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## STABILITY IN BIRD COMMUNITIES DURING THE SECONDARY SUCCESSION OF A FOREST ECOSYSTEM\*

**ABSTRACT:** For five phases (FI-FV) of the secondary succession of a deciduous forest the stability (as a constancy and resistance) has been determined of the breeding avifauna in respect of the density ( $N$ ) and species diversity ( $H'$ ). The assessment of total variability (= directional variability of succession + random variability) and random variability (independent of changes related to the trend of succession) indicates that with the progress of secondary succession the stability of birds generally increases, although not in every case is it at its lowest in the initial phase (FI), and not always at its highest in the climax phase (FV).

**KEY WORDS:** Stability, directional and random variability, diversity, abundances, secondary succession, bird communities, deciduous forest, southern Poland.

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### 1. INTRODUCTION

Stability is one of the basic concepts used in ecology which express the state of inner structure and functional properties of biocoenotic units. The term is closely related to the

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ecological equilibrium understood in a broader sense, and to the theory of homeostasis and regulation (Trojan 1978). The problem of dependence of stability on diversity and vice versa is very often considered. However, views on these problems, important from a cognitive and practical point of view, differ very much, being based primarily on theoretical speculations (McNaughton 1977, Collier et al. 1978, Trojan 1978, Ricklefs 1979 and others). Itself the notion of stability is ambiguous (constancy, inertia, elasticity = toleration = resilience, amplitude, persistence = resistance = endurance, cyclic stability, trajectory stability) and has a large number of definitions (Levontin 1969, Margalef 1969, May 1973, Golley 1975, Noy-Meir 1975, Orians 1975, Whittaker 1975 and others). For this reason, one is inclined to adopt a single conventional concept of stability, depending on the aim of a study.

In the present paper stability is interpreted as a constancy of certain structural and functional characteristics of avian communities in different phases of succession. Those communities were regarded to be more stable whose characters showed smaller deviations from the mean values (total variability, or directional + random variability), or the resultant of successional changes (random, or fluctuant variability) in the particular phases of this process. However, random variability informs of a stability understood as a persistence rather than constancy.

The aim of the studies here presented was to demonstrate (1) how the constancy of bird communities changes, with regard to the characteristics chosen, during the different phases of maturation of a deciduous forest, (2) what the fluctuant (random) variability of bird communities is like during this process, (3) what relations there are between the measure of stability of the avifauna and the size (species richness and abundances) and diversity of bird communities.

## 2. STUDY AREA

The studies were carried out in the northern part of Niepołomice Forest (southern Poland), in a complex of deciduous woods known under the name of Grobla (50°06' N and 20°22' E). Dominant in these woods are *Quercus robur* L., *Carpinus betulus* L. and *Alnus glutinosa* L., members of the two chief forest formations found in this area: an oak-hornbeam stand and an alderwood (Denisiuk et al. 1977 and other papers published in *Studia Naturae Ser. A*, Nos. 6, 7 and 8 in the editorial cycle: Nature of the northern part of Niepołomice Forest and its conservation, parts I–III, 1971, 1973, 1975). In spite of the management based on felling and drainage, the natural, or almost natural features of the forest communities have been preserved.

The sample sites were marked out in areas comparable in respect of habitat, but differing in age and spatial structure of the vegetation (Głowaciński 1975).

The physical conditions of the forest area under study are subject to annual changes, often exceeding 10%, and in some cases even 50%, relative to the average state. This has been demonstrated particularly well in relation to the local climate (Klein 1978).

## 3. METHODS

The successional series was studied by direct observation continued for several years simultaneously in five developmental phases of the forest: phase I — a 1–5-year clearing, phase II

— a 7–11-year thicket, phase III — a 15–19-year thicket, phase IV — a wood about 95 years old, and phase V — a wood over 150 years old.

In each phase the birds were censused for a period of at least three consecutive years. In the general assessment of instability, censuses of four-year periods have been presented separately, in most cases separated by a one-year pause (see Tables I–V). In the analysis, primarily the variations in density of the breeding pairs ( $N$ ) and in bird species diversity ( $H'$ ) were taken into account. Other characteristics such as the number of species ( $S$ ) and mean biomass ( $\bar{B}_{ind.}$ ) of a bird in a community, were analysed only complementarily.

The avian species were described by the mapping method (see Głowaciński 1975) during the breeding seasons 1967–1970 (mature forest stages) and 1971–1975 (initial and transitory stages). Most of the data for this study have already been used in earlier publications (Głowaciński 1975, 1978, Głowaciński and Weiner 1977).

