Annual fluctuations of land bird communities in different successional stages of boreal forest

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Bird communities in four different phases of secondary forest succession (clear cut, seedling stand, young mixed forest, climax conifer forest) were censused by the line transect method in northeastern Finland in 1980—85. Yearly variations in bird density and species diversity, as well as community compositional stability of the successional bird communities, were measured. The bird community of the clear cut was the most stable, while the other phases did not deviate from each other in stability. Relative density variation of long-distance migrants (as a group) was lower that that of short-distance migrants or sedentary species. There was a strong negative correlation between the population variability and average population density among the studied succession stages for each of the abundant species.

The finding that clear cut supports the most stable bird community contradicts the general theory of succession; however, clear cut is an artificial habitat which cannot be included in the natural forest succession series. The negative correlations between density variation and average density of the species in different successional stages support the idea that the optimum habitats of species are occupied more regularly than marginal ones. An identical pattern might also be caused by chance. The lower the density (or smaller the sample) the greater the role of stochasticity. Some evidence is presented that the population densities of species in studied habitats behave as a Poisson variate, i.e. they are 'random samples' from stable source populations.

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1. Introduction

A classic principle of ecology, that northern species-poor communities are less stable than more southern species-rich ones (e.g. MacArthur 1955), was questioned by May (1973). He showed that a simple system can be even more stable than a complex one, at least in theoretical models. The stability of land bird communities has been found to decrease with increasing latitude within Europe (Järvinen 1979, 1981), but not in North America (Noon et al. 1985). Stability is also a problematic concept in the framework of succession theory. It has been assumed (e.g. Odum 1969) that pioneer communities are less stable than climax ones, but this has not been properly verified; Głowaciński's (1981) work on Central European forest bird communities is among the few quantitative studies. The idea has been derived

from the 'principle' that diversity begets stability, and diversity usually increases in the course of succession. An important question here is, what does stability actually mean (see e.g. Botkin & Sobel 1975, Connell & Sousa 1983)? If succession is defined as a process at the beginning of which community change is rapid, and which ceases when no major change takes place, stability self-evidently increases during succession (Horn 1974); for a far more critical view see Peters (1976). On the other hand, if stability is defined as the ability to recover from disturbance, it tends to decrease from pioneer to climax, as is pertinently said by Horn (1974). "Disturb early succession and it becomes early succession. Disturb a climax community and it becomes an early successional stage that takes a long time to return to climax" (see also Głowaciński's (1981) introduction to the problem).

Noon et al. (1985) put forward an idea that bird communities in habitats with a simple vegetation structure (e.g. open habitats) could be less stable than those in more complex environments (e.g. forests) (see e.g. Wiens & Rotenberry 1980 and Noon et al. 1985 and references therein). This idea may be applied to forest succession, as the complexity of vegetation increases with increasing forest age, at least to the subclimax phase (e.g. Margalef 1968).

We have censused breeding bird communities in different phases of secondary forest succession near the Arctic circle in northern Finland. Our objective here is to compare the stability of bird communities in these habitats. The species diversity of bird communities does not increase steadily during forest succession in our study area, but is highest in the early stages of succession and again in climax (Helle 1985a, 1985b). Therefore, if diversity creates stability, we predict that the bird communities of young and old forest phases are more stable than those in stands of median age. The other purpose of this study is to assess the population variability among individual bird species.

2. Material and methods

2.1. Study area and bird censuses

Our study area lies in northern Finland some 20 km south of the Arctic Circle in the Oulanka National Park and its nearby areas (approx. 66°N, 29°E). The area has been thoroughly described in other papers (Helle 1984, 1985a). Four different phases of secondary forest succession were studied:

A: Clear-felling, about 5–8 years old (censused 1982-85);
B: Seedling stand, clear-felled some 25–30 years earlier (censused 1980–85);
C: Mixed young stand, cutting and/or burning about 70 years earlier (censused 1981–83, 1985).
D: Old conifer forest, age at least 150 years (censused 1980–85).

The succession stages roughly correspond to age classes I, III, IV and V in Helle (1985a) in the same area. The stages studied in this paper do not, however, form a proper succession series, as the study areas of stages A–C are in more productive sites than those of D. In stage A there is no tree or shrub layer; B is dominated by birch and pine seedlings some 3–5 metres high; spruce, pine, birch and aspen form the mixed stand of stage C; climax forest (D) includes old, pure pine and spruce stands. The studied stages are not, of course, entirely homogeneous: there are scattered trees (mainly dead hardwoods) in clear cuts, while small treeless areas can be found in forest proper (caused by storms or forest fires). Our study area is very sparsely populated and the distance between the census routes and human habitation is usually several kilometres.

Birds censusing was carried out using the Finnish line transect method (Järvinen & Väisänen 1977, 1983). Observations made inside a belt of 25 m either side of a walking line form the main belt data; all observations, irrespective of their distance, form the survey belt data. In this study we use the survey belt data only, to provide adequate samples. Pair densities are calculated using the species-specific coefficients of detectability calculated by Järvinen & Väisänen (1983) for northern Finland. For each species we tested whether our main belt/supplementary belt ratio (supplementary belt = survey belt − main belt) differed from the figures from which the coefficients are derived, as recommended by Järvinen & Väisänen (1983, p.98). For five species our main belt percentage was significantly ($P<0.05$) higher than in the data of Järvinen & Väisänen (1983). This difference is probably due to differences in average habitat structure between the two studies. The following new coefficients were calculated and used in further calculations: *Numenius phaeopus* 1.544, *Tringa nebularia* 1.696, *Motacilla flava* 8.793, *Phylloscopus trochilus* 3.266 and *Corvus corone* 1.367.

Each stage had two separate transect lines. These were exactly the same in each study year in phase A, C and D, while in B about 20% of the routes varied slightly. Using the survey belt data in this kind of study creates a problem, as a proportion of the distant observations comes from a "wrong" habitat. However, as the habitat patches studied are large (at least 30 ha) and uniform, we consider this effect to be of minor importance, if not negligible.

