Robson for helping with the English and to the Emil Aaltonen Foundation for financial support.

Selostus: **Metsäkasvillisuuden sukkessio ja pesimälinnuston elinympäristönvalinta Koillis-Suomessa**

Pohjois-Kuusamossa tutkittiin viiden eri-ikäisen metsäkasvillisuuden ikävaiheen (2, 10, 25, 75 ja 150 vuotta) pesimälinnustoa vuosina 1980–82, erikseen kuivilla ja tuoreilla kankailla. Linnut laskettiin 36 näytealalta (1167 ha) kertalaskentamenetelmällä.

Kuivilla kankailla yksi laji 36:sta (metsäkirvinen) pesi kaikissa viidessä tutkitussa ikävaiheessa; tuoreilla kankailla viiden vaiheen lajeja oli kolme 44:stä (punakylkirastas, pajulintu, urpiainen). Lajien esiintymisen painopiste avohakkuu-vanhametsä -akselilla määritettiin tiheyksien perusteella. Lajien runsaudella painotettu esiintymisen painopiste oli sama kuivilla ja tuoreilla kankailla. Vastaava elinympäristönvalinnan väljyyttä kuvaava ’habitaattiamplitudi’ oli tuoreilla mailla selvästi suurempi kuin kuivilla kankailla. Ero johtui pääasiassa tuoreilla kankailla runsaana esiintyvästä ja monenlaisissa maastoissa viihtyvästä pajulinnusta. Lajien elinympäristönvalintaa kuvaava ryhmittely jakoi runsaimmat lajit viiteen ryhmään, mikä jossain määrin johtui siitä, että tutkittuja ikävaiheita oli viisi ja nämä olivat linnustoltaan selvästi toisistaan poikkeavat.

Lajien ekologisen väljyyden ja suhteellisen runsauden välillä oli positiivinen korrelaatio – mikä oli odotettua. Aineiston runsaimmista lajeista ei yksikään poikennut selvästi tästä yleistrendistä.

Runsaimpien lajien tiheyksiä verrattiin viiteen näytealueilta mitattuun tai arvioituun kasvillisuuden tunnukseen (korkeus; pohja-, pensas ja puukerroksen yhteispeittävyys; lehvästön korkeusjakauman tasaisuus; lehtipuuston (pensaston) osuus puiden ja pensaiden kokonaislehvämäärästä; puu- ja pensaslajien lukumäärä 20 aarin alueella). Minkään lajin tiheys ei ollut merkitsevästi riippuvainen lehtipuuosuudesta. Peipon, järripeipon, punakylkirastaan ja harmaasiepon tiheydet korreloivat positiivisesti kaikkien muiden kasvillisuusmuuttujien kanssa.

Tutkimuksessa tarkastellaan myös menetelmällisiä ongelmia. Näytteen kokoon liittyvä on kysymys: johtuuko tietyn lajin runsaus siitä, että se pystyy asuttamaan monenlaisia ympäristöjä vai havaitaanko laji monenlaisessa ympäristössä sen takia, että se on niin lukuisa? Aineiston runsaimpien lajien erilaisten näytekokojen ei havaittu vaikuttavan mainittavasti tutkimuksessa käytettyyn ekologisen amplitudin mittaan.

References

Ahlén, I. 1975: Forestry and the bird fauna in Sweden. – Ornis Fennica 52:39–44.

Ahlén, I. 1976: Forestry and the vertebrate fauna. – *In* Tamm, C.O. (ed.): Man and the Boreal Forest. Ecol. Bull.(Stockholm) 21:59–62.

Alatalo, R. V. 1980: Bird communities in boreal forests. – Abstracts of Uppsala Dissertations from the faculty of Sciences, 582. 16 pp. Uppsala.

Alatalo, R. V. 1981: Habitat selection of forest birds in the seasonal environment of Finland. – Ann. Zool. Fennici 18:103–114.

Bendell. J. F. 1974: Effects of fire on birds and mammals. – *In* Kozlowski, T. T. & Ahlgren, C. E. (eds.): Fire and Ecosystems, pp. 73–138, Academic Press, New York.