Species diversity was calculated according to Shannon's function ( $H'$ ) derived from the information theory:

$$H' = - \sum_{i=1}^S pn_i \log_2 pn_i,$$

where  $S$  is the number of species in a community,  $pn_i$  = a fraction of the total number of individuals  $n$ , belonging to the  $i$ -th species.

The variability that describes the succession consists of two components: (1) directional variability, expressing the trend of succession and (2) non-directional variability which does not result from the trend of succession, and which in this paper is conventionally termed as random or fluctuant.

The total variability in the particular phases of succession (directional + fluctuant) has been defined by means of the coefficient of variation ( $CV$ ):

$$CV = \frac{SD \cdot 100}{\bar{x}}$$

where  $SD$  = standard deviation, and  $\bar{x}$  = the arithmetic mean. Additionally, for the estimation of the annual variations in the value of  $H'$ , the between-year (inter-stage) component of diversity ( $DIV_{diff}$ ) was calculated on the basis of the index used by Järvinen and Väisänen (1976):

$$DIV_{diff} = H'_{TOT} - H'$$

where  $H'_{TOT}$  = diversity in the whole period of a succession phase, and  $H'$  = average annual diversity. This formula is an expansion of the mathematical formula, introduced by Horn (1966), MacArthur, Recher and Cody (1966), and Cody (1970).

Random (fluctuant) variability was determined separately by calculating the relative residual difference (expressed as a fraction or in per cent) between the real dependent variable ( $Y_{real}$ ) and expected dependent variable ( $Y_{exp}$ ) for each value of  $X$  (Fig. 1). The expected dependent variable was determined on the basis of a linear regression equation for the values of

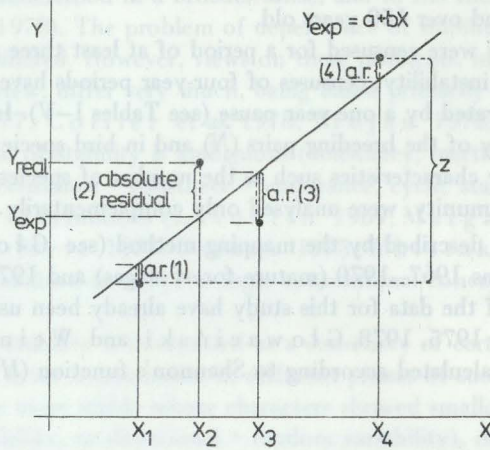


Fig. 1. Calculating the absolute residual (a.r.) between the real independent variable ( $Y_{\text{real}}$ ) and expected dependent variable ( $Y_{\text{exp}}$ ) on the basis of linear regression equations for any successional phase used as an example

$X$  is the independent variable of time,  $z$  – the difference between the extreme values of the  $Y_{\text{real}}$  variable

$N$ ,  $H'$  and  $S$  as a function of time. From the immediate difference of the real and expected value for each year (stage) the absolute residual was obtained.

$$|Y_{\text{real}} - Y_{\text{exp}}| = \text{absolute residual} \quad (1)$$

The absolute residual was then converted to relative values

$$\frac{|Y_{\text{real}} - Y_{\text{exp}}|}{Y_{\text{exp}}} = \text{relative residual} \quad (2)$$

Finally, for each succession phase the average relative residual was found:

$$\frac{\sum_{i=1}^N \text{rel. resid.}_i}{N} = \text{average relative residual} \quad (3)$$

where  $N$  = number of stages (years) in a phase. The higher the variability coefficient derived from regression, the greater the variability of the characteristics studied.

## 4. RESULTS

## 4.1. DIRECTIONAL AND RANDOM VARIABILITY

The direction of changes in the basic structural and energetic characteristics of bird communities in the course of succession in a clearing is most often progressive, with a clear peak in the phase of older thickets (Głowaciński and Weiner 1977). This is in parallel accompanied by a fall in the rate of avian succession (Głowaciński and Järvinen 1975), which decisively affects the total variability of the avifauna in the course of succession.