2.2 Stability measurements

Stability is here understood as in Järvinen's (1979) study: a community is the more stable the less its properties (e.g. density, diversity, densities of individual species) vary from year to year. To measure stability we selected the following five criteria from those used by Järvinen (1979) and Noon et al. (1985); these seem to be the least sensitive to random variation (note our modification in index 2):

1) Coefficient of variation ($CV\%$) in bird density, $CV(D)$; the standard deviation of the densities of different study years divided by their average density multiplied by 100;

2) $CV(\%)$ of number of species, $CV(S')$; the observed number of species is not used, as this is heavily affected by sample size; as a sample size free measure of species richness the expected number of species in a random sample of 93 pairs is used (rarefaction method, James & Rathbun 1981; 93 pairs is the smallest sample in the data).

3) $CV(\%)$ of species diversity, $CV(H')$; the sample size corrected Shannon's index is used (Hutcheson 1970);

4) $CV(\%)$ of evenness of species-abundance distribution, $DV(J')$; evenness is calculated as $J' = H'/\ln S$ (S = the number of species);

5) Average individual turnover, IT; the average of the index rD calculated from the consecutive years' data. $rD = 100 \ (\exp DIV_{diff} - 1)$, where the term $DIV_{diff} = H'_{1+2} - 0.5(H'_1 + H'_2)$; H'_1 and H'_2 are the species diversities of consecutive years (1 and 2), H'_{1+2} the species diversity value for the pooled data of these years.

The index values increase with increasing instability and should thus be called "instability indices'. However, to avoid confusion when comparing the results with earlier studies we have not relinquished the practice of calling them stability indices.

In computing the index IT we used successive years' data only (in stage C not all the study years were successive) to avoid bias included in the census internal (see e.g.

Table 1. Lengths of transects (km), the number of species and pairs observed and average census dates (in June) in the studied forest succession stages in Northeastern Finland.

Stage	1980	1981	1982	1983	1984	1985	Total
Clear cut							
length			6.6	6.6	6.6	6.6	26.4
species			24	28	26	25	40
pairs			127	138	129	124	518
date			27	30	18	24	
Seedling stand							
length	11.0	11.0	10.0	10.3	7.9	7.9	58.1
species	22	20	22	36	30	24	53
pairs	173	120	186	263	175	169	1086
date	23	19	25	30	19	25	
Young mixed forest							
length		8.0	8.0	8.0		8.0	32.0
species		28	25	28		30	42
pairs		199	217	230		130	776
date		22	20	29		17	
Climax conifer forest							
length	11.1	11.1	11.1	11.1	11.1	11.1	66.6
species	22	19	23	36	33	24	47
pairs	93	164	153	214	232	136	992
date	23	24	18	20	17	24	

Diamond & May 1977). As stages A and C have been censused in four, but B and D in six, seasons, we could not compare the whole periods without reservation. The correlation coefficients between all the study years and shared study years (when all the stages have been studied) concerning density, species diversity and evenness were 0.946, 0.973, 0.964, respectively (critical value for $P<0.05$ is 0.950 ($N=4$)). The high correlations support the use of the whole data; this, of course, makes the data base broader.

It has been suggested that logarithmically transformed data should be preferred in studying population or community variability (e.g. Williamson 1972). We did not follow this recommendation, however. The transformation should have been done here from $N+1$ bird pairs, because many species have not been observed every year in a given succession phase. The proportion of these nil-observations is so high that it is unclear whether or not the transformation would have improved the quality of the data.

3. Characteristics of bird communities studied

Table 1 presents the observed numbers of pairs and species as well as the lengths of transects by succession stages and by years. The whole material comprises 183.1 km of transect line, 3372 bird pairs and 73 species. The primary data are included in the Appendix.

Instead of a thorough community analysis here, we record only the main characteristics of the bird communities studied. The average bird density, species diversity and evenness for each community are depicted in Table 2. Table 3 shows the average densities and proportions of sedentary species, short-distance migrants and long-distance migrants in these communities.

Succession stage A (clear cuts) is dominated by typical open habitat species, the two most numerous being *Motacilla flava* and *Anthus pratensis*. In seedling stands (B) the open habitat species still occur but forest species are already abundant, *M. flava* and *Phylloscopus trochilus* being the most frequent. The forest stages (C and D) are dominated by typical forest species *Ph. trochilus*, *Fringilla montifringilla* and *F. coelebs* (see Appendix).

