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# Short-term fluctuations of bird communities and populations in virgin and managed forests in Northern Finland

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Bird communities of virgin and managed coniferous forests were censused by the line transect method in Northern Finland in 1982–87. Managed forests were thinned, dry pine-dominated forests and virgin climax, dry pine and moist spruce-birch forests. I assessed the stability of bird communities in these different forest types by measuring variation in bird density, species richness, species diversity, evenness component of diversity and average individual turnover between consecutive years. I also compared annual fluctuations of the five most common species (*Fringilla montifringilla, Phylloscopus trochilus, Carduelis flammea, Phoenicurus phoenicurus* and *Turdus iliacus*) in virgin and managed forests.

The stability indices did not reveal any clear patterns between different forest types, presumably because of the irregularity of seed crops (affecting seed eaters) and the unpredictability of weather conditions in late spring and early summer (affecting migratory insectivores). These two aspects of environmental unpredictability probably make stability patterns in different habitats similar to each other in the north.

The effect of forest management on the stability of bird communities and populations is discussed. Species preferring virgin forests (*Parus cinctus, Perisoreus infaustus, Pinicola enucleator, Bombycilla garrulus, Picoides tridactylus, Phoenicurus phoenicurus, Tetrao urogallus*) fluctuated less in virgin compared with managed forests, but these species have always comprised only a minor proportion of the community. Thus, bird communities of virgin forests have probably not been more stable earlier, when forest management was not so intensive.

Density fluctuations of *Ph. trochilus* and *Phoenicurus phoenicurus* were most pronounced in their marginal habitats, whereas similar fluctuations could not be seen in *F. montifringilla, T. iliacus* or *C. flammea*. The northern species *F. montifringilla* and *C. flammea* possess specific adaptations to the environmental unpredictability, such as low site tenacity and breeding nomadism, which probably decrease differences in the density variation of these species between forest habitats. The mass appearence of *Loxia leucoptera* in 1987 indicates that local bird communities studied also reflect changes occurring outside the study area, on a regional or a continental level.

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## 1. Introduction

Populations and communities fluctuate in time and vary in space. The concept of stability is connected with these variations, and it can be defined as the ability of an ecological system to exhibit resistance to short-term perturbations (Connell & Sousa 1983). It is generally believed that northern species-poor communities are unstable compared with those at lower latitudes. The latitudinal decrease of community stability can be presumed to be a result of a northward decrease in species diversity, productivity, and/or climatic (environmental) predictability. In his study of bird community stability in Europe, Järvinen (1979) observed that northern communities were the least stable, and he suggested this to be due to environmental unpredictability in the north. In contrast, Noon et al. (1985) did not observe any clear latitudinal stability gradients in breeding bird communities in North America.

In this paper I examine fluctuations of bird communities and populations in coniferous forests of northern Finland, in an area situated 200 km north of the Arctic Circle. In particular, I compare stability patterns of bird communities in virgin climax forests and managed forests. Forest management presumably gives rise to changes in bird populations, whereas virgin forests, being structurally more constant, should not exert such environmental effects on them.

There have only been a few studies on bird community dynamics in northern forests: a thorough 20-year research in a subalpine birch forest in Swedish Lapland (Enemar et al. 1984) and the study of Helle & Mönkkönen (1986) on a successional series of coniferous forest. Both these studies have been carried out in areas situated south of the Arctic Circle.

## 2. Material and methods

The data originate from line transect censuses (Järvinen & Väisänen 1977) carried out in northern Finland, in the coniferous forests around Sodankylä Vuotso (68°N, 27°E, Fig. 1) in 1982–87. The area is situated at the northwestern tip of the northern taiga belt. I distinquished three forest types along the line transects: virgin spruce-birch forest, virgin pine-dominated forest, and managed pine-dominated forest. Virgin forests were censused in the Sompio Nature Reserve and managed forests in the Tankajoki and the Sotajoki area (Fig. 1).

Spruce-birch forests were moist, with spruce as a dominating tree species, and virgin pine-dominated forests barren, with only few birches. In spruce-birch forests, coniferous and deciduous bushes were common, whereas the bush layer was almost totally lacking in virgin pine forests. Most of the virgin spruce-birch and pine forests censused were over 200 years old. Managed pine-dominated forests were thinned, with young trees as undergrowth. Cuttings were carried out mainly in the late 1950s and in the 1960s, but silviculture has also been practised later (not, however, during the census years). Dead trees had been removed, and deciduous trees and bushes were more abundant here than in virgin pine forests.

The Finnish line transect method is a one-visit census, in which birds are counted separately on a 50-m wide main belt and outside it, on a supplementary belt (Järvinen & Väisänen 1976). In the present study both main and supplementary belt observations were taken into account in order to increase the sample size, because average bird densities in these northern forests are very low. For calculating the density estimates I used correction coefficients given by Järvinen & Väisänen (1983). If the ratio of main/supplementary belt observations differed significantly from those of Järvinen & Väisänen (1983), I calculated a new species-specific correction coefficient (see Virkkala 1987a). All species nesting only on mires were excluded from the data.