In the first two succession phases (FI and FII) directional changes decidedly dominate over random changes, in phase III the rate of directional changes falls, while the role is increased of oscillations which remain at a similar level during the subsequent two phases (FIV and FV), being already of the nature of cyclic fluctuations (Tables I–V). Analyses of the ecological parameters of the avian communities participating in the succession (especially comparisons of the parameters, e.g.  $N$  and  $S$ ,  $N$  and  $H'$ ,  $\bar{B}_{ind}$  and  $H'$ , or  $H'$  and  $P:A$ ; Figs. 2–4 and Głowaciński and Weiner 1977) clearly show in which periods of succession and to what

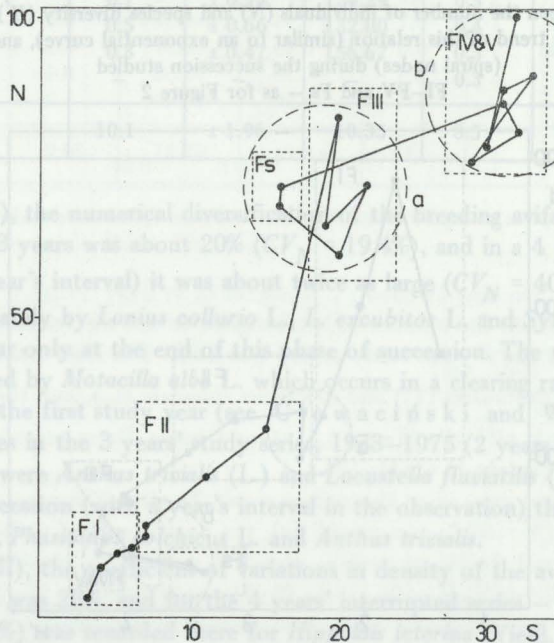


Fig. 2. Relationship between the number of individuals ( $N$ ) and the number of species ( $S$ ) in the avian communities studied, indicating a general trend of this relation (similar to a logarithmic curve) and random variability (spiral nodes  $a$  and  $b$ ) during the succession in the clearing

FI–FV – succession phases,  $F_s$  – a complementary successional phase of a wood 35–40 years old, left out in the basic analyses, because it contained only two developmental stages

extent the total variability is affected by random variability. The example summaries (Figs. 2–4) indicate that random variability contributes to directional variability mainly in later suc

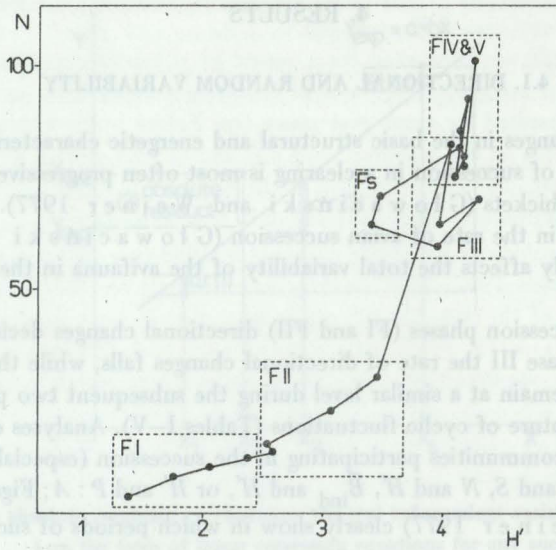


Fig. 3. Relationship between the number of individuals ( $N$ ) and species diversity ( $H'$ ) of the avian communities, indicating a general trend of this relation (similar to an exponential curve), and random variability (spiral nodes) during the succession studied  
FI–FV and  $F_s$  – as for Figure 2

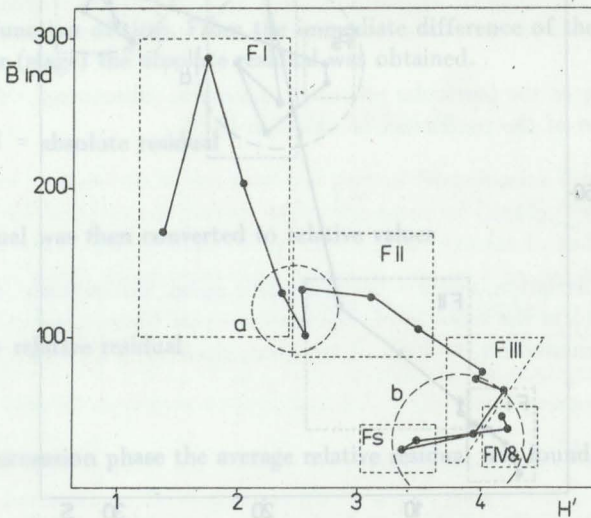


Fig. 4. Relationship between the average biomass of a bird ( $\bar{B}_{ind}$ ) in the communities and the species diversity ( $H'$ ) of the bird communities, indicating a general trend of this relation (regressive, probably rectilinear), and random variability ( $a$  and  $b$  spirals) during the succession studied  
FI–FV and  $F_s$  – as for Figure 2

cessional phases, the time and magnitude of the fluctuations (marked with spirals on the curves) depending on the parameters analysed. Noteworthy is the fact that the total variability of the avifauna parameters compared may have a different course, e.g. similar to a logarithmic (Fig. 2), exponential (Fig. 3) and rectilinear (Fig. 4) course.