4. Stability of communities and populations

The stability indices do not reveal a consistent pattern in bird community stability in the age gradient studied (Fig. 1, Table 2). The indices $CV(D)$ and $CV(S')$ show stage A to be clearly more stable than the other stages, which do not differ from each other. According to diversity-based indices — $CV(H')$ and $CV(J')$ — the ends of the studied gradient — clear-felling and climax forest — are more stable than the successional phases between them (B and C). The index IT is relatively constant among different stages. In order to reduce the information from the five indices (Table 2) to a single figure, each successional stage was ranked from one (lowest index value) to four (highest index value) within each index, and these rank points then summed. This procedure shows stage A to be the most stable:
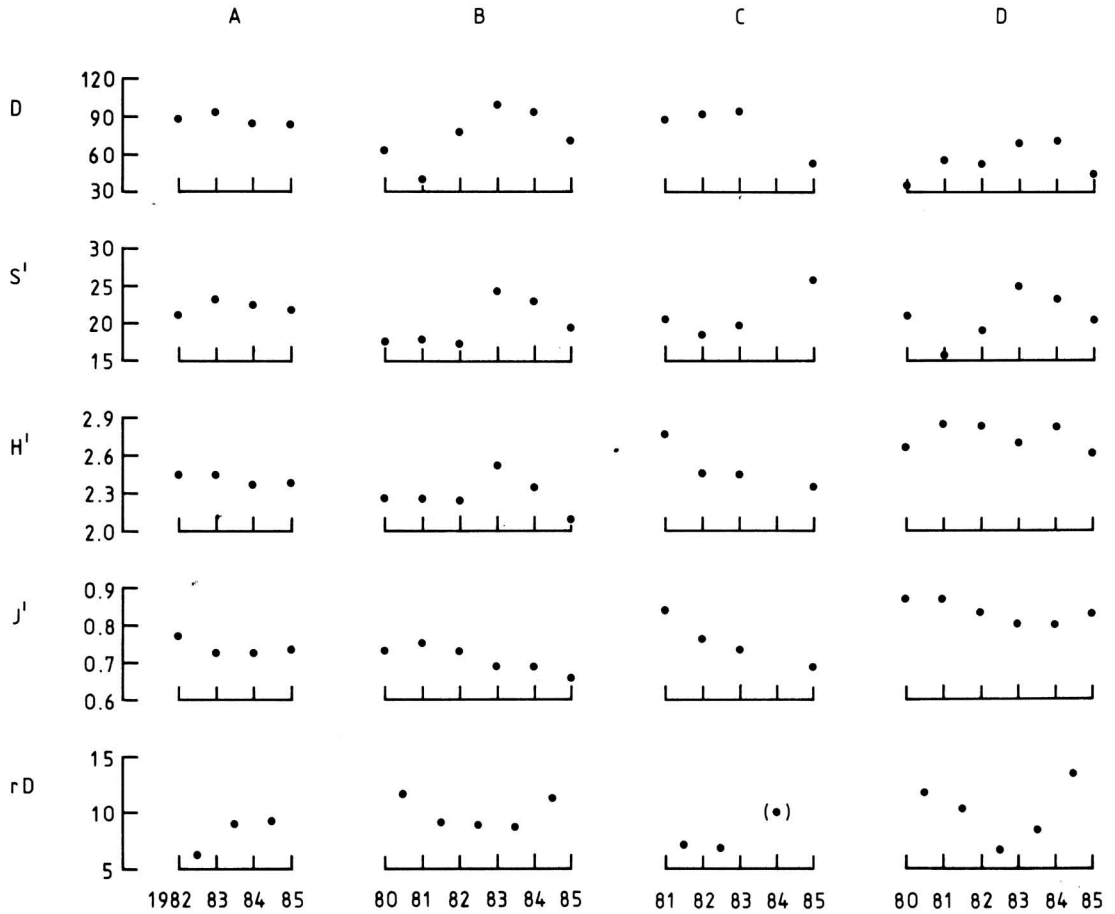
A 5   B 13   C 16   D 13

Fig. 1. Pair density (D), number of species (S'), species diversity (H') and the evenness component of diversity (J') observed in study years in different phases of forest succession (A−D); rD indicates the difference in community composition between consecutive years (see Sect. 2.2. for detailed definitions of the parameters). A: clear cut, B: seedling stand, C: young mixed forest, D: climax conifer forest.

The three other stages have similar values, stage C being only slightly less stable than B and D.

The stability indices are not heavily correlated. Of the 10 mutual correlations between them, one is significant ($CV(D)$ vs. $CV(S')+0.976$, $P<0.05$) and one nearly significant ($CV(H')$ vs. $CV(J')+0.947$, $P<0.1$). The indices need not be strongly correlated, they can reflect different aspects of stability. A detailed study of the mutual correlations shows that the indices form three groups: 1) $CV(D)$, $CV(S')$, 2) $CV(H')$, $CV(J')$, 3) IT. This accords with the finding of Noon et al. (1985) that the indices (they had nine altogether) tend to form

Table 2. Average pair density (pairs/km^2), species diversity (H'), evenness (J') and the values of stability indices used (defined in the text) in the forest successional stages studied.

	Clear cut	Seedling stand	Young mixed	Climax conifer
Pair density	86	75	81	54
Species diversity	2.41	2.29	2.50	2.74
Evenness	0.74	0.71	0.76	0.83
Stability indices:				
$CV(D)$	6.1	28.6	25.0	28.6
$CV(S')$	5.1	15.4	16.1	15.4
$CV(H')$	1.6	5.3	7.4	3.7
$CV(J')$	2.6	4.6	8.4	4.0
IT	7.8	9.6	8.5	10.1

Fig. 2. Relationship between average pair density (pairs/km^2) and coefficient of variation in pair density in sedentary species and partial migrants (lower case letters), short-distance migrants (capitals) and long-distance migrants (letters in squares); see text for details. Symbols refer to studied successional phases: A: clear cut, B: seedling stand, C: young mixed forest, D: climax conifer forest. A least square regression line is shown.
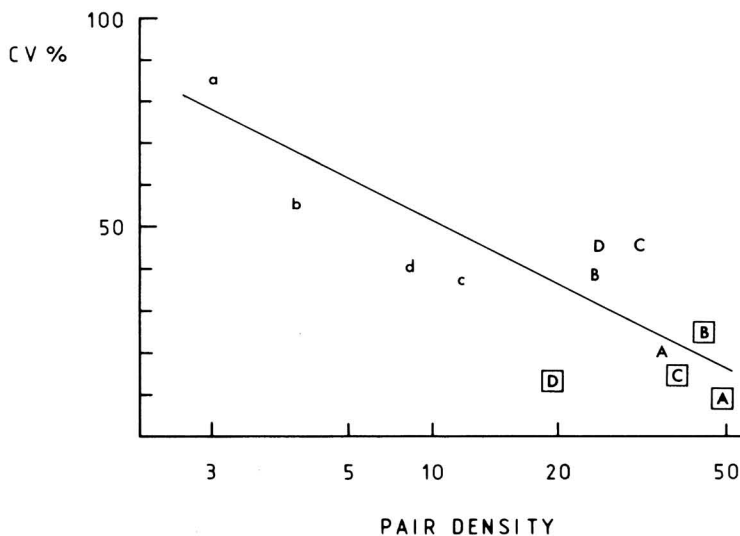
three groups, reflecting density variation, diversity variation, and community compositional stability (see also Järvinen 1979).

