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Annual variation of northern Finnish forest and fen bird assemblages in relation to spatial scale

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Censuses made yearly in 1983–89 were used to study the year-to-year variation in bird species assemblages in four localities in virgin coniferous forest and four localities in open flark fen. The censuses in forests were made in an area of 100 km^2 and those in fens in 1000 km^2. The variation in the density of the assemblages did not differ between the pooled samples from forests and fens or between the separate localities. The temporal density variation (V^2) of the assemblages in separate fens was significantly larger than that of the pooled data of the other fens in three out of four cases, whereas no difference was observed between separate and pooled samples in coniferous forests. In the passerine species the density variation in the different sites was similar in magnitude in both forests and fens, whereas the variation in waders in fens differed in magnitude between the sites. Compensatory fluctuations in the density of species prevailed in the fens, but neither compensatory nor parallel fluctuation patterns were observed in the bird assemblages in coniferous forests. The results indicate that the variation patterns of waders in fens are different from those of passerines in fens or forests. Waders are probably more susceptible than passerines to environmental variation between sites, such as differences in the water level. The fact that the variation of bird assemblages in fens was observed to be smaller on a larger spatial scale than the variation in separate localities, while this was not the case in forests, may be due to differences in species characteristics between fens and forests or to the larger spatial scale adopted in the study of birds of fens.

1. Introduction

Between-habitat differences in the annual variation patterns of bird populations and communities have been discussed in several studies during the past decade (e.g., Järvinen 1979, Wiens & Rotenberry 1981). In North America some studies based on local plots have indicated that bird communities in forests are less variable (e.g., Winternitz 1976) than those in open shrub steppes and grasslands (Rotenberry & Wiens 1980). This has been attributed to the simpler habitat structure on open ground. However, in a large study of the temporal variation of bird communities over North America, Noon et al. (1985) did not observe any clear differences between forests and open land. Studies on individual local plots are susceptible to problems arising from heterogeneous data sets, the spatial scales adopted and population variation between sites in a homogeneous habitat (see e.g. Wiens 1989).

For instance, the dynamics of bird communities and populations are usually studied within small plots some tens of hectares in size, and

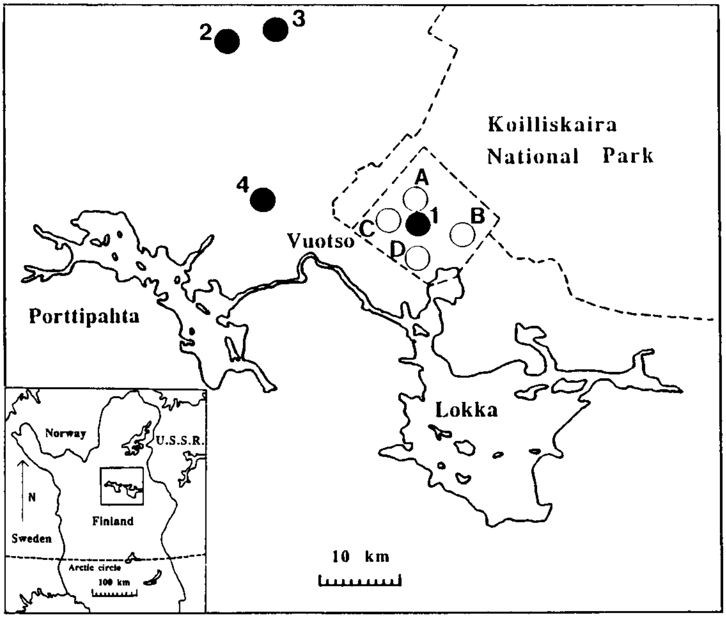


Fig. 1. Situation of the censuses areas in northern Finland. closed circles represent transects in fens and open circles transects in virgin coniferous forests in Sompio Nature Reserve. 1 = Vosavaaranaapa, 2 = Vuijemi, 3 = Sotajoki, 4 = Kelta-aapa; A = Vosavaara, B = Heikkilänvaara, C = Purnunnenä, D = Pyhä Nattanen.

information on the temporal variation of populations in larger areas is lacking. Wiens (1981), using a 'checkerboard' model, suggested that due to randomness in the spatial distribution of birds from year to year, bird numbers in a small study plot may vary considerably between consecutive years although the populations in a larger area may have been stable. Therefore, counts on small plots, although precise, may not tell us much about year-to-year variation in the density of populations on a larger spatial scale.