## 4.2. VARIATIONS IN THE DENSITY OF AVIFAUNA

Tables I–V illustrate in detail the diversification, expressed by the coefficient of variation ( $CV$ ), of the density of avian communities ( $N$ ) from year-to-year in consecutive phases of succession. Specified in the tables are also dominant species (density > 5% of total community), and the so-called subdominants (2–5%). These bird groups are decisive for the stability of the whole communities.

Table I. Phase I of succession – a 1–5-year clearing  
Coefficient of variation ( $CV$ ) of breeding pair density ( $N$ ) in the 3 years' period (1973–1975) and 4 years' period (1971 and 1973–1975) with one year's interval in research in 1972

| Species                       | 1973–1975 |        |        | 1971, 1973–1975 |        |        |
|-------------------------------|-----------|--------|--------|-----------------|--------|--------|
|                               | $\bar{N}$ | $SD$   | $CV$   | $\bar{N}$       | $SD$   | $CV$   |
| <i>Emberiza citrinella</i>    | 3.6       | ± 1.06 | 29.44  | 3.2             | ± 1.02 | 31.88  |
| <i>Anthus trivialis</i>       | 3.0       | ± 0.00 | 0.00   | 2.3             | ± 1.30 | 56.52  |
| <i>Phasianus colchicus</i>    | 1.4       | ± 0.28 | 20.00  | 1.2             | ± 0.50 | 41.67  |
| <i>Locustella fluviatilis</i> | 0.9       | ± 0.19 | 21.11  | 0.5             | ± 0.36 | 72.00  |
| <i>Sylvia communis</i>        | 0.7       | ± 0.94 | 134.29 | 0.5             | ± 0.87 | 174.00 |
| <i>Lanius excubitor</i>       | 0.5       | ± 0.66 | 132.00 | 0.4             | ± 0.60 | 171.43 |
| <i>Lanius collurio</i>        | 0.3       | ± 0.47 | 156.67 | 0.3             | ± 0.43 | 143.33 |
| <i>Motacilla alba</i>         | —         | —      | —      | 0.3             | ± 0.43 | 143.33 |
| All species                   | 10.1      | ± 1.96 | 10.35  | 8.5             | ± 3.30 | 40.00  |

In phase I (Table I), the numerical diversification of the breeding avifauna during continuous studies lasting 3 years was about 20% ( $CV_N = 19.4\%$ ), and in a 4 years' observation series (divided by a year's interval) it was about twice as large ( $CV_N = 40.0\%$ ). The diversifying effect is caused mainly by *Lanius collurio* L., *L. excubitor* L. and *Sylvia communis* Lath. – species which appear only at the end of this phase of succession. The variability of the avifauna is also influenced by *Motacilla alba* L. which occurs in a clearing rather by chance, and was only recorded in the first study year (see Głowaciński and Weiner 1977). The most stable species in the 3 years' study series, 1973–1975 (2 years after a complete cutting of the wood) were *Anthus trivialis* (L.) and *Locustella fluviatilis* (Wolf), whereas during the 5 years of succession (with a year's interval in the observation) the most stable were *Emberiza citrinella* L., *Phasianus colchicus* L. and *Anthus trivialis*.

In phase II (Table II), the coefficient of variations in density of the avifauna for the continuous 3 years' series was 28%, and for the 4 years' interrupted series – 33.7%. The greatest variability ( $CV_N > 70\%$ ) was recorded there for *Hippolais icterina* (Vieill.), *Turdus philomelos* C. L. Brehm, *Phylloscopus trochilus* (L.), *Ph. collybita* (Vieill.) and *Turdus merula* L. These are birds which enter the succession series only at the end of this phase (Głowaciński and Weiner 1977). The least variable, relatively ( $CV_N < 20\%$ ), were *Phasianus colchicus*, *Lanius collurio*, *Emberiza citrinella* and *Anthus trivialis*, that is, species which had appeared there still in the first phase of succession.