Long-distance migrants seem to be more stable (as a group) than short-distance migrants or sedentary species (Fig. 2). This kind of conclusion has to be qualified, however, because the lower the density (or the smaller the sample) the greater the relative density variation caused by chance. Thus, the comparison of the species groups should be made by using the regression line calculated for the points as reference (Fig. 2), which may be taken as the average amount of stochastic variation. After this correction the differences between the species groups are minor, the short-distance migrants being slightly more variable than long-distance migrants or sedentary species.

When assessing the population variability of individual species in different phases of succession it is reasonable to restrict the study to the most abundant species to avoid inadequate samples. The correlation between the average

density and coefficient of variation in densities in different successional stages is negative for all of the most abundant species (Table 4). As already stated, this kind of result is expected to be caused by chance as well. The easiest way to avoid the effect of sampling variance on the correlation between the average density and variability is to remove the effect of sample size with the partial correlation technique. We found this method problematic here, however, because the correlation between sample size and density is quite close to unit in the most numerous species of our data; thus these two variables (sample size and density) are "indistinguishable'.

It would appear to be a safe assumption that the densities of species populations behave as a Poisson variate (e.g. Svensson et al. 1984), which means that there is a certain amount of stochastic variation in local densities (increasing with decreasing density), although the source population is stable from year to year. If this assumption is correct the variance

Table 3. Average densities (D, pairs/km^2) and proportions (%) of sedentary species (including partial migrants), short-distance migrants (wintering areas mainly in Europe) and long-distance migrants (wintering grounds mainly in Africa) in the forest succession stages studied. The division is based on Väisänen (1984) and completed by data from von Haartman et al. (1963–72).

| | Clear cut | | Seedling stand | | Young mixed | | Climax conifer | |
	D	%	D	%	D	%	D	%
Sedentary species	3.0	3.5	4.6	6.2	12.3	15.1	8.9	16.6
Short-distance migrants	34.8	40.2	24.9	33.2	30.8	37.8	25.9	48.2
Long-distance migrants	48.7	56.3	45.4	60.6	38.3	47.1	18.9	35.2

Table 4. Average density (D, pairs/km^2) and year-to-year variation ($CV(\%)$) among the most numerous species in the data having been observed in all the successional stages studied. Coefficients of correlation between average density (log transformed) and year-to-year variation are given (r value for $P<0.05$ is 0.950, $N=4$). CV_{exp} indicates the coefficient of variation which is expected to be caused by chance, i.e. assuming that the densities of the species in different years behave as a Poisson variable (see also text).

	Clear cut			Seedling stand			Young mixed			Climax conifer			
	D	CV	CV_{exp}	D	CV	CV_{exp}	D	CV	CV_{exp}	D	CV	CV_{exp}	r
Phylloscopus trochilus	10.0	31.1	22.2	20.0	26.1	14.2	22.7	23.3	13.4	3.9	57.0	27.4	−0.966
Fringilla montifringilla	5.6	44.4	29.8	4.0	71.1	31.1	13.1	35.7	17.7	11.7	46.3	15.9	−0.810
Turdus iliacus	4.9	42.1	35.4	11.8	55.5	20.7	4.7	62.0	32.9	0.9	84.3	65.5	−0.478
Anthus trivialis	1.9	70.3	48.5	2.7	58.5	37.5	5.9	23.9	25.4	3.0	23.7	30.4	−0.798
Phoenicurus phoenicurus	1.0	75.9	66.7	0.6	106.5	73.5	1.3	59.5	53.5	2.6	49.7	32.6	−0.941
Carduelis flammea	0.5	151.4	89.4	1.4	83.3	51.2	2.8	64.5	35.4	1.0	109.9	49.0	−0.979
C. spinus	0.2	115.5	141.4	0.4	116.8	88.3	2.7	77.1	32.4	1.4	72.5	38.3	−0.918
Loxia curvir/pytyops	0.9	73.4	51.6	0.4	125.1	62.8	1.1	67.2	42.6	0.6	80.4	47.1	−0.925
Cuculus canorus	0.3	42.6	66.7	0.2	76.4	65.7	0.5	36.0	45.9	0.4	44.3	46.3	−0.906
Tringa glareola	2.9	42.2	43.6	1.3	87.2	59.4	0.2	115.5	141.4	0.4	113.9	92.6	−0.938

of the densities of a species in different years should equal its average density. Following this method we calculated the expected values for coefficients of variation using the formula $CV(\%)_{exp} = 100 \ \bar{x}^{-0.5}$), where $\bar{x}$ is the average number of pairs observed in study years (Table 4). The ratio "observed variation per expected variation' can then be used for comparing the population variability among the most numerous species (Fig. 3). *Fringilla montifringilla* and *Carduelis flammea* show the highest population variability, whilst *Cuculus canorus* and *Tringa glareola* seem to have the most stable population densities of the species studied. Interestingly, after eliminating the effect of sampling variance, there is a nearly significant, positive correlation between the amount of variation and average density of species ($r= +0.624$, $P<0.1$).

5. Discussion

The values of stability indices obtained here agree roughly with those reported by Järvinen & Väisänen (1976) for several northern European land bird communities. A detailed comparison between this study and earlier contributions is, however, beyond our present interest. Below, we try to explain our results on bird community stability, which were not in accordance with the classic theory of succession (see Introduction).

Firstly, one methodological point deserves mention. When studying bird community stability in the context of succession, it is preferable to separate community changes caused

by succession (which are directional) and those caused by stochasticity (which are non-directional), as was stressed by Głowaciński (1981) (for a discussion on a similar problem, see also Helle & Mönkkönen 1985). The importance of this aspect can be exemplified as follows. We have censused birds at a given site in consecutive years and calculated coefficients of variation to measure bird community variation. It is possible, for example, that total bird density has increased evenly in that area within the study period, and the $CV(\%)$ perhaps suggests considerable density variation. This would lead to an incorrect interpretation, however. If the increasing trend in bird density is exactly linear, the result should be interpreted so that there is a marked successional trend but no stochastic variation. Głowaciński (1981) introduced a method to estimate the significance of these two components: if there is a successional trend in any parameter used to describe community stability, it is removed and the residuals are then used to measure the amount of stochastic variation (random fluctuations) in a community. Fig. 1 shows that in our data the problem is not serious: the year-to-year change in any stability index is not directional but more or less fluctuating. Hence, we did not adopt the Głowacińskian approach, but used the index $CV(\%)$ instead.