The other factor complicating the conclusions drawn from the annual variation patterns of birds in different habitat types is that population fluctuations may differ in separate homogeneous habitat patches in agreement with the metapopulation model (see Hanski 1989, 1991). In such a case, local populations may show considerable, non-parallel fluctuation due to environmental and demographic stochasticity, but local variations may be compensated between separate homogeneous patches. The assemblage composition may also be more stable on the regional than on the local scale (Rotenberry & Wiens 1980, Wiens 1986). In comparisons of the annual variation patterns of bird communities between different habitat types, the effects of the spatial scale should be taken into account and replicated samples of bird censuses in different sites should be adopted.

In this study I compare bird community and population dynamics in Northern Finnish mires and coniferous forests on the basis of seven-year data from annual censuses. The community dynamics may differ between mires and forests due to the large differences in the structure of the vegetation and the bird species composition of these two habitats. I also study whether year-to-year variation in bird species assemblages is compensated among local sites, so that the assemblages are more stable on a larger spatial scale.

Table 1. Length of line transects in fens and virgin coniferous forests.

Habitat	Transect	Length (km)
Fen	Vosavaaranaapa	1.3
	Vuijemi	2.5
	Sotajoki	1.2
	Kelta-aapa	1.2
Virgin coniferous forest	Vosavaara	4.4
	Heikkilänvaara	5.0
	Purnunnenä	4.4
	Pyhä Nattanen	6.0

2. Material and methods

The bird counts were conducted using the Finnish line transect census (Järvinen 1976, 1981, Järvinen et al. 1991). The Finnish line transect method is a one-visit census, in which birds are recorded separately on the 50-m wide main belt and outside it, on a supplementary belt; the main and supplementary belts together compose the survey belt. To achieve adequate sample sizes I used observations from the whole survey belt.

Censuses were carried out yearly between 11 and 27 June in 1983–89. I myself censused 90% of the transects. The transects traversed four mire areas and four virgin coniferous forests (Fig. 1).

The mires were flark fens bordered by pine bogs. The transects, totalling 6.2 km yearly (Table 1), crossed the fen areas. In the virgin coniferous forests 40% of the total transect length (19.8 km, Table 1) was located in pine forests and 60% in spruce-birch forests. The birds in virgin coniferous forests were counted in Sompio Nature Reserve; for a detailed description of these forests, see Virkkala (1987, 1989).

In calculating the density from the survey belt observations, I used species-specific correction coefficients (K, Järvinen & Väisänen 1983). If the main/supplementary belt ratio of a given species differed significantly (χ^2-test, $P < 0.05$) from that presented in Järvinen & Väisänen (1983), I calculated a new correction coefficient based on the present data. For instance, in the case of the mire birds I used a new correction coefficient only for the Yellow Wagtail *Motacilla flava* ($K = 3.48$). I used the density-dependent correction coefficient (y, see Järvinen & Väisänen 1983) in both fens ($y = 0.790$) and forests ($y = 0.795$).

In analysing the data for fens, I included only species known to breed or forage regularly in mires (von Haartman et al. 1963–72), because many observations in the supplementary belt came from totally different habitats, for instance forests. The proportion of the mire-nesting species was 85% of the original main belt observations in the fens. Two-thirds of the remaining observations relate to species which prefer forest edges (Redwing *Turdus iliacus*, Redpoll *Carduelis flammea* and Willow Warbler *Phylloscopus trochilus*, see Helle & Järvinen 1986, Virkkala 1987), and I also observed these species at the edge of a mire and a forest. As the excluded species comprise only a minor proportion of the total assemblage, I do not think that this procedure affects the results.

In studying the year-to-year variation and stability of bird assemblages and populations I used the coefficient of variation (CV, %) and variances (V^2) in bird density. For comparisons of variances (but not for CVs) the original density values were ln (natural logarithm)-transformed. In certain cases only variances were compared as there were no proper statistical tests, e.g., for comparison of three or more CVs (see Sokal & Braumann 1980).