Brown, J. L. 1969: The buffer effect and productivity in tit populations. – Amer. Nat. 103:347–354.

Cody, M. L. 1974: Competition and the structure of bird communities. – Princeton Univ. Press, Princeton.

Dement'ev, G. P. & Gladkov, N. A. (eds.) 1966–70: Birds of the Sovjet Union. – Israel Program for Scientific Translation, Jerusalem.

Engström, K. 1955: The dependence of the bird fauna on the composition of the forest. – Medd. Statens Skogsforskningsinstitut 45(2):1–47 (in Swedish with English Summary).

Franzreb, K. E. 1977: Bird population changes after timber harvesting of a mixed conifer forest in Arizona. – USDA For. Serv. Res. Pap. RM-184, 26 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colorado.

Fretwell, S. D. 1972: Populations in a seasonal environment. – Princeton Univ. Press, Princeton.

Glowacinski, Z. 1975: Succession of the bird communities in the Nielopomice Forest (Southern Poland). – Ekol. Pol. 23:231–263.

Glowanciński, Z. 1979: Some ecological parameters of avian communities in the successional series of cultivated pine forest. – Bull. Acad. Pol. Sci., serie des sciences biol. Cl. II 27:169–177.

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

Haapanen, A. 1966: Bird fauna of the Finnish forests in relation to forest succession. II. – Ann. Zool. Fennici 3:176–200.

Haapanen, A., Ulmanen, I. & Valste, J. 1966: Observations on the bird fauna in Koitilaiskaira (Finnish Lapland). – Ornis Fennica 43:45–54.

v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. – Otava, Helsinki.

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

Heck, K. L., van Belle, G. & Simberloff, D. 1975: Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. – Ecology 56:1459–1461.

Helle, P. 1983: Bird communities in open ground/climax forest edges in Northeastern Finland. – Oulanka Reports 3:39–46.

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

Helle, P. 1985: Effects of forest regeneration on the structure of bird communities in Northern Finland. – Holarctic Ecology 8:120–132.

Helle, P. & Mönkkönen, M. 1985: Oulangan kansallispuiston metsälinnustosta erityisesti 15 viime vuoden aikana (Summary: On the Forest bird fauna of the Oulanka National Park, northern Finland). – Aureola 10:21–30.

Helle, P., Sulkava, S. & Mela, M. 1983: Oulangan kansallispuiston ja sen lähialueen pesimälinnusto. – Oulun yliopiston Oulangan biologisen aseman monisteita 5:1–20.

Hildén, O. 1965: Habitat selection in birds. A review. – Ann. Zool. Fennici 2:53–75.

Huttunen, P. 1980: Early land use, especially the slash-and-burn cultivation in the commune of Lammi, southern Finland, intrepreted mainly using pollen and charcoal analyses. – Acta Bot. Fennica 113:1–45.

Järvinen, O. 1978: Species-specific census efficiency in line transects. – Ornis Scand. 9:165–167.

Järvinen, O. 1980: Ecological zoogeography of Northern European bird communities. – Unpubl. Dr. Thesis, Dept. Zool., Univ. Helsinki.

Järvinen, O. & Sammalisto, L. 1976: Regional trends in the avifauna of Finnish peatland bogs. – Ann. Zool. Fennici 13:31–43

Järvinen, O. & Väisänen, R. A. 1976: Finnish line transect censuses. – Ornis Fennica 53:115–118.

Järvinen, O. & Väisänen, R. A. 1977: Line transect method: a standard for field work. – Polish Ecol. Studies 3:11–15.

Järvinen, O. & Väisänen, R. A. 1978a: Recent changes in forest bird populations in northern Finland. – Ann. Zool. Fennici 15:279–289.

Järvinen, O. & Väisänen, R. A. 1978b: Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. – J. Ornithol. 119:441–449.

Järvinen, O. & Väisänen, R. A. 1979: Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric species in Finland. – Oikos 33:261–271.

Järvinen, O. & Väisänen, R. A. 1980: Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. – Ann. Zool. Fennici 17:67–85.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana (Summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975). – Silva Fennica 11:284–294.