In phase III (Table III), the variability of the  $N$  character in the shorter continuous, and the longer interrupted period was about 10% ( $CV_N = 7.3$  and 12.7%). Of the species enumerated above the populations of the following showed the highest values of the coefficient of

variation ( $CV_N > 50\%$ ): *Sylvia curruca* (L.), *Luscinia luscinia* (L.) and *Phasianus colchicus* – species fairly chimerical, temporarily disappearing during this phase of succession. A fairly high stability ( $CV_N < 20\%$ ) was maintained by *Turdus merula*, *Oriolus oriolus* (L.) and *Phylloscopus trochilus*, species for which the older thicket provides rather an optimum habitat.

Table II. Phase II of succession – a 7–11-year thicket  
Other explanations as for Table I

| Species                       | 1973–1975 |        |        | 1971, 1973–1975 |        |        |
|-------------------------------|-----------|--------|--------|-----------------|--------|--------|
|                               | $\bar{N}$ | SD     | CV     | $\bar{N}$       | SD     | CV     |
| <i>Emberiza citrinella</i>    | 5.4       | ± 1.82 | 33.52  | 5.2             | ± 1.63 | 31.35  |
| <i>Lanius collurio</i>        | 3.8       | ± 1.11 | 29.44  | 3.7             | ± 0.97 | 26.22  |
| <i>Anthus trivialis</i>       | 3.4       | ± 2.09 | 60.93  | 3.1             | ± 0.78 | 24.02  |
| <i>Sylvia communis</i>        | 2.5       | ± 2.18 | 86.17  | 2.2             | ± 2.00 | 93.02  |
| <i>Phasianus colchicus</i>    | 1.8       | ± 0.33 | 18.64  | 1.5             | ± 0.50 | 32.68  |
| <i>Phylloscopus trochilus</i> | 1.4       | ± 1.11 | 77.62  | 1.1             | ± 1.14 | 105.56 |
| <i>Sylvia borin</i> (Bodd.)   | 0.8       | ± 0.37 | 46.25  | 0.8             | ± 0.51 | 63.75  |
| <i>Turdus philomelos</i>      | 0.9       | ± 0.83 | 92.22  | 0.7             | ± 0.85 | 126.87 |
| <i>Hippolais icterina</i>     | 0.7       | ± 0.94 | 140.30 | 0.5             | ± 0.87 | 174.00 |
| <i>Phylloscopus collybita</i> | 0.6       | ± 0.46 | 76.67  | 0.5             | ± 0.47 | 104.44 |
| <i>Turdus merula</i>          | 0.5       | ± 0.39 | 73.58  | 0.4             | ± 0.41 | 102.50 |
| Other species*                | 1.3       | ± 0.96 | 104.40 | 1.2             | ± 0.91 | 110.98 |
| All species                   | 23.1      | ± 6.71 | 28.31  | 20.9            | ± 7.17 | 33.69  |

\**Luscinia luscinia*, *Sylvia atricapilla* (L.), *Locustella fluviatilis*, *Sylvia curruca*, *Lanius excubitor*, *Oriolus oriolus*.

In phase IV, in which the number of species grew to 26, the coefficient of variation of the  $N$  character over the 3 years' study period was 3.8%. The least stable ( $CV_N > 30\%$ ) were *Coccothraustes coccothraustes* (L.) and *Erithacus rubecula* (L.), and the most stable ( $CV_N < 10\%$ ) were *Ficedula albicollis* (Temm.), *Anthus trivialis*, *Parus caeruleus* L., *Turdus philomelos* and *Fringilla coelebs* L. (Table IV).

In phase V, the last one, when the avifauna was the richest in species ( $\bar{S} = 31.5$ ) and of the highest density ( $\bar{N} = 87.1$  pairs per 10 ha), the coefficients of variation in  $N$  during the continuous shorter and the longer periods were 8.8, and 10.5%. Most stable ( $CV < 5\%$ ) was the population of *Ficedula albicollis*, while *Phylloscopus sibilatrix* (Bechst.), *Parus major* L. and *Coccothraustes coccothraustes* were characterized by a greater variation in numbers ( $CV \approx 20\%$ ) (Table V).

Generally, the variability of density of the whole avian communities in the particular years of succession in the clearing decreased from phases I and II to the pre-climax mature wood stage (phase IV), whereafter a slight growth followed of the coefficient of variation of the  $N$  value at the climax stage (phase V, Fig. 5). A greater diversity of numbers of the avifauna could be seen in the longer, 4 years' study period than in the 3 years' phase (Table VI).