3. Results

The average density of mire-nesting birds in the combined data for the four fens was 63 pairs/km^2 (Table 2). Altogether 17 mire-nesting species were observed, 12—14 being recorded each year. In the combined data for fens, the coefficient of variation (CV, %) of the density of these species was 7.3%, the yearly density varying between 56 and 68 p/km^2 (Fig. 2). In virgin coniferous forests the mean density was 78 p/km^2 (Table 3, Fig. 2) and the CV of the density of the pooled data 13.2%. The CVs of the bird density of the pooled data sets did not differ significantly (t-test) between forests and fens.

The mean density in fens varied between 49 and 87 p/km^2 and the CVs of density between 15 and 20% (Table 4). The variances (V^2) of density were significantly higher (F-test) in a local fen in three out of four pairwise comparisons between the V^2 of the local fen and that of the pooled data for the other fens; in every comparison the local fen was excluded from the pooled data.

The mean density in coniferous forests varied locally between 61 and 97 p/km^2 (Table 4) and yearly over all forests between 60 and 89 p/km^2 (Fig. 2). The CVs of the density of the local samples (15–21%) did not differ from those in fens. The variances (V^2) of assemblages in separate coniferous localities were not significantly higher than those in the pooled data for the other forests (Table 4).

The CVs of the density of the three most common species in virgin coniferous forests and

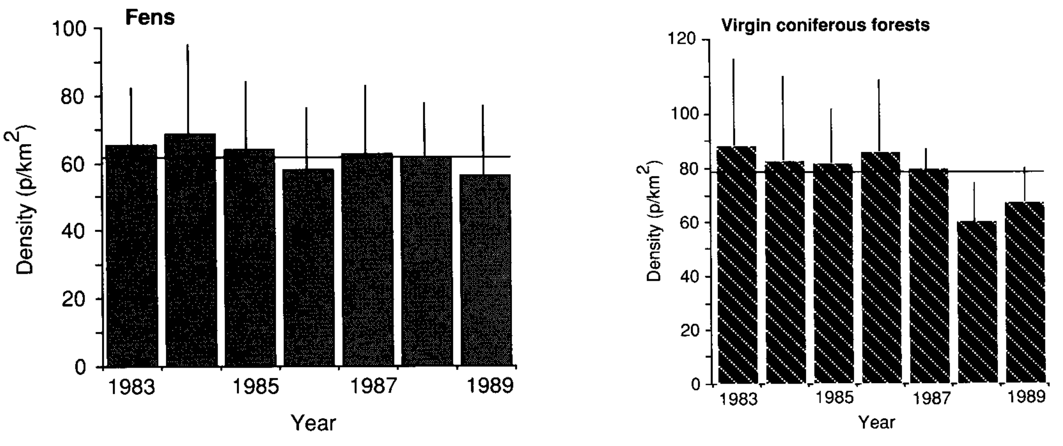


Fig. 2. Yearly bird densities (based on survey belt data) with SD:s in fens and virgin coniferous forests. The horizontal line indicates the mean density in 1983–89

fens are presented in Table 5. With the exception of the Redpoll, the yearly densities of the three most common species did not vary more in fens than in forests. Because of the pronounced variation in the seed crop of the birch, the density of seed-eating Redpolls fluctuates strongly from year to year (Enemar & Nyström 1981, Enemar et al. 1984).

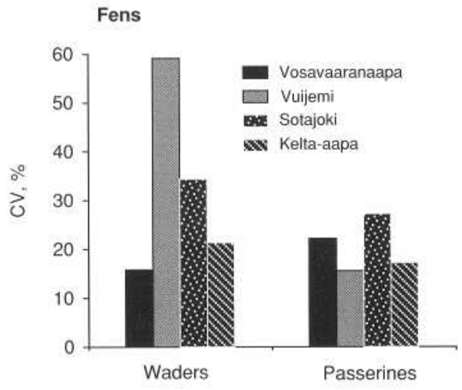
In fens, waders comprise, on the average, 28% of the bird pairs and passerines 71%. The

Table 2. Yearly numbers of observations on the survey belt and mean densities (pairs/km^2) of species nesting and foraging regularly on mires.