The length of the transects (km) and average census dates in different forest types in the study years are presented in Table 1.

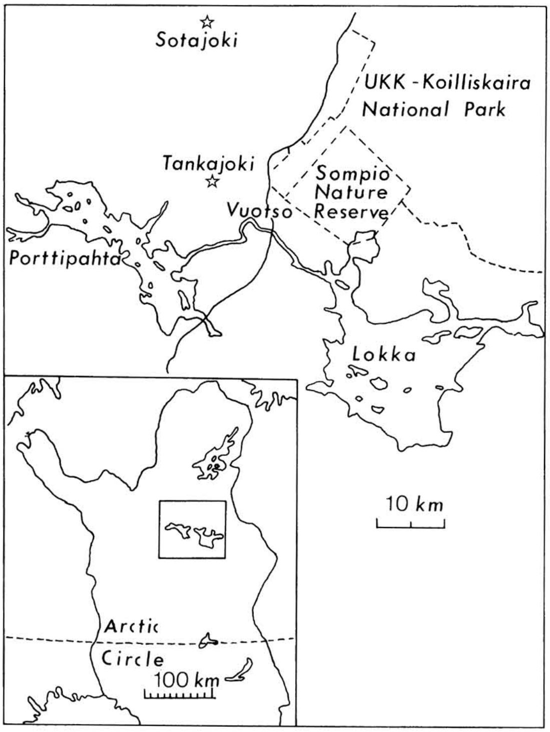

Fig. 1. Situation of the study areas in northern Finland.

Censuses of virgin forests were based on four transects repeated yearly and those of managed forests on three transects (in 1982 on only one transect). When studying the density fluctuations of particular species or species groups in managed forests, only the data from 1983–87 were used, because of the small sample size in 1982.

The stability of bird communities was measured using the following indices presented by Järvinen (1979) (see also Noon et al. 1985, Helle & Mönkkönen 1986):

1) Coefficient of variation (*CV%*) of the total bird density, *CV(D)*.

2) *CV* of the number of species *CV(S')*. I used the expected number of species in a random sample of 50 pairs, calculated by rarefaction (see Simberloff 1978).

3) *CV* of species diversity *CV(H')*. Sample size corrections were made according to Hutcheson (1970).

Table 1. Length of transects (km) and average census dates (within parentheses) in different forest types.

| Forest type | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Total |
|---|---|---|---|---|---|---|---|
| Virgin spruce | 11.7 (27.6) | 11.7 (26.6) | 11.7 (21.6) | 11.7 (22.6) | 11.7 (23.6) | 11.7 (19.6) | 70.2 |
| Virgin pine | 8.1 (27.6) | 8.1 (25.6) | 8.1 (23.6) | 8.1 (21.6) | 8.1 (22.6) | 8.1 (18.6) | 48.6 |
| Managed pine | 2.1 (22.6) | 9.6 (16.6) | 9.6 (16.6) | 9.6 (11.6) | 9.1 (16.6) | 9.6 (15.6) | 49.6 |

4) *CV* of evenness component of diversity $CV(J')$. Evenness is calculated as $J'=H'/\ln S$. Only the data from 1983–87 were used.

5) Average individual turnover, *IT*, the average of the index *rD*.

$$rD = 100(\exp DIV_{diff} - 1),$$

in which

$$DIV_{diff} = H'(1 + 2) - (H'(1) + H'(2))/2.$$

$H'(1)$ and $H'(2)$ are species diversities of successive years; $H'(1 + 2)$ species diversity of the pooled data of these years. This index is affected by the average change in the composition of the community (Järvinen 1979).

The interpretation and importance of different stability indices used is discussed in more detail by Järvinen (1979). The stability indices acquire higher values, when instability increases.

## 3. Results

Bird densities differed between the three forest types (Table 2, Friedman's two-tailed variance analysis, $P < 0.01$) and the difference was significant between virgin forests and virgin spruce and managed pine forests (Tukey's test, $P < 0.05$). Species diversity and evenness did not greatly differ between the forest habitats. In spruce-birch forest species diversity seemed to be, however, somewhat lower (non-significantly) than in more barren virgin and managed pine forests. The values for species diversity were lower than in similar forest types in Kuusamo (66°N, 29°E; values about 2.5–3.0; Helle 1985, Helle & Mönkkönen 1986). This difference was due to the high proportion of the brambling *Fringilla montifringilla* (about 40%, see Table 3) in my study area.