5.1 Stability vs. diversity and habitat productivity

Three explanations are generally used to account for differences in community stability:

Fig. 3. Relationship between the observed vs. expected density variation and average density among the ten most abundant species of the data. Expected values are calculated assuming that the densities of species vary as a Poisson variate, the variance of the densities equalling their mean (see also text). Species explanations:

1 — *Phylloscopus trochilus*
2 — *Fringilla montifringilla*
3 — *Turdus iliacus*
4 — *Anthus trivialis*
5 — *Phoenicurus phoenicurus*
6 — *Carduelis flammea*
7 — *C. spinus*
8 — *Loxia curvirostra/ pytyopsittacus*
9 — *Cuculus canorus*
10 — *Tringa glareola*
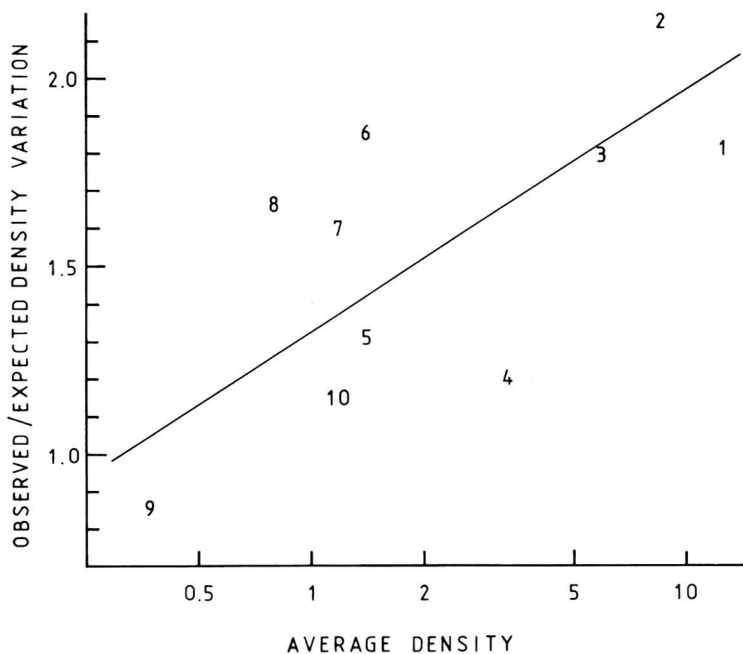
community stability will increase with 1) increasing diversity, 2) increasing productivity and 3) increasing climatic predictability (for an explicit review of these hypotheses see Järvinen (1979)). The last explanation seems to be the most important as regards the geographical variation in stability in Europe (Järvinen 1979, A. Järvinen 1983), but it is outside the present discussion, because our succession stages lie in a very restricted area hardly differing in their predictability of weather conditions (for such a case see Stenseth et al. 1979).

The productivity hypothesis states that stability increases with habitat productivity, since more species have their density maxima in highly productive habitats than in poorly productive ones; in optimum habitats, territories are occupied annually (or nearly so), and population fluctuations are therefore minor, whereas suboptimal or marginal habitats have larger annual fluctuations (e.g. Enemar 1966, Fretwell & Lucas 1971, v. Haartman 1971). To test this explanation we calculated the correlations between the stability indices and average pair densities of different succession stages (which reflect the productivity of a habitat). Negative correlations are expected, if the hypothesis holds true. The test does not support the explanation (Table 5): three out of five are

negative, two positive, although none are statistically significant.

According to the diversity hypothesis, community stability increases with the number of species (e.g. MacArthur 1955, Goodman 1975; see however May 1973), because in a species-rich community a change in a species' population is more easily compensated by other species than in a species-poor community. One test of this hypothesis is to correlate the stability index values with the species diversities of different successional stages. If the hypothesis holds true, negative correlations should dominate. This is not the case, rather the contrary is true (see Table 5); all the correlations are far from significant.

Another test of this explanation is to assess whether the year-to-year changes in species

Table 5. Correlations between the stability indices (see text) and the average species diversity (H'), pair density (D) and sample size (N) in the successional stages studied. The critical value for $P<0.05$ is $r=0.950$ ($N=4$).

	$CV(D)$	$CV(S')$	$CV(H')$	$CV(J')$	IT
H'	0.268	0.260	−0.073	0.034	0.418
D	−0.651	−0.533	0.023	0.144	−0.897
N	0.840	0.924	0.971	0.859	0.051

populations compensate for each other or whether they take place in parallel. If the diversity hypothesis is correct, compensatory fluctuations should be more important. We analysed the data using the method introduced by Pielou (1972) (see also Schluter 1984): if the species fluctuate entirely independently of each other, the sum of the variances of species' densities is equal to the variance of annual total densities; if this ratio is below one, parallel fluctuations are stronger than compensating ones, and if the ratio exceeds one, compensating changes dominate. The computed figures show that in stage A compensating population changes are important, whereas they are clearly not in stages B−D:

A 2.45　　B 0.39　　C 0.28　　D 0.28

All the figures deviate significantly ($P<0.05$) from one, that is, from the situation which is expected to be caused by chance (see Schluter 1984 for the details of the test). The ratios above closely fit the patterns observed in $CV(D)$ and $CV(S')$ (Table 2): stage A was found to be the most stable successional stage, and it is the only stage showing compensating population fluctuations as being important. The high figure obtained for successional stage A may emerge from interspecific interactions such as competition, but compensating population fluctuations may arise from other causes, too. One possible explanation is that vegetation succession in successional phase A is rapid and different species are favoured in different years because of this succession.