	83	84	85	86	87	88	89	Mean
Pluvialis apricaria	4	2	4	1	1	2	1	0.9
Vanellus vanellus	–	–	1	–	–	–	–	0.05
Limicola falcinellus	–	–	1	–	2	–	1	0.3
Philomachus pugnax	1	1	3	–	–	–	–	0.5
Lymnocryptes minimus	2	2	9	3	4	4	4	0.2
Gallinago gallinago	6	3	11	7	6	9	9	2.0
Numenius phaeopus	3	3	5	2	2	5	–	0.5
Tringa erythropus	2	1	5	2	1	1	2	1.1
T. nebularia	–	–	–	1	–	–	1	0.05
T. glareola	41	34	21	22	22	25	19	12.2
Asio flammeus	3	–	–	–	–	1	–	0.3
Anthus pratensis	20	25	31	25	34	40	26	18.8
Motacilla flava	25	34	22	35	29	17	18	14.4
Luscinia svecica	1	3	6	2	1	1	3	1.6
Saxicola rubetra	2	–	–	–	–	2	–	0.3
Acrocephalus schoenobaenus	3	1	1	1	1	2	2	0.8
Emberiza schoeniclus	12	13	8	7	12	7	15	8.9
								62.9

Table 3. Number of observations of bird species on the survey belt in virgin coniferous forests in 1983–89. The mean density (pairs/km^2) in 1983–89 is presented.

	83	84	85	86	87	88	89	Mean
Accipiter gentilis	1	1	–	–	–	1	–	0.1
Falco columbarius	–	1	1	–	–	–	–	0.03
Lagopus lagopus	2	4	4	6	2	–	1	1.4
Tetrao urogallus	4	3	3	1	2	6	1	2.1
Numenius phaeopus	7	6	3	4	3	1	–	0.2
Tringa erythropus	–	–	1	–	1	1	1	0.1
T. nebularia	–	–	2	–	–	–	–	0.03
T. ochropus	–	–	1	–	–	–	–	0.03
Cuculus canorus	16	19	16	16	11	7	6	0.5
Surnia ulula	1	–	–	–	1	–	1	0.1
Dryocopus martius	1	–	–	1	–	–	–	0.02
Picoides tridactylus	–	–	1	–	–	1	–	0.2
Anthus trivialis	8	15	14	12	9	7	8	1.3
A. pratensis	–	–	2	–	2	6	1	0.05
Motacilla flava	–	–	2	1	5	–	–	0.1
M. alba	–	–	–	2	1	1	1	0.2
Bombycilla garrulus	–	–	–	–	–	3	–	0.05
Corvus corax	2	4	2	–	1	–	–	0.03
Perisoreus infaustus	1	5	4	2	1	3	1	1.2
Prunella modularis	2	–	–	3	2	4	3	0.3
Phylloscopus trochilus	141	92	90	138	112	119	124	12.3
Ph. sibilatrix	–	1	–	–	–	–	–	0.02
Regulus regulus	2	1	–	–	–	–	4	0.3
Ficedula hypoleuca	–	1	6	1	4	4	5	0.5
Muscicapa striata	–	7	2	4	1	–	2	0.8
Oenanthe oenanthe	2	10	11	10	11	4	11	1.9
Phoenicurus phoenicurus	44	61	27	43	64	52	54	4.5
Luscinia svecica	–	1	2	–	2	1	2	0.2
Erithacus rubecula	3	–	3	–	–	–	7	0.3
Turdus iliacus	37	43	40	55	29	23	19	3.9
T. philomelos	42	29	37	28	9	4	14	1.7
T. pilaris	–	–	1	–	–	–	–	0.03
Parus cinctus	5	6	7	6	4	5	6	3.4
P. montanus	–	–	–	1	–	–	–	0.05
Fringilla montifringilla	309	231	229	207	225	130	178	31.9
F. coelebs	1	–	–	–	–	–	–	0.02
Carduelis spinus	1	15	2	–	1	–	1	0.3
Carduelis flammea	41	23	57	104	34	32	32	4.7
Pinicola enucleator	1	4	6	4	2	5	7	0.9
Loxia curvirostra/ pytyopsittacus	1	24	2	7	27	5	8	0.6
Loxia leucoptera	–	–	–	–	31	1	–	0.7
Emberiza rustica	2	3	3	4	2	3	–	1.0
E. schoeniclus	–	–	–	1	2	3	1	0.3
								78.36