Stability indices did not reveal any clear patterns between different forest types (Fig. 2, Table 2). In

Table 2. Average density, species diversity, evenness, expected number of species in a random sample of 50 pairs (smallest sample) and the values of stability indices used in different forest types.

| | Virgin spruce | Virgin pine | Managed pine |
|---|---|---|---|
| Density (pairs/km$^2$) | 94.2 | 59.6 | 68.2 |
| Species diversity ($H'$) | 1.97 | 2.17 | 2.11 |
| Evenness ($J'$) | 0.63 | 0.72 | 0.70 |
| Exp. no. of species ($S'$) | 12.0 | 10.7 | 11.0 |
| Stability indices: | | | |
| $CV(D)$ | 12.7 | 12.0 | 9.5 |
| $CV(H')$ | 8.1 | 6.8 | 5.6 |
| $CV(J')$ | 7.2 | 2.9 | 4.0 |
| $CV(S')$ | 8.7 | 12.7 | 13.6 |
| *IT* | 7.1 | 8.3 | 12.1 |

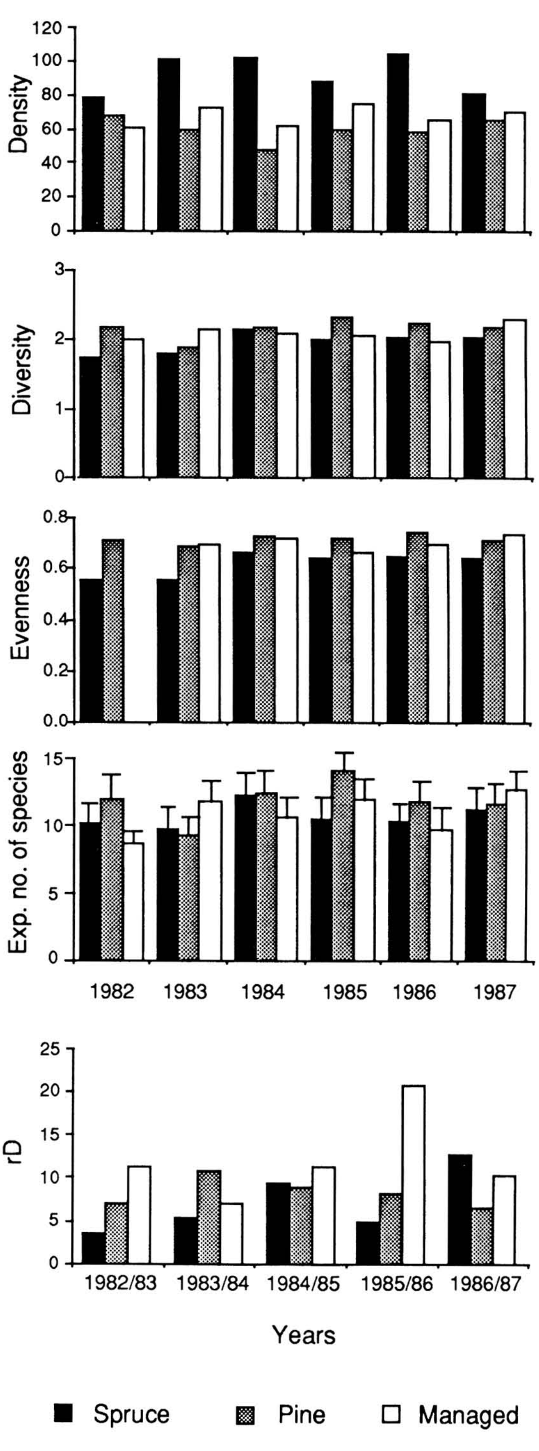

Fig. 2. Values of density (pairs/km$^2$), species diversity ($H'$), evenness component of diversity ($J'$), species richness (rarefaction estimate per 50 pairs with standard deviation) and *rD* in different forest types in the study years (1982–87).

Table 3. Densities (pairs/km²) and proportions (%, in parentheses) of the ten most abundant species in the different forest types.

| Virgin spruce forest | | Virgin pine forest | | Managed pine forest | |
|---|---|---|---|---|---|
| *Fringilla montifringilla* | 40.6 (43.1) | *F. montifringilla* | 22.4 (37.5) | *F. montifringilla* | 22.0 (32.3) |
| *Phylloscopus trochilus* | 14.6 (15.5) | *Ph. phoenicurus* | 7.6 (12.7) | *Ph. trochilus* | 14.7 (21.6) |
| *Carduelis flammea* | 6.3 (6.7) | *Ph. trochilus* | 5.6 (9.4) | *C. flammea* | 8.1 (11.9) |
| *Turdus iliacus* | 5.9 (6.3) | *C. flammea* | 4.6 (7.7) | *T. iliacus* | 5.0 (7.3) |
| *Parus cinctus* | 3.3 (3.5) | *Oenenthe oenanthe* | 3.5 (5.9) | *Ph. phoenicurus* | 3.2 (4.7) |
| *Turdus philomelos* | 3.0 (3.2) | *P. cinctus* | 2.7 (4.5) | *Muscicapa striata* | 2.7 (4.0) |
| *Tetrao urogallus* | 3.0 (3.2) | *T. iliacus* | 2.3 (3.8) | *Motacilla flava* | 1.9 (2.8) |
| *Phoenicurus phoenicurus* | 2.7 (2.9) | *Lagopus lagopus* | 2.3 (3.8) | *Oe. oenanthe* | 1.8 (2.6) |
| *Emberiza rustica* | 1.8 (1.9) | *Perisoreus infaustus* | 1.9 (3.2) | *Anthus pratensis* | 1.7 (2.5) |
| *Pinicola enucleator* | 1.7 (1.8) | *Anthus trivialis* | 1.1 (1.8) | *A. trivialis* | 1.5 (2.2) |