5.2 Other factors affecting stability and stability indices

Several studies have indicated that northern European populations of long-distance migrants are more stable than those of short-distance migrants (e.g. Svensson 1977, Solonen 1981, Fig. 1; see, however, Berthold & Querner 1979). Noon et al. (1985) have reported a negative correlation between the proportion of long-distance migrants and diversity variation in North American land bird communities; they suggest that the long-distance migrants might "buffer' bird communities against large year-to-year diversity variation. In order to assess the role of the migratory groups distinguished (sedentary species, short-distance migrants, long-distance migrants, see Sect. 3) from the point of view of community stability

we correlated the stability index values of different successional stages with the respective average pair densities of these species groups. One of the 15 correlations (three species groups, five indices) is significant: the density of short-distance migrants vs. IT ($r=0.956$, $P<0.05$). This suggests that they are short-distance, rather than long-distance, migrants which are of major importance to bird community stability. It has to be stressed, however, that every fifteenth correlation is fairly easily significant due to random variation only.

As the samples for our data (per year per stage) are not large, the possibility that the results respecting stability are affected by chance has to be assessed. If this effect is important we would expect successional stages with the smallest samples to have the highest values for stability indices, and *vice versa*. As shown in Table 5, this effect is not important: in fact, all five correlations are positive, with one significant one! The test is only partially satisfactory, since the size of samples *per se* is inevitably not the most effective factor, but rather the size of sample in relation to the diversity of bird communities. We were not able to construct such a test, however.

Järvinen & Lokki (1978) presented a method of estimating the variance in pair numbers caused by the incompleteness of one-visit censuses. They assumed a one-visit census to be a binomial process and the census efficiency of all the species about the same (not far from 0.5). The expected CV% in pair density in the studied successional stages calculated according to the formula given by Järvinen & Lokki (1978 p.89) are as follows:

A 7.2　　B 6.1　　C 5.9　　D 6.4

The observed density variation in clear cuts ($CV(\%)$ 6.1, Table 2) nearly equals that expected (7.2%), indicating that the observed variation may be sampling variance only. In the other successional phases (B−D), on the other hand, the observed coefficients of variation are about 4.5 times larger (see Table 2) than those expected on the grounds of one-visit sampling variance (above), i.e. the year-to-year changes are "real". As to the other stability indices used, the sampling variance cannot be estimated.

5.3 Population variability among individual species

Our first result, a negative correlation between average population density and popula-

tion variability (Table 4) seemed to agree well with the idea that species occupy optimum habitats (where densities are high) more regularly than marginal ones (where densities are low) (for references see Sect. 5.1., Hildén 1965). However, differences in sample size explained most of this pattern supporting the importance of scale in ecological studies (see e.g. Wiens 1981). It should be noticed that chance works in the present data, in principle at least, at two levels: firstly, there is the sampling variance of the one-visit census technique (all the birds in a given area are not observed, see e.g. Järvinen 1978, Järvinen et al. 1978, Hildén 1981), and secondly, there is the "natural' stochasticity of populations. The latter is demonstrated by the checkerboard model of Wiens (1981).

In Section 4 we assumed that census samples behave as a Poisson variable and we presented the expected amount of variation for the most numerous species (Table 4). The mean ratios for observed vs. expected population variability in different successional stages studied (A−D) are 1.22, 1.74, 1.51 and 1.66, respectively (the difference between stages A and B is significant, $P<0.05$, t-test). The population variations observed are on average 1.5 times larger than the expected ones. It should be stressed that the variance caused by one-visit sampling should be added to the expectations before we can obtain a figure for true population variation. Järvinen & Lokki (1978) showed that if censusing is assumed to be a binomial process (which seems to be a safe assumption), the variance is then $p(1-p)N$, where p is the probability of detecting and N number of pairs. Based on this formula and the known efficiency of one-visit censusing (e.g. Järvinen 1978) the expected variance is about 1.3 (Poissonian and sampling variance together). This approach requires so many assumptions, however, that a more detailed analysis is not justified.

Finally, we offer an example which demonstrates the importance of scale (associated with the sample size problem) in the study of population processes; this view has been particularly stressed by Wiens (1981). The density variation $CV(\%)$ of the most abundant species of the data, *Phylloscopus trochilus*, is the following in different successional stages: A 31.1, B 26.1, C 23.3 and D 57.0. These figures are based on equal areas studied for each stage. What will the density variations amount to, if they were calculated, not per unit area, but per unit

sample size? If the average sample size per year is the same in every succession stage (concerning *P. trochilus*) the lengths of the transects should be A 4.3, B 2.2, C 1.9, and D 11.1 km (per season). We checked from our original notes these distances and counted the numbers of pairs observed and their variation. The "sample size free density variation' $CV(\%)$ for the studied successional stages are as follows: A 51.5, B 52.2, C 60.6 and D 57.0. These figures equate well with each other compared to those obtained earlier (calculated per unit area). This empiric sample size standardization stresses the utmost importance of sample size (or population density or area size) in the study of annual fluctuations.

6. Concluding remarks

The result obtained on the stability of bird communities during forest succession does not agree with the traditional view. Although we showed that the sample size *per se* is not an important factor contributing to the result (on a community level), the samples are quite naturally "noisy". The index IT, which measures the compositional stability of a community, is very useful in a successional context (see Głowaciński & Järvinen 1975), since the community change during succession is one of the most steady features of succession (e.g. Christiansen & Peet 1984). The IT values, however, were not in accordance with the theory, but were relatively constant among the successional stages. This might mean that they reflect nothing but "noise' (or pseudo-turnover, see Helle & Mönkkönen 1985). We also have an alternative explanation. Bird communities of old forest may have been more stable than those in other forested habitats, but since continuous forests have been heavily fragmented by intensive forestry in the last few decades (e.g. Järvinen et al. 1977, Helle 1985c), the fragments of primeval forest no longer support their original stable bird community, but reflect the same changes in bird populations as in the surrounding large areas of secondary vegetation (see also Väisänen et al. 1986). Whitcomb et al. (1977) suggested that forest fragmentation in North America may have increased turnover rates in bird communities. We do not have adequate data to test this hypothesis, but it seems to be a promising topic for further studies.