The random variability of density ( $N$ ) of the bird communities in the particular phases was as shown in Table VII.



Table III. Phase III of succession – an older, 15–19-year thicket  
Other explanations as for Table I

| Species                              | 1973–1975 |        |       | 1971, 1973–1975 |        |        |
|--------------------------------------|-----------|--------|-------|-----------------|--------|--------|
|                                      | $\bar{N}$ | SD     | CV    | $\bar{N}$       | SD     | CV     |
| <i>Phylloscopus trochilus</i>        | 9.2       | ± 0.87 | 9.46  | 9.2             | ± 0.75 | 8.20   |
| <i>Sylvia atricapilla</i>            | 9.0       | ± 0.82 | 9.11  | 7.5             | ± 2.69 | 35.87  |
| <i>Emberiza citrinella</i>           | 5.3       | ± 1.47 | 27.89 | 7.6             | ± 4.15 | 54.97  |
| <i>Sylvia borin</i>                  | 4.9       | ± 1.22 | 25.05 | 5.9             | ± 2.08 | 35.25  |
| <i>Erithacus rubecula</i>            | 3.7       | ± 1.70 | 46.32 | 2.8             | ± 2.16 | 78.55  |
| <i>Turdus philomelos</i>             | 3.5       | ± 1.05 | 29.75 | 3.2             | ± 1.08 | 33.75  |
| <i>Coccothraustes coccothraustes</i> | 3.7       | ± 1.22 | 33.24 | 3.8             | ± 1.09 | 29.07  |
| <i>Turdus merula</i>                 | 3.4       | ± 0.17 | 5.00  | 3.2             | ± 0.37 | 11.56  |
| <i>Hippolais icterina</i>            | 2.7       | ± 1.89 | 70.79 | 3.5             | ± 2.18 | 62.29  |
| <i>Phylloscopus collybita</i>        | 2.1       | ± 0.84 | 39.44 | 2.6             | ± 1.09 | 41.92  |
| <i>Anthus trivialis</i>              | 1.8       | ± 0.59 | 32.78 | 3.3             | ± 2.56 | 78.77  |
| <i>Oriolus oriolus</i>               | 2.0       | ± 0.00 | 0.00  | 2.3             | ± 0.43 | 19.11  |
| <i>Fringilla coelebs</i>             | 2.3       | ± 1.25 | 53.65 | 1.8             | ± 1.48 | 84.57  |
| <i>Luscinia luscinia</i>             | 1.7       | ± 1.27 | 73.41 | 1.9             | ± 1.12 | 60.54  |
| <i>Streptopelia turtur</i> (L.)      | 1.7       | ± 0.47 | 28.14 | 1.9             | ± 0.57 | 30.00  |
| <i>Carduelis chloris</i> (L.)        | 1.7       | ± 0.47 | 28.14 | 1.8             | ± 0.43 | 24.57  |
| <i>Lanius collurio</i>               | 1.3       | ± 0.47 | 35.34 | 1.5             | ± 0.50 | 33.33  |
| <i>Phasianus colchicus</i>           | 1.3       | ± 0.94 | 70.68 | 1.5             | ± 0.87 | 58.00  |
| <i>Sylvia curruca</i>                | 1.3       | ± 0.94 | 70.68 | 1.0             | ± 1.00 | 100.00 |
| Other species*                       | 3.3       | ± 1.59 | 48.18 | 4.8             | ± 2.78 | 57.92  |
| All species                          | 65.9      | ± 4.86 | 7.27  | 71.1            | ± 9.06 | 12.67  |

\* *Phylloscopus sibilatrix*, *Sylvia communis*, *Locustella fluviatilis*, *Columba palumbus* L., *Garrulus glandarius* (L.), *Carpodacus erythrinus* (Pall.), *Pica pica* (L.).