spruce forests, $CV(S')$ seemed to be lower, and $CV(J')$ higher. Individual turnover was somewhat higher in managed forests than in virgin forests. None of the differences in stability indices between forests was statistically significant ($F$-test). The highest correlations between stability indices were: $CV(D)$ correlated negatively with $IT$ ($r=-0.999$, $P<0.05$), and there was also a high positive correlation between $CV(D)$ and $CV(H')$ ($r=0.944$, ns) and a negative correlation between $CV(H')$ and $CV(S')$ ($r=-0.947$, ns) and $CV(H')$ and $IT$ ($r=-0.951$, ns).

Table 4. Year-to-year variation of density ($CV$,%) in the five most abundant species in the three forest types.

| | Virgin spruce | Virgin pine | Managed pine |
|---|---|---|---|
| *Fringilla montifringilla* | 15.8 | 20.2 | 34.4 |
| *Phylloscopus trochilus* | 23.5 | 37.9 | 17.9 |
| *Carduelis flammea* | 76.8 | 50.0 | 51.5 |
| *Phoenicurus phoenicurus* | 41.8 | 25.2 | 44.0 |
| *Turdus iliacus* | 37.3 | 37.4 | 8.6 |

### *Fluctuation of dominant species*

The densities and proportions of the ten most abundant species in the forest types are shown in Table 3. *F. montifringilla* was a clear dominant in all forest types. Species typical of the northern taiga, such as capercaillie *Tetrao urogallus*, three-toed woodpecker *Picoides tridactylus*, Siberian jay *Perisoreus infaustus*, Siberian tit *Parus cinctus*, pine grosbeak *Pinicola enucleator* and rustic bunting *Emberiza rustica* comprised 11.4% of the community in spruce forest and 10.5% in virgin pine forest, but only 1.0% in managed pine forest.

Five species, viz. *F. montifringilla, Ph. trochilus*, the redpoll *Carduelis flammea, Phoenicurus phoenicurus* and the redwing *Turdus iliacus*, reached mean densities of more than two pairs/km² in all three forest types (see Table 3). Density variations for these species ($CV(D)$) are presented in Table 4. Other species were scarce or absent in one or two of the forest types, and thus the density variation of these species was not considered separately: in very low densities stochastic variation has a profound effect on the results (e.g., Helle & Mönkkönen 1986). Again, in the case of the five most common species there were great variations in average density, although, the negative correlation of sample size (number of observations) in these five species in different forest types ($N=15$) and the corresponding values of $CV(D)$ was not significant ($r=-0.449$). Thus it can be considered that stochastic variation due to small sample size probably has a minor effect on the observed fluctuation of these species.

If density variations were greatest in areas of low density, high negative correlations should prevail between $CV(D)$ and average density (see Table 4). Correlations ($r$) over the three forest types are for *Ph. trochilus* are $-0.965$ (ns) and for *Phoenicurus phoenicurus* $-0.980$ (ns), whereas other species have either weak correlations or none at all (*F. montifringilla, T. iliacus, C. flammea*). *T. iliacus* is, however, the only species, in which $CV(D)$ differs significantly between two forest types: managed/virgin pine forest, managed pine/spruce forest ($P<0.05$ for both comparisons, $F$-test). *C. flammea* plainly has the highest density variation, whereas the average density variation in all forests is of the same order of magnitude in *F. montifringilla, Ph. trochilus* and *T. iliacus*.

*Species preferring virgin/managed forests*

Species preferring virgin, climax forests ( *Parus cinctus, Perisoreus infaustus, Pinicola enucleator,* the waxwing *Bombycilla garrulus, Picoides tridactylus, T. urogallus* and *Ph. phoenicurus,* e.g., Järvinen & Väisänen 1979a) have decreased in northern Finland as a consequence of increased silviculture (Järvinen et al. 1977, Väisänen 1983, Helle & Järvinen 1986, Väisänen et al. 1986). On the other hand, *Ph. trochilus, T. iliacus, C. flammea* and the yellow wagtail *Motacilla flava* have increased (Väisänen 1983, Väisänen et al. 1986), which can at least partly be explained by the effects of forestry (see Virkkala 1987a). *CV*s in the density of these species groups were compared (in parentheses average density, pairs/km$^2$):

| Forest pref. | Spruce | Pine | Managed |
|---|---|---|---|
| Virgin | 15.0(11.5) | 25.6(13.0) | 46.2 (3.8) |
| Managed | 33.8(27.0) | 33.6(12.6) | 20.4 (29.8) |

*CV* in density differs significantly in species of virgin forests between spruce and managed forests ($P<0.05$, *F*-test). Species preferring virgin forests also appear to have a lower year-to-year variation in virgin forests compared with that of species preferring managed forests (non-significant, however).