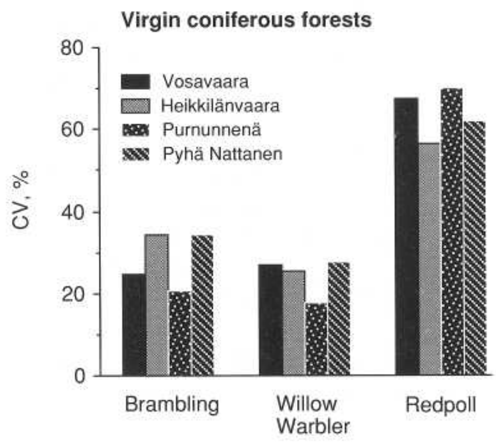


Fig. 3. CV values for the density of waders and passerines in fens and for the density of the three most common species in virgin coniferous forests in the different localities.

wader densities were more variable than the passerine densities: in the pooled data for fens the CV was significantly larger in the group of waders (26.3%) than in the passerines (7.4%, $P < 0.05$, t-test).

Fig. 3 presents the CV of the density of waders and passerines in the different fen localities and the value for the most common species, which also had the largest samples, in the different forests. Individual species could not be compared in the fens, due to the small sample sizes. Individual fens did not differ in the variability (CV, Fig. 3) of passerine densities, but were very different when waders were considered: in the fens the between-site variation in the variances (V^2) of the wader density was statistically significant,

Table 4. Mean density (pairs/km^2), year-to-year variation in density (CV, %, original values) and variances (V^2, ln-transformed) in fen and coniferous forest areas in 1983–89. In parentheses the V^2 values of the pooled data for fens/forests, with which the local sample was compared; in every comparison the local sample was excluded from the pooled data. The statistical significance was determined with the F-test.

Area	Density	CV	V^2	P
Fens				
Vosavaaranaapa	79.8	15.3	0.03 (0.02)	ns
Vuijemi	48.8	21.0	0.05 (0.01)	<0.05
Sotajoki	50.2	20.2	0.06 (0.01)	<0.01
Kelta-aapa	87.0	17.7	0.04 (0.01)	<0.05
Virgin coniferous forests				
Vosavaara	97.3	19.9	0.04 (0.02)	ns
Heikkilänvaara	60.8	20.6	0.04 (0.02)	ns
Purnunnenä	92.2	14.9	0.02 (0.02)	ns
Pyhä Nattanen	69.0	18.3	0.03 (0.02)	ns

but not in that of the passerines (Table 6). In the forests, the density variation in the different localities was similar in magnitude in all the three passerine species: the variances in the densities did not differ significantly (Table 6).

The variance sum of populations can be compared with the total variance in the community. If parallel density fluctuations of species prevail, the variance ratio (variance sum of populations/ total variance of community) should be less than one, and if compensatory fluctuations are common, this ratio should exceed one (Järvinen 1979).

The variance ratio in fens was 3.95 and in coniferous forests 0.85. Thus, in fens compensatory fluctuations were common: the variance ratio differs significantly from zero ($P < 0.01$, for the test, see Schluter 1984). In virgin coniferous forests neither compensatory nor parallel fluctuations were observable.

4. Discussion

4.1. Methodological problems

I used a single-census method, which may cause some problems in the patterns observed (e.g., for mire-nesting birds, see Kouki & Järvinen 1980). However, due to the synchronized breeding of the different species and the openness of the habitats, the census efficiency is fairly high in the north (Järvinen et al. 1978). The observability of birds may differ from year to year, particularly in waders in fens, due to differences in the phenology (Väisänen & Järvinen 1977, Väisänen, pers. comm.). Possible insufficiencies in the data due to this source of error do not, of course, affect the between-site comparisons.

4.2. Effects of spatial scale on temporal variation in northern bird species assemblages

The density variation (CV,%) in bird communities of separate peatlands reported here (15–20%) is similar in magnitude to the values of earlier studies: 17% for Northern Finland (five-year study, O. Hildén, pers. comm. in Järvinen 1979) and 19% for Northern Sweden (20 years; Svensson et al. 1984). In a study of temporal density variation of bird communities in a successional series in Northeastern Finland, Helle & Mönkkönen (1986) obtained values for CV between 25 and 28% in the three different types of coniferous forests (six-year study).