Johnston, D. W. &. Odum, E. P. 1956: Breeding bird population in relation to plant succession on the Piedmont of Georgia. – Ecology 37:50–61.

Kaakinen, K. 1976: Avohakkuualueiden pesimälinnustosta erityisesti Sotkamon seudulla. – Unpubl. M.Sc. Thesis, Dept. Zoology, Univ. Oulu.

Kalela, A. 1961: Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. – Arch. Soc. 'Vanamo' 16 (suppl.):65–83.

Lack, D. 1971: Ecological isolation in birds. – Blackwell, Oxford-Edinburgh.

Lack, D. & Lack, E. 1951: Further changes in bird life caused by afforestation. – J. Anim. Ecol. 20:173–179.

Mela, M. 1975: Oulangan kansallispuiston ja sen lähiympäristön linnusto vuosina 1967–1973. Unpubl. M.Sc. Thesis, Dept. Zoology, Univ. Oulu.

Merikallio, E. 1946: Über die regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonderes in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I. Allgemeiner Teil. – Ann. Zool. Soc. 'Vanamo' 12:1–140.

Merikallio, E. 1951: Der Einfluss der letzten Wärmeperiode (1939–49) auf die Vogelfauna Nordfinnlands. – Proc. X Int. Ornithol. Congr. (Uppsala):484–493.

Mikkonen, A. V. 1983: Peippo. – *In:* Hyytiä, K., Kellomäki, E. & Koistinen, J. (eds.): Suomen Lintuatlas, pp. 434–435. SLY:n Lintutieto Oy, Helsinki.

Mönkkönen, M. 1984: Metsäkasvillisuuden sukkession vaikutukset Pohjois-Savon metsälinnustoon. – Siivekäs 5:41–51.

Nilsson, S. G. &. Ebenman, B. 1981: Density changes and niche differences in island and mainland Willow Warbler Phylloscopus trochilus at a lake in southern Sweden. – Ornis Scand. 12:62–67.

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

Palmgren, P. 1930: Quantitativen Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands. – Acta Zool. Fennica 7:1–218.

Partridge, L. 1978: Habitat selection. – *In* Krebs, J. R. & Davies, N. B. (eds.): Behavioural ecology: an evolutionary approach, pp. 351–376, Blackwell, Oxford.

Prodon, R. & Lebredon, J.-D. 1981: Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. – Oikos 37:21–38.

Renkonen, O. 1938: Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. – Ann. Zool. Soc. 'Vanamo' 6:1–226.

Soveri, J. 1940: Die Vogelfauna von Lammi, ihre regionale Verbreitung und Abhängigkeit von den ökologischen Faktoren. – Acta Zool. Fennica 27:1–176.

Söyrinki, N., Salmela, R. & Suvanto, J. 1977: Oulangan kansallispuiston metsä- ja suokasvillisuus (Summary: The forest and mire vegetation of the Oulanka National Park, Northern Finland). – Acta Forest. Fennica 154:1–150.

Stoddard, H. L. Jr. 1963: Bird habitat and fire. – Proc. 2nd Annu. Tall Timbers Fire Ecol. Conf.:163–175.

Svärdson, G. 1949: Competition and habitat selection in birds. – Oikos 1:157–174.

Tiainen, J. 1981: Habitat preferences by breeding forest passerines in an area in S. Finland. – 2nd Proc. Nordic Congr. Ornithol. 1979:38–42.

Tomialojć, L., Walankiewicz, W. & Wesolowski, T. 1977: Method and preliminary result of the bird census in primeval forest of Bialowieza National Park. – Pol. Ecol. Studies 3:215–223.

Ulmanen, I. & Valste, J. 1965: Sodankylän Koitelaiskairan linnustosta 1962–64. – Lintumies 1:51–56.

Väisänen, R. A. 1983: Pohjois-Suomen maalinnuston kannanmuutokset viime vuosikymmeninä (Summary: Long-term population changes of the most abundant north Finnish land birds during the past 40 years). – Aureola 8:58–65.