*Migratory groups*

I divided the bird species into different groups according to migratory habits (see von Haartman et al. 1963–72), and the density variation of these groups in different forests were studied (Table 5). Sedentary species seem to have the greatest year-to-year variation in density, but due to their low density (and small number of observations) stochastic factors influence the results. The value of *CV(D)* of short-distance migrants is lower in spruce forests and higher in virgin pine forests compared with that of long-distance migrants.

Table 5. Coefficient of variation in density and average density (in parentheses) of sedentary species, short-distance migrants and long-distance migrants.

| | Virgin spruce | Virgin pine | Managed pine |
|---|---|---|---|
| Sedentary species | 25.8 (9.2) | 49.2 (7.4) | 76.8 (2.1) |
| Migrant species | | | |
| short-distance | 13.1 (61.3) | 20.7 (32.1) | 11.8 (38.4) |
| long-distance | 20.1 (23.7) | 5.4 (20.2) | 10.4 (29.4) |

*Seed specialists*

Seed specialist species fluctuate as a result of variation in the seed crop. During the study period (1982–87) I recorded three exceptional years in terms of seed specialist abundance. In 1984 the crossbills *Loxia curvirostra* and *pytyopsittacus* and the siskin *Carduelis spinus* were abundant. *Carduelis flammea* had a peak year in 1986, when it was the second most numerous species in virgin and managed forests and the third in spruce forests. An exceptionally good spruce seedcrop occurred in 1986 (E. Numminen, pers. comm.) and as a consequence the two-barred crossbill *Loxia leucoptera* occurred in the area in large numbers in 1987. The density of *L. leucoptera* in 1987 was 4.8 pairs/km$^2$ ($N=21$) in spruce forests and 3.3 p/km$^2$ ($N=10$) in virgin pine forests, whereas I recorded it only once during the previous years. *L. leucoptera* was the third most numerous species in spruce forests and the fifth in virgin pine forests in 1987.

## 4. Discussion

### 4.1. Census method

Because the line transect method is a one-visit census, all the birds are not observed, which may affect the results obtained in this study. However, in northern areas the efficiency of line transects is presumably high (Järvinen et al. 1978), and only a minor proportion of the supplementary belt observations in my data came from "wrong" habitats, because uniform forests cover large areas and the forest types are clearly separated from each other. I thus presume that errors involved with the line transect method are parallel in different forest habitats.

On the other hand, the mapping method could also cause problems. Bird densities in these northern forests are low (in the order of 50–100 pairs/km$^2$) with one species dominating (*Fringilla montifringilla*). Thus study plots should be very large to avoid problems presented by Wiens (1981) in his "checkerboard" model: in a very sparsely packed habitat the annual redistribution of individuals may produce substantial variations in the number of individuals independant of annual changes in the habitat. The line transect method is not as susceptible to within-habitat random redistribution of individuals as study plot methods, because transects cover larger areas.

### 4.2. Stability indices

The bird community in virgin forests was not more stable than that of managed forests according to the stability indices used. Density variation appeared lower than the 20–30% previously reported for northern European forests (Järvinen 1979, Enemar et al. 1984, Helle & Mönkkönen 1986). This may be because the dominant species, *Fringilla montifringilla*, fluctuates less in this area, which is close to the centre of its distribution (see Järvinen & Väisänen 1979b). The other index values are similar to those reported by Helle & Mönkkönen (1986).

Because individual turnover seemed to be somewhat higher in the managed forests, I studied whether compensatory or parallel density fluctuations dominate in the different forest types. The variance sum of population fluctuations of individual species was compared with the variance of bird community fluctuations. If parallel density fluctuations prevail, the variance ratio should be less than one, and if compensatory fluctuations are common, this ratio should exceed one (Järvinen 1979). Variance ratios in these three forests were:

| Spruce | Pine | Managed |
|---|---|---|
| 0.72 | 1.06 | 2.59 |

In virgin forests no clear patterns emerge, whereas in managed forest compensatory fluctuations seem to be general and the variance ratio deviates significantly from one ($P<0.05$, see Schluter 1984).

In my data, an increase in species diversity is not associated with an increase in community stability, because the negative correlation between average diversity and $CV(D)$ is far from significant ($r = -0.423$).

In the study area silvicultural management was carried out mainly 20–30 years before the study, and thus annual changes in forest structure were small. The situation might have been different, if these forests had been cut just before the study began. Management of forests (mainly thinning) can also be considered as a moderate perturbation of forest habitat compared to the large-scale clearcuttings of northern Finland.

My results suggest that differences in forest habitats in the north do not greatly affect community stability, and hence support Järvinen (1981) who found that geographical location is of greater importance in determining community stability patterns than habitat.