In the pooled data the temporal density variation of bird species assemblages did not differ between coniferous forests and fens: although structurally more heterogeneous, coniferous forests did not support more stable bird assemblages than fens. Nor did the density variation of local communities differ between forests and fens.

Although similar in magnitude over all the samples, the annual variation in assemblages in fens and virgin coniferous forests did differ in certain aspects. On a larger spatial scale the bird assemblages in coniferous forests were not more stable: none of the differences between local and pooled samples was significant. In fens there seemed to be a tendency for the assemblages to vary less on a larger spatial scale. The results are not unambiguous, however. The sample sizes in

Table 5. Year-to-year variation of density (CV, %) in the most numerous species in fens and virgin coniferous forests.

Species	Fens	Coniferous forests
Meadow Pipit *Anthus pratensis*	23.4	–
Yellow Wagtail *Motacilla flava*	28.2	–
Wood Sandpiper *Tringa glareola*	30.9	–
Brambling *Fringilla montifringilla*	–	25.4
Willow Warbler *Phylloscopus trochilus*	–	17.3
Redpoll *Carduelis flammea*	–	59.8

local fens are rather small compared with those in forests. The variances tend to increase with decreasing sample size, the smaller the sample size, and, therefore, small samples are susceptible to random 'noise'. It should, however, be noted that although the sample sizes in local fens are small compared with the sizes in forests, the CV values are similar in these two habitats.

The present data seem to provide fairly convincing evidence that bird assemblages in open fens are not more variable than assemblages in forests. On the contrary, there are indications that fens support less variable bird assemblages than forests. However, this cannot be verified with the present data. Interestingly, Helle & Mönkkönen (1986) observed that the bird assemblage of open clear-felled areas had significantly smaller temporal variation than that of coniferous forests. They suggested that open habitats, such as clear cuts and open bogs, may be more predictable in time and space than forests (see also Helle & Mönkkönen 1990).

The explanation of the different variation pattern of bird assemblages in fens and forests on the two spatial scales is problematic, because between-transect distances were greater in fens than in forests, and as a consequence the avian biota of forests was censused in a smaller area (about 100 km^2) than that of the fens (1000 km^2) (See Fig. 1). On a larger spatial scale pooled assemblages may be more stable, irrespective of the habitat characteristics of fens and forests.

It is possible that the regional population dynamics are reflected in the fens, whereas the forests covering in a smaller area, are more affected by local factors. For instance, the habitat selection patterns of individuals of a given species may be more similar in a smaller area. Haila et al. (1989) observed changes in the territory selection of individuals from year to year, and they concluded that birds are probably able to perceive year-to-year variation in the relative quality of different habitats. This means that in a small plot or area temporal variation in bird numbers can be considerable, although in a larger area the population may be more stable. The compensatory fluctuations of species in fens also indicated stability of assemblages on a large spatial scale.

Table 6. Variances (V^2) in the group of waders and passerines in the different localities in fens and of the most common species in coniferous forests in 1983–89. The variances are based on ln-transformed density values. The statistical significance of the differences in variances between the sites was determined with Bartlett's test (B_c) of the homogeneity of variances.

Fens						
Species group	Vosavaa-ranaapa	Vuijemi	Sota-joki	Kelta-aapa	B_c	P
Waders	0.03	0.59	0.13	0.06	22.03	<0.001
Passerines	0.07	0.03	0.08	0.03	4.27	ns

Coniferous forests						
Species	Vosa-vaara	Heikkilän-vaara	Purnun-nenä	Pyhä Nattanen	B_c	P
Fringilla montifringilla	0.07	0.21	0.10	0.04	6.08	ns
Phylloxcopus trochilus	0.07	0.07	0.09	0.03	3.17	ns
Carduelis flammea	0.27	0.14	0.29	0.27	1.32	ns

4.3. Annual variation of bird populations in fens and forests

The basic difference in the year-to-year density variation of bird populations between forests and fens was that the variation of waders in fens differed between the sites, whereas the variation of passerines seemed to be similar in magnitude in the different sites in both forests and fens. Passerines comprise 94% of the bird pairs in the assemblage of coniferous forests. In fens, the availability of food for birds, such as waders, is probably connected with the water level (see Järvinen & Sammalisto 1976, Järvinen & Väisänen 1978), which may also vary between fens. Therefore, it is possible that between-site variation in the availability of food for waders is high. Marsh-nesting passerines are probably not so dependent on the variation in the water level, as these species, e.g. the Yellow Wagtail and Meadow Pipit *Anthus pratensis*, are also numerous in very dry peatlands (Järvinen & Sammalisto 1976, Kouki & Häyrinen 1991). Unfortunately, the population dynamics of waders in northern mires has not been thoroughly studied (see, however, Hildén 1967, Väisänen & Järvinen 1977) and the reasons for the year-to-year variation patterns of waders should be clarified in detail.