Table IV. Phase IV of succession – a wood 95 years old  
Coefficient of variation (CV) of breeding pair density (N) in the 3 years' (1967–1969) period

| Species                              | 1967–1969 |        |       |
|--------------------------------------|-----------|--------|-------|
|                                      | $\bar{N}$ | SD     | CV    |
| <i>Ficedula albicollis</i>           | 10.8      | ± 0.45 | 4.17  |
| <i>Fringilla coelebs</i>             | 9.1       | ± 0.82 | 9.03  |
| <i>Parus caeruleus</i>               | 8.3       | ± 0.45 | 5.45  |
| <i>Erithacus rubecula</i>            | 6.2       | ± 1.91 | 30.71 |
| <i>Parus major</i>                   | 5.1       | ± 0.71 | 13.98 |
| <i>Phylloscopus sibilatrix</i>       | 4.8       | ± 1.09 | 22.61 |
| <i>Anthus trivialis</i>              | 4.3       | ± 0.19 | 4.47  |
| <i>Sturnus vulgaris</i> L.           | 3.8       | ± 1.02 | 26.77 |
| <i>Sylvia atricapilla</i>            | 3.7       | ± 0.45 | 12.33 |
| <i>Turdus merula</i>                 | 3.6       | ± 0.53 | 14.93 |
| <i>Sitta europaea</i>                | 2.8       | ± 0.39 | 13.73 |
| <i>Turdus philomelos</i>             | 2.5       | ± 0.22 | 8.66  |
| <i>Emberiza citrinella</i>           | 2.5       | ± 0.40 | 15.94 |
| <i>Muscicapa striata</i> (Pall.)     | 2.1       | ± 0.60 | 29.13 |
| <i>Coccothraustes coccothraustes</i> | 1.9       | ± 0.67 | 35.26 |

Table IV continued

| Species                       | 1967-1969 |           |           |
|-------------------------------|-----------|-----------|-----------|
|                               | <i>N</i>  | <i>SD</i> | <i>CV</i> |
| <i>Dendrocopos major</i> (L.) | 1.6       | ± 0.16    | 10.13     |
| Other species*                | 7.1       | ± 0.62    | 10.00     |
| All species                   | 80.2      | ± 3.08    | 3.84      |

\**Streptopelia turtur*, *Parus palustris* L., *Hippolais icterina*, *Oriolus oriolus*, *Certhia brachydactyla* C. L. Brehm, *C. familiaris* L., *Luscinia luscinia*, *Phylloscopus collybita*, *Dendrocopos medius* (L.), *D. minor* (L.), *Columba palumbus*, *Troglodytes troglodytes* (L.), *Phasianus colchicus*, *Locustella fluviatilis*, *Picus canus* Gmel., *Caprimulgus europaeus* L., *Crex crex* (L.).

Table V. Phase V of succession – a wood over 150 years old  
Coefficient of variation (*CV*) of breeding pair density (*N*) in the 3 years' (1967-1969) and 4 years' (1967-1970) periods

| Species                              | 1967-1969 |           |           | 1967-1970 |           |           |
|--------------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
|                                      | $\bar{N}$ | <i>SD</i> | <i>CV</i> | $\bar{N}$ | <i>SD</i> | <i>CV</i> |
| <i>Ficedula albicollis</i>           | 12.5      | ± 0.35    | 2.80      | 12.8      | ± 0.52    | 4.08      |
| <i>Fringilla coelebs</i>             | 9.6       | ± 1.68    | 17.59     | 10.1      | ± 1.72    | 17.06     |
| <i>Parus caeruleus</i>               | 9.1       | ± 1.12    | 12.38     | 9.3       | ± 1.05    | 11.30     |
| <i>Sturnus vulgaris</i>              | 9.0       | ± 1.96    | 21.78     | 8.8       | ± 1.87    | 21.74     |
| <i>Erithacus rubecula</i>            | 7.8       | ± 1.30    | 16.67     | 8.3       | ± 1.49    | 17.95     |
| <i>Parus major</i>                   | 4.5       | ± 0.35    | 18.89     | 5.0       | ± 1.18    | 23.47     |
| <i>Sitta europaea</i>                | 4.4       | ± 0.43    | 9.77      | 4.5       | ± 0.46    | 10.22     |
| <i>Sylvia atricapilla</i>            | 3.6       | ± 0.24    | 6.67      | 4.1       | ± 0.84    | 20.49     |
| <i>Coccothraustes coccothraustes</i> | 3.5       | ± 0.71    | 20.42     | 3.4       | ± 0.61    | 17.96     |
| <i>Phylloscopus sibilatrix</i>       | 3.1       | ± 0.71    | 23.23     | 3.4       | ± 0.90    | 26.27     |
| <i>Anthus trivialis</i>              | 2.7       | ± 0.12    | 4.44      | 3.3       | ± 1.02    | 31.25     |
| <i>Turdus merula</i>                 | 2.3       | ± 0.38    | 16.40     | 2.5       | ± 0.44    | 17.58     |
| <i>Dendrocopos major</i>             | 1.7       | ± 0.21    | 12.30     | 1.7       | ± 0.20    | 10.77     |
| Other species*                       | 13.3      | ± 2.08    | 15.64     | 13.9      | ± 2.03    | 14.60     |
| All species                          | 87.1      | ± 7.63    | 8.77      | 91.1      | ± 9.56    | 10.50     |