Głowacinski (1981) observed in his study of bird community fluctuations in a Polish forest successional sere that climax forest (age about 150 years) comprised the most stable bird community. By contrast, in a corresponding study in northern Finland, Helle & Mönkkönen (1986) found that the clear-felled areas (age 5–8 years) had the most stable community. Helle & Mönkkönen suggested, however, "that bird communities of old forests may have been more stable than those in other forested habitats, but because continuous forests have been heavily fragmented by the intensive forestry in the last decades, the fragments of primeval forests no longer support their original stable community". For instance, in eastern deciduous forests of North America forest habitat fragmentation has been severe and has probably greatly increased avian turnover rates (Whitcomb et al. 1977, 1981). Although forest management has been very extensive and intensive in northern Finland, the virgin forests in my study area were situated in a very large virgin forest tract (hundreds of square kilometers in UKK-Koilliskaira National Park and Sompio Nature Reserve) and species preferring virgin forests have probably not decreased in these forests during the last few decades (Virkkala 1987a). Fluctuations in this species group were lower in virgin than in managed forests, but these species comprise only 22% of bird pairs in virgin pine forests and 12% of those in spruce forests, while 70–80% of bird pairs in northern Finnish virgin forests are forest habitat generalists, species such as *Fringilla montifringilla, Phylloscopus trochilus, Turdus iliacus* and *Carduelis flammea* (see Virkkala 1987b). Species preferring virgin forests even before (in the 1940–50s) comprised a minor proportion of the bird community in virgin forests (Virkkala 1987a). Thus my data do not support the idea that virgin forests were more stable previously.

Climatic unpredictability is a plausible explanation for the lack of between-habitat differences in stability patterns in my data. Variances of monthly average temperatures in Helsinki (60°20′N) in May and June of 1982–87 were 2.8 and 2.9 and in Sodankylä (67°20′N) 4.8 and 5.4, respectively; the northwards increase in variances of average monthly temperatures is discussed by Skre (1971). Most of the migratory birds (90% of the total bird community in my study area) return in May, but the average temperature in May varies more in the north. The occurrence of cold spells in late spring and early summer probably influence the numbers of insectivores (see

Ojanen 1979), which comprise about 80% of communities in these forests. A very cold period occurred, e.g., in Mid-June of 1982, with daily snow during a period of two weeks. The unpredictability of the weather in spring and early summer affects bird communities similarly in all habitats. The situation is different in more southern areas, e.g., in Poland, where climatic conditions are more predictable and thus have less effect on bird communities. Järvinen (1979) also assumed that the northward decrease in bird community stability in Europe was a consequence of the northward increase in the environmental (climatic) unpredictability.

### 4.3. Fluctuation of bird populations

Bird populations tend to fluctuate more in low density areas (suboptimal or marginal habitat) than in high density areas (optimal or suitable habitat) (e.g. von Haartman 1971). Density can, however, be a misleading indicator of habitat quality without the existence of demographic data (van Horne 1983). Density fluctuations in *Phylloscopus trochilus* and *Phoenicurus phoenicurus* were most pronounced in their marginal habitats, whereas similar fluctuations could not be seen in *Fringilla montifringilla, Turdus iliacus* and *Carduelis flammea.*

Hogstad (1975) observed that in Norwegian subalpine forests the two most abundant species (as also in my study area) *F. montifringilla* and *Ph. trochilus* fluctuated inversely to each other. No similar correlation was found in my study area, for correlations between the densities of these species were not significant (spruce forest, $r$=–0.037, $N$=6, ns; virgin pine forest, $r$=0.662, $N$=6, ns; managed pine forest, $r$=–0.498, $N$=5, ns).

Densities of *F. montifringilla* did not fluctuate as greatly as reported in earlier studies (Mikkonen 1983, Enemar et al. 1984). In subalpine birch forests of Norway and Sweden the densities of *F. montifringilla* are most obviously the highest in years with high densities of caterpillars of the geometrid moth *Epirrita (Oporinia) autumnata* (Enemar et al. 1984, Hogstad 1985, Lindström 1987). In the coniferous forests of my study area, birch, in which this moth occurs, comprises only a minor proportion of the stand. Moreover, there are no large birch forests in this region. Thus peak *F. montifringilla* years as a consequence of the mass occurrence of *Epirrita autumnata* are probably not being observed in these coniferous forests.

The decline of *F. montifringilla* in the 1940s has been suggested to be a result of very cold winters (Merikallio 1951). Interestingly, there were two very cold winters in the whole of Central and Northern Europe during the study period: 1984/85 and 1986/87, but the populations of *F. montifringilla* did not collapse in my study area. For instance, the densities of *F. montifringilla* were 36.0, 18.2 and 12.4 pairs/km$^2$ in spruce, virgin pine and managed pine forests in 1986, respectively, and the corresponding densities in 1987 were 34.4, 24.3 and 20.0 p/km$^2$. However, local and regional density fluctuations of *F. montifringilla* may differ because of the low site tenacity observed in this species (Mikkonen 1983, Lindström 1987).

The great density fluctuations observed in *C. flammea* are in accordance with earlier results reporting the irregularity in abundance of this species as a consequence of variation in the seed crop of birch (e.g. von Haartman et al. 1963–72, Enemar & Nyström 1981, Enemar et al. 1984). The low site tenacity of *F. montifringilla* and the breeding nomadism of *C. flammea* (see Enemar & Nysröm 1981) probably decrease the differences in density variations between forest habitats. Low site tenacity and breeding nomadism can also be regarded as adaptations to the environmental unpredictability in the north.