Finally, there is one important question of

principle left. The stability of the bird community of a clear-felling was observed to be highest among the successional phases studied. Clear cut is a very artificial phase of forest succession, however: it includes unnaturally sparse vegetation and it is often heavily ploughed in our study area. A natural beginning of forest succession, after a forest fire or storm, is probably never so bare. Does our stage A belong to *forest succession* at all, as it is mainly occupied by species of *open habitats* (mires, shores, meadows etc.)? If the clear cut is excluded from our succession series, the result is not, however, in accordance with the general

theory of succession, which was supported by Głowaciński (1981) in his study on deciduous forest succession in Central Europe. Interestingly, clear cut showed, in some stability parameters, greater stability than a 7−11 year old thicket also in Głowaciński's (1981) data.

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Appendix. Primary data of bird censuses in different stages of forest succession in Kuusamo, northeastern Finland in 1980—85. The average densities (D, pairs/km^2) of the species are given for each successional phase; the figure 0.0 indicates densities below 0.05 pairs/km^2. See text for details.

	Clear cut					Seedling stand							Young mixed forest					Climax conifer forest						
	82	83	84	85	D	80	81	82	83	84	85	D	81	82	83	85	D	80	81	82	83	84	85	D
Buteo buteo	0	1	0	0	0.1	0	0	0	1	0	0	0.0	0	0	0	0		1	0	0	0	0	0	0.0
B. lagopus	0	0	2	0	0.1	0	0	0	0	0	0		0	0	0	0		0	0	0	0	0	0	
Falco tinnunculus	0	0	1	1	0.1	1	0	0	1	0	0	0.0	0	0	0	0		0·	0	0	0	0	0	
F. columbarius	0	0	0	0		0	0	1	0	0	0	0.0	0	0	0	0		0	0	0	0	0	0	
Bonasa bonasia	0	0	0	0		0	0	0	0	0	0		3	1	0	0	1.6	1	2	1	2	1	1	1.5
Lagopus lagopus	0	0	0	0		1	0	0	0	1	0	0.5	0	0	0	0		0	0	0	0	0	0	
Tetrao tetrix	0	1	1	0	0.3	3	2	0	0	0	0	0.3	0	0	0	0		0	0	0	0	0	0	
T. urogallus	0	0	0	0		0	0	0	1	0	0	0.3	0	0	0	0		0	0	0	0	1	0	0.3
Grus grus	0	1	0	0	0.0	0	0·	0	1	0	0	0.0	0	0	0	0		0	0	0	0	0	0	
Pluvialis apricaria	0	0	1	1	0.3	0	0	0	0	0	0		0	0	0	0		0	0	0	0	0	0	
Vanellus vanellus	0	1	1	1	0.4	0	0	0	0	0	0		0	0	0	0		0	0	0	0	0	0	
Gallinago gallinago	6	6	4	4	1.6	3	0	0	1	0	1	0.2	0	0	0	1	0.1	0	0	0	0	0	0	
Numenius phaeopus	2	2	1	1	0.4	2	4	2	4	4	1	0.5	0	0	0	0		0	0	0	0	0	0	
N. arquata	0	0	2	0	0.1	0	0	0	0	0	0		0	0	0	0		0	0	0	0	0	0	
Tringa nebularia	2	1	3	5	0.7	0	1	2	4	1	4	0.4	0	0	0	0		0	0	0	0	0	0	
T. ochropus	0	0	0	0		0	0	0	0	0	0		2	1	1	1	0.6	1	0	0	3	3	0	0.4
T. glareola	4	6	3	8	2.9	0	2	1	6	5	6	1.3	0	0	1	1	0.2	0	0	0	2	3	2	0.4
Actitis hypoleucos	1	2	2	0	0.8	0	0	0	0	0	0		0	0	0	0		0	0	0	0	0	0	
Cuculus canorus	2	1	3	3	0.3	5	0	1	2	4	4	0.2	5	3	7	4	0.5	2	7	3	7	5	4	0.4
Surnia ulula	0	2	0	0	0.5	0	0	0	0	0	0		0	0	1	0	0.2	0	0	0	0	0	0	
Asio flammeus	0	0	0	0		0	1	0	2	0	0	0.2	0	0	0	0		0	0	0	0	0	0	
Apus apus	0	0	0	1	0.0	0	0	0	1	0	0	0.0	0	2	0	0	0.0	0	1	0	0	0	0	0.0
Jynx torquilla	0	0	0	0		0	0	0	0	0	0		1	0	0	1	0.1	0	0	0	0	0	0	
Dryocopus martius	0	0	0	0		0	0	0	1	0	0	0.0	0	0	0	0		0	0	1	1	0	1	0.0
Dendrocopos major	0	0	0	0		0	0	0	0	1	2	0.3	1	0	0	0	0.2	0	0	1	0	1	1	0.2
Hirundo rustica	0	0	0	0		0	0	0	1	0	0	0.0	0	0	0	0		0	0	0	0	0	0	
Anthus trivialis	5	1	3	8	1.9	2	6	10	17	6	10	2.7	18	19	14	11	5.9	10	16	10	9	10	10	3.0
A. pratensis	26	26	20	16	17.1	21	5	16	9	3	1	4.9	0	0	0	0		0	0	0	0	1	0	0.1
Motacilla flava	15	17	15	18	21.6	14	6	12	21	23	6	12.4	0	0	0	0		0	0	0	0	0	0	0.1