The results of the present study can be considered with reference to a 'sink-source' model (Wiens & Rotenberry 1981). In this model the landscape consists of habitat patches of different quality for a given species (Wiens 1989). The within-site density variation of waders differs in magnitude between fens, and, therefore, waders seem to be suitable for a study based on the 'sink-source' model, although no demographic data are available. For the passerine species, both the fens and virgin coniferous forests are fairly homogeneous habitats in terms of temporal density variation. It is important to note that the between-site variation patterns of species and species groups, such as waders and passerines, differ widely from each other. Therefore, landscape ecological models like the 'sink-source' model may not necessarily be applicable to all species, but should be studied in relation to specified species or groups.

I have earlier argued that the similar stability patterns in the bird communities and populations of virgin and managed forests in the north are due to environmental unpredictability because of the irregularity of seed crops of trees (affecting seed eaters) and unpredictability of weather conditions in spring, especially the occurrence of cold spells (affecting migratory insectivores) (Virkkala 1989, 1991). As a consequence of these components of environmental unpredictability, the year-to-year variation of bird populations and communities seems to be similar in different forest habitats. In the fens, the passerine species also have similar variation patterns in different sites, but waders have not. The local characteristics of the fens may affect the waders differently.

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Selostus: **Pohjoissuomalaisten soiden ja metsien linnuston ajallinen vaihtelu suhteessa tutkittuun alueelliseen mittakaavaan**

Linnuston ajallista vaihtelua tutkittiin neljällä suo- ja metsäalueella Sodankylän Vuotson ympäristössä. Tutkimus perustui vuosina 1983–89 toistettuihin lintulaskentoihin. Tutkimussuot sijaitsivat noin 1000:n ja metsät noin 100 km^2:n alueella. Tutkimuksessa selvitetään: (1) Miten soiden ja luonnontilaisten havumetsien linnuston vaihtelu eroaa toisistaan? (2) Onko kokonaislinnuston vaihtelu pienempää alueellisella kuin paikallisella tasolla? Lintupopulaatioiden ja -yhteisöjen ajallinen vaihtelu on yleensä suurempaa mitä suppeammalla alueella laskenta on suoritettu eli mitä pienempää mittakaavaa tutkimuksessa on käytetty. Laajemmalla alueellisella tasolla lintupopulaatioiden yksittäisten paikkojen satunnaisvaihtelu kompensoituu. Vuosien välistä vaihtelua on työssä mitattu varianssin ja vaihtelukertoimen avulla.

Kokonaislintutiheyden vuosien välinen vaihtelu ei eronnut soiden ja metsien välillä, kun kaikkia suo- ja metsäalueita tarkasteltiin. Yksittäisten soiden lintutiheyden vuosien välinen vaihtelu oli suurempaa kolmella suolla neljästä verrattaessa muiden soiden yhteiseen lintutiheyden vaihteluun. Sen sijaan metsissä linnuston tiheysvaihtelussa ei ollut eroa yksittäisten metsäalueiden ja muiden metsien välillä. Metsien yleisimpien lajien, järripeipon, pajulinnun ja urpiaisen, sekä soiden varpuslintujen tiheysvaihtelussa ei ollut eroa paikkojen välillä. Sen sijaan kahlaajien vuosien välisen vaihtelun suuruus erosi toisistaan eri soilla. Tämä voi johtua siitä, että kahlaajat ovat varpuslintuja (keltavästäräkki, niittykirvinen) herkempiä reagoimaan soiden veden pinnan vaihteluun, joka voi olla myös erilaista eri soilla. Erot linnuston vaihtelussa soiden ja metsien välillä voivat johtua joko alueellisen mittakaavan eroista tai metsä- ja suolintulajien erilaisesta vuosien välisestä vaihtelusta.

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