The high numbers of *Loxia leucoptera* in 1987 show that considerable population movements occur in the taiga belt of Eurasia. This species is distributed from northern Russia across Siberia, but in years when there is a good spruce seed crop it also breeds in northern Finland, at the western tip of the taiga belt (von Haartman et al. 1963–72, Pulliainen 1983). The seed crops of trees are very irregular in these northern latitudes (northern Finland, see Leikola et al. 1982 and references therein) and as a consequence seed eaters fluctuate greatly both temporally and spatially.

The invasion of *L. leucoptera* indicates that local bird communities in my study area also reflect changes on a regional scale or possibly even on a continental scale (see Wiens 1981).

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## Appendix

Yearly number of observations and average densities (D, pairs/km$^2$) of bird species in different forests. Average densities in virgin forests are based on the data of 1982–87 and in managed pine forest on those of 1983–87.

| | Virgin spruce forest | | | | | | | Virgin pine forest | | | | | | | Managed pine forest | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 82 | 83 | 84 | 85 | 86 | 87 | D | 82 | 83 | 84 | 85 | 86 | 87 | D | 82 | 83 | 84 | 85 | 86 | 87 | D |
| *Accipiter gentilis* | 1 | 1 | 1 | – | – | – | 0.2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Falco columbarius* | – | – | – | – | – | – | – | – | – | 1 | 1 | – | – | 0.1 | – | – | – | – | – | – | – |
| *Lagopus lagopus* | – | 1 | 4 | 2 | 3 | – | 1.6 | 3 | 1 | – | 2 | 3 | 2 | 2.3 | – | 2 | – | 1 | – | 3 | 1.3 |
| *Tetrao urogallus* | 2 | 4 | 3 | 3 | 1 | 1 | 3.0 | – | – | – | – | – | 1 | 0.3 | – | – | – | – | – | – | – |
| *T. tetrix* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | 0.1 |
| *Numenius phaeopus* | – | – | – | – | – | – | – | 2 | 7 | 6 | 3 | 4 | 3 | 0.5 | – | 2 | 4 | 6 | 1 | 3 | 0.3 |
| *Tringa ochropus* | – | – | – | 1 | – | – | 0.05 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *T. erythropus* | – | – | – | – | – | – | – | – | – | – | 1 | – | – | 0.1 | – | 2 | – | 1 | 1 | – | 0.3 |
| *T. nebularia* | – | – | – | – | – | – | – | – | – | – | 2 | – | – | 0.05 | – | – | 2 | – | – | – | 0.04 |
| *Cuculus canorus* | 10 | 11 | 14 | 7 | 16 | 7 | 0.7 | 11 | 5 | 5 | 9 | 8 | 4 | 0.6 | – | 6 | 14 | 14 | 3 | 9 | 0.6 |
| *Surnia ulula* | – | – | – | – | – | – | – | – | 1 | – | – | – | 1 | 0.2 | – | 1 | – | – | – | – | 0.1 |
| *Picoides tridactylus* | – | – | – | – | – | – | – | – | – | – | 1 | – | – | 0.1 | – | – | – | – | – | – | – |
| *Dryocopus martius* | – | – | – | – | 1 | – | 0.02 | – | 1 | – | – | – | – | 0.02 | – | – | 1 | 1 | – | – | 0.04 |
| *Anthus trivialis* | 2 | 5 | 12 | 9 | 9 | 8 | 1.6 | 8 | 3 | 3 | 5 | 3 | 1 | 1.1 | 2 | 7 | 3 | 6 | 7 | 8 | 1.5 |
| *A. pratensis* | 3 | 1 | 1 | – | 1 | – | 0.4 | – | – | – | – | – | 1 | 0.1 | – | 2 | 1 | 4 | 3 | 10 | 1.7 |
| *Motacilla flava* | 1 | 2 | 1 | 2 | 1 | 3 | 0.3 | – | – | – | 1 | 1 | 2 | 0.1 | 4 | 9 | 14 | 12 | 8 | 9 | 1.9 |
| *M. alba* | – | – | – | – | – | – | – | – | – | – | – | 2 | 1 | 0.3 | – | – | – | 2 | – | 3 | 0.5 |
| *Bombycilla garrulus* | – | – | – | – | – | – | – | 1 | – | – | – | – | – | 0.05 | – | – | – | – | – | – | – |
| *Perisoreus infaustus* | 2 | 1 | 2 | – | 1 | 1 | 0.9 | 3 | – | 3 | 4 | 1 | – | 1.9 | – | 1 | – | – | – | 1 | 0.4 |