Wasilewski, A. 1961: Certain aspects of the habitat selection of birds. – Ecol. Polska, Ser, A 9:111–137.

Whittaker, R. H. 1970: Communities and ecosystems. – Macmillan, New York.

Wiens, J. A. 1977: On competition and variable environments. – Am. Scientist 65:590–597.

Wiens, J. A. 1983: Avian community ecology: an iconoclastic view. – *In:* Brush, A. H. & Clark, G. A. (eds.): Perspectives in ornithology, pp. 355–403. Cambridge Univ. Press, Cambridge.

Zackrisson, O. 1977: Influence of forest fires on the North Swedish boreal forest. – Oikos 29:22–32.

Received June 1984

Appendix. Primary data from the censuses made in different stages of forest succession in Northeastern Finland. Age of stages: I = about 2, II = 10, III = 25, IV = 75 and V = 150 years. In addition to the pair numbers, abbreviations for those species which occur in Figs 1, 3 and 4 and habitat amplitudes (HA, defined in the text) are included.

	Dry series						Moist series					
	I	II	III	IV	V	HA	I	II	III	IV	V	HA
Bonasa bonasia											2	1
Lagopus lagopus			1			1						
Tetrao tetrix								1				1
Numenius phaeopus (N pha)	1	2				1.95		2				1
Tringa nebularia (T neb)	2	1				1.35	1					1
T. glareola							2					1
Cuculus canorus (C can)			1		1	1.91				2	1	1.91
Surnia ulula							1					1
Asio flammeus		1				1						
Apus apus											1	1
Jynx torquilla (J tor)		1				1			1	1		1.93
Dryocopus martius					1	1						
Dendrocopos major											1	1
Anthus trivialis (A tri)	1	2	4	7	5	4.33		7	3	5	11	3.03
A. pratensis (A pra)							3		1			1.30
Motacilla flava (M fla)	1	4	1			2.53	2	4	2			2.52
M. alba (M alb)	5	1	3			1.19	6	3				1.67
Bombycilla garrulus			1			1						
Troglodytes troglodytes										1		1
Erithacus rubecula (E rub)				3	2	1.85				5	2	1.62
Phoenicurus phoenicurus (P pho)					5	1					3	1
Saxicola rubetra (S rub)	1	4				1.94	2	2	2			2.76
Oenanthe oenanthe (O oen)	3					1	5	3				1.76
Turdus pilaris					1	1				1		1
T. philomelos (T phi)					2	1					7	1
T. iliacus (T ili)		2	2		3	2.98	2	1	9	8	2	3.49
T. viscivorus											1	1
Sylvia curruca			1			1						
S. borin (S bor)									1	4	1	2.12
Phylloscopus collybita (P col)				5	2	1.60				3		1
Ph. trochilus (P tro)		17	14	3	5	2.76	3	9	33	20	18	3.74
Regulus regulus (R reg)				4		1					1	1
Muscicapa striata (M str)			2	2	6	2.57				3	4	1.99
Ficedula hypoleuca (F hyp)					1	1				2	6	1.67
Parus montanus (P mon)										2	1	1.73
P. cinctus											1	1
P. cristatus				1	1	1.98						
P. major (P maj)		1				1				1	1	1.99
Certhia familiaris (C fam)											5	1
Perisoreus infaustus											1	1
Corvus corone										1		1
. corax				1		1						
Fringilla coelebs (F coe)			1	7	5	2.28				13	7	1.76
F. montifringilla (F mon)		2	3	9	8	3.24			4	11	18	2.65
Carduelis spinus (C spi)				2	2	1.98				4	5	2.00
C. flammea (C fla)				1	2	1.88 1	2	6	5	3		4.17
Loxia curvirostra (L cur)											3	1
L. pytyopsittacus					1	1					1	1
Carpodacus erythrinus (C ery)		1	1			1.98		3	1			1.39
Pyrrhula pyrrhula				2		1						
Emberiza citrinella	1					1						
E. hortulana (E hor)		3				1		1				1
E. rustica (E rus)							1				2	1.83