	Clear cut					Seedling stand							Young mixed forest					Climax conifer forest						
	82	83	84	85	D	80	81	82	83	84	85	D	81	82	83	85	D	80	81	82	83	84	85	D
M. alba	4	0	2	0	1.5	1	0	3	2	0	0	0.7	0	0	0	0		0	1	0	0	0	0	0.1
Bombycilla garrulus	0	1	0	0	0.1	0	0	0	2	2	0	0.2	0	0	0	0		0	0	0	0	2	0	0.1
Erithacus rubecula	0	0	0	0		0	0	0	0	0	0		7	6	3	1	2.3	6	7	3	16	13	7	3.4
Luscinia svecica	0	0	0	0		0	0	0	0	0	0		0	0	0	1	0.2	0	0	0	0	0	0	
Phoenicurus phoenicurus	2	0	3	4	1.0	0	0	1	3	5	3	0.6	3	4	6	1	1.3	9	9	5	8	19	8	2.6
Saxicola rubetra	9	6	11	2	4.8	14	6	9	4	1	1	2.8	0	0	0	0		0	0	0	0	0	0	
Oenanthe oenanthe	5	4	0	4	3.2	7	0	8	1	0	0	1.8	0	0	0	0		0	0	0	0	0	0	
Turdus pilaris	0	1	0	2	0.5	0	0	0	0	1	0	0.1	0	0	0	1	0.1	0	0	1	0	2	0	0.2
T. philomelos	0	0	1	0	0.1	0	0	0	2	1	1	0.1	3	4	2	4	0.7	5	8	4	7	24	6	1.5
T. iliacus	9	12	7	4	4.9	13	14	40	52	32	17	11.8	12	10	14	1	4.7	1	3	4	1	5	0	0.9
T. viscivorus	0	0	0	1	0.1	0	0	0	0	0	1	0.0	0	1	1	1	0.3	0	1	1	2	0	1	0.2
Sylvia curruca	0	0	0	0		0	0	0	0	0	1	0.1	0	0	0	0		0	0	0	0	0	0	
S. communis	0	0	0	0		0	0	0	0	0	0		0	0	0	0		0	0	0	0	1	0	0.1
S. borin	0	0	0	0		0	3	0	0	0	4	0.3	1	0	1	1	0.2	0	1	0	0	0	0	0.0
Phylloscopus borealis	0	0	0	0		0	0	0	0	0	0		0	0	0	0		0	0	1	0	0	0	0.1
Ph. sibilatrix	0	0	0	0		0	0	0	0	0	0		0	0	0	0		0	0	0	0	1	0	0.0
Ph. collybita	0	0	0	0		0	0	0	0	1	0	0.0	2	5	4	0	0.8	5	3	4	3	2	3	0.7
Ph. trochilus	11	22	23	25	10.0	57	50	58	72	47	72	20.0	41	60	71	50	22.7	5	18	21	19	3	14	3.9
Regulus regulus	0	0	0	0		0	0	0	0	0	0		2	0	0	0	0.5	0	1	2	1	1	2	0.8
Muscicapa striata	0	0	0	0		1	0	0	0	1	0	0.3	5	4	2	2	3.5	3	5	4	7	6	1	3.3
Ficedula hypoleuca	0	0	0	0		0	0	0	0	1	0	0.1	2	2	1	0	0.7	3	6	4	4	2	4	1.5
Parus montanus	0	0	0	0		0	0	0	0	0	0		2	0	4	2	1.9	0	1	1	2	2	0	0.7
P. cinctus	0	0	0	0		0	0	0	0	0	0		1	0	0	0	0.3	0	0	0	1	1	2	0.7
P. cristatus	0	0	0	0		0	0	0	0	0	0	0.0	0	0	1	0	0.3	0	3	0	0	0	0	0.5
P. major	0	0	0	0		0	1	0	0	1	0	0.2	1	0	0	3	0.6	0	1	2	2	1	4	0.7
Certhia familiaris	0	0	0	0		0	0	0	0	0	0		0	1	0	0	0.3	0	2	0	0	1	0	0.5
Lanius excubitor	1	2	0	1	0.7	0	0	0	1	0	0	0.1	0	0	0	0		0	0	0	0	0	0	
Perisoreus infaustus	0	0	0	1	0.4	0	0	1	0	0	0	0.2	0	1	0	0	0.3	0	0	3	1	0	0	0.7
Pica pica	0	0	0	0		0	0	0	0	0	0		1	0	3	1	0.5	0	0	0	0	0	0	
Corvus corone	0	0	0	0		3	1	1	1	2	2	0.2	2	2	2	2	0.3	1	0	0	1	0	3	0.1
C. corax	1	1	0	1	0.1	0	0	0	1	0	0	0.0	0	0	1	1	0.0	0	0	2	0	0	0	0.0
Fringilla coelebs	0	0	0	0		0	1	3	4	1	2	0.6	14	27	15	1	6.1	10	11	25	21	34	22	6.3
F. montifringilla	15	6	16	8	5.6	1	8	10	18	12	22	4.0	27	40	42	18	13.1	17	32	30	63	60	34	11.7
Carduelis spinus	0	1	1	0	0.2	1	3	0	5	1	0	0.4	17	6	14	1	2.7	3	9	4	10	14	1	1.4
C. flammea	1	4	0	0	0.5	6	7	3	12	2	0	1.4	14	6	10	2	2.8	2	10	2	10	1	0	1.0
Loxia leucoptera	0	0	0	0		0	0	0	0	1	0	0.1	0	0	0	0		0	0	0	0	0	0	
L. curvirostra/ pytyopsittacus	5	7	1	2	0.9	0	0	2	6	6	1	0.4	8	9	4	1	1.1	1	4	8	5	9	0	0.6
Carpodacus erythrinus	1	1	1	0	0.3	1	3	1	1	4	2	0.6	0	0	0	0		0	0	1	1	1	0	0.1
Pinicola enucleator	0	0	0	0		0	0	0	0	1	0	0.2	0	0	0	1	0.3	0	0	0	0	0	0	
Pyrrhula pyrrhula	0	0	0	0		0	0	0	2	0	1	0.2	0	1	2	5	0.8	2	1	2	4	0	1	0.5
Emberiza citrinella	1	0	0	0	0.1	2	0	0	0	0	0	0.1	0	0	1	1	0.2	0	0	0	0	0	0	
E. hortulana	1	0	0	0	0.2	0	1	0	0	0	0	0.1	0	0	0	0		0	0	0	0	0	0	
E. rustica	0	0	0	0		0	0	0	2	0	0	0.4	3	1	0	1	1.7	4	1	3	1	1	3	2.1
E. schoeniclus	2	2	1	2	1.8	3	0	1	2	4	2	1.4	0	1	2	0	0.6	0	0	1	0	1	0	0.2