| *Corvus corone* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 0.02 |
| *C. corax* | 1 | 1 | 2 | 1 | – | 1 | 0.04 | 1 | 1 | 2 | 1 | – | – | 0.05 | – | – | – | 1 | – | – | 0.01 |
| *Prunella modularis* | 2 | 2 | – | – | 2 | 2 | 0.3 | 1 | – | – | – | – | – | 0.05 | – | – | – | – | – | – | – |
| *Phylloscopus trochilus* | 62 | 101 | 74 | 75 | 117 | 91 | 14.6 | 24 | 40 | 18 | 15 | 21 | 21 | 5.6 | 8 | 74 | 65 | 68 | 88 | 59 | 14.7 |
| *Ph. sibilatrix* | – | – | 1 | – | – | – | 0.03 | 1 | – | – | – | – | – | 0.05 | – | – | – | – | – | – | – |
| *Ph. borealis* | – | – | – | – | 1 | – | 0.05 | 1 | – | – | – | – | – | 0.01 | – | – | – | – | – | – | – |
| *Regulus regulus* | 1 | 2 | 1 | – | – | – | 0.4 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Ficedula hypoleuca* | 1 | – | – | 3 | – | 2 | 0.3 | 1 | – | 1 | 3 | 1 | 2 | 0.5 | – | – | – | 1 | – | 1 | 0.2 |
| *Muscicapa striata* | 2 | – | 7 | – | 3 | 1 | 1.3 | – | – | – | 2 | 1 | – | 0.4 | – | 8 | – | 4 | 5 | 2 | 2.7 |
| *Oenanthe oenanthe* | – | – | – | – | – | – | – | 6 | 2 | 10 | 11 | 10 | 11 | 3.5 | – | 5 | 5 | 4 | 1 | 11 | 1.8 |
| *Saxicola rubetra* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 4 | – | – | – | – | 0.3 |
| *Phoenicurus phoenicurus* | 21 | 11 | 20 | 7 | 17 | 21 | 2.7 | 38 | 34 | 42 | 20 | 26 | 37 | 7.6 | 2 | 20 | 25 | 5 | 17 | 15 | 3.2 |
| *Luscinia svecica* | – | – | 1 | 2 | – | 2 | 0.3 | – | – | – | – | – | – | – | – | 2 | 2 | 6 | 4 | 2 | 1.4 |
| *Erithacus rubecula* | – | 3 | – | 3 | – | – | 0.3 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Turdus iliacus* | 16 | 27 | 40 | 35 | 45 | 20 | 5.9 | 8 | 9 | 4 | 6 | 13 | 9 | 2.3 | 8 | 22 | 19 | 24 | 20 | 21 | 5.0 |
| *T. philomelos* | 6 | 32 | 28 | 32 | 27 | 9 | 3.0 | 3 | 10 | 1 | 5 | 1 | – | 0.6 | 1 | – | – | 5 | – | – | 0.2 |
| *T. viscivorus* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 0.04 |
| *T. pilaris* | – | – | – | – | – | – | – | – | – | 1 | – | – | – | 0.1 | – | – | – | 1 | – | – | 0.1 |
| *Parus montanus* | – | – | – | – | 1 | – | 0.1 | – | – | – | – | – | – | – | – | – | 1 | – | – | – | 0.1 |
| *P. cinctus* | 7 | 4 | 3 | 4 | 4 | 3 | 3.3 | 5 | 1 | 3 | 3 | 2 | 1 | 2.7 | – | – | 1 | – | – | – | 0.2 |
| *Fringilla coelebs* | – | 1 | – | – | – | – | 0.03 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *F. montifringilla* | 183 | 220 | 179 | 155 | 149 | 148 | 40.6 | 78 | 89 | 52 | 74 | 58 | 77 | 22.4 | 21 | 95 | 78 | 119 | 44 | 75 | 22.0 |
| *Carduelis spinus* | – | 1 | 14 | 1 | – | 1 | 0.5 | – | – | 1 | 1 | – | – | 0.1 | – | 1 | – | – | – | – | 0.04 |
| *C. flammea* | 14 | 23 | 18 | 45 | 73 | 15 | 6.3 | 19 | 18 | 5 | 12 | 31 | 19 | 4.6 | 8 | 25 | 40 | 17 | 62 | 34 | 8.1 |
| *Pinicola enucleator* | 1 | 1 | 4 | 5 | 3 | 1 | 1.7 | – | – | – | 1 | 1 | 1 | 0.5 | – | – | – | – | – | – | – |
| *Loxia curvir./phytops.* | – | 1 | 16 | 1 | 6 | 14 | 0.6 | 2 | – | 8 | 1 | 3 | 13 | 0.6 | – | 1 | 1 | 1 | 1 | – | 0.1 |
| *L. leucoptera* | 1 | – | – | – | – | 21 | 0.8 | – | – | – | – | – | 10 | 0.6 | – | – | – | – | – | – | – |
| *Emberiza pusilla* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 0.1 |
| *E. rustica* | 1 | 2 | 2 | 3 | 4 | 2 | 1.8 | – | – | 1 | – | – | – | 0.2 | – | – | – | – | – | – | – |
| *E. schoeniclus* | 4 | 1 | 1 | 1 | 1 | 2 | 0.8 | – | – | – | – | – | – | – | 1 | 4 | 3 | – | 1 | 2 | 1.1 |

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