\**Certhia brachydactyla*, *C. familiaris*, *Turdus philomelos*, *Columba palumbus*, *Muscicapa striata*, *Troglodytes troglodytes*, *Oriolus oriolus*, *Streptopelia turtur*, *Emberiza citrinella*, *Dendrocopos medius*, *Parus palustris*, *Phylloscopus collybita*, *Dendrocopos minor*, *Strix aluco* L., *Dryocopus martius* (L.), *Columba oenas* L., *Luscinia luscinia*, *Picus canus*, *Caprimulgus europaeus*, *Phoenicurus phoenicurus* (L.), *Locustella fluviatilis*, *Sylvia borin*, *Tringa ochropus* L.

The summary of the results obtained for all the phases of the successional series under study indicates a low random variability of the value of *N* in phase I, a relatively great increase in the variability of *N* in phase II, a considerable fall in phase III, and then in phase IV, and a new, considerable growth of the fluctuant variability in phase V (Fig. 6).

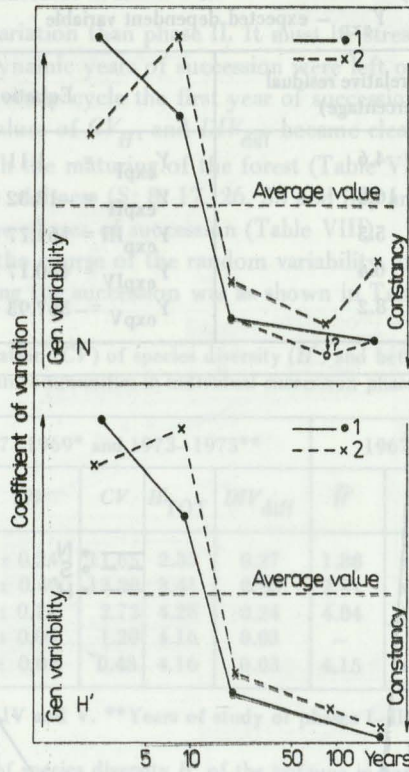


Fig. 5. Total variability of density ( $N$ ) and species diversity ( $H'$ ) of the bird communities in the consecutive successional phases  
 1 – values for 3 consecutive study years, 2 – values for 4 study years. Logarithmic time scale

Table VI. Variation in numbers of the avian communities in each of the succession phases over the 3 and 4 years' periods

| Phases of succession | 1967–1969* and 1973–1975** |      |       | 1967–1970* and 1971–1975** |      |       |
|----------------------|----------------------------|------|-------|----------------------------|------|-------|
|                      | $\bar{N}$                  | SD   | CV    | $\bar{N}$                  | SD   | CV    |
| I                    | 10.1                       | 1.96 | 19.35 | 8.5                        | 3.30 | 40.00 |
| II                   | 23.1                       | 6.71 | 28.31 | 20.9                       | 7.17 | 33.69 |
| III                  | 65.9                       | 4.86 | 7.27  | 71.1                       | 9.06 | 12.67 |
| IV                   | 80.2                       | 3.08 | 3.84  | —                          | —    | —     |
| V                    | 87.1                       | 7.63 | 8.77  | 91.1                       | 9.56 | 10.50 |

\*Years of study of phases IV and V. \*\*Years of study of phases I–III.

Table VII. Fluctuant variability of numbers  $N$  of the avifauna in consecutive successional phases I–V  
 $Y_{\text{exp}}$  – expected dependent variable

| Phases of succession | Average relative residual (percentage) | Equations of regression                 |
|----------------------|--|---|
| I                    | 4.6                                    | $Y_{\text{expl}} = 1.11 + 2.257 X$      |
| II                   | 16.0                                   | $Y_{\text{explII}} = -18.32 + 4.240 X$  |
| III                  | 5.5                                    | $Y_{\text{explIII}} = 161.77 - 5.291 X$ |
| IV                   | 0.4                                    | $Y_{\text{explIV}} = 440.17 - 3.750 X$  |
| V                    | 8.2                                    | $Y_{\text{explV}} = -367.93 + 3.020 X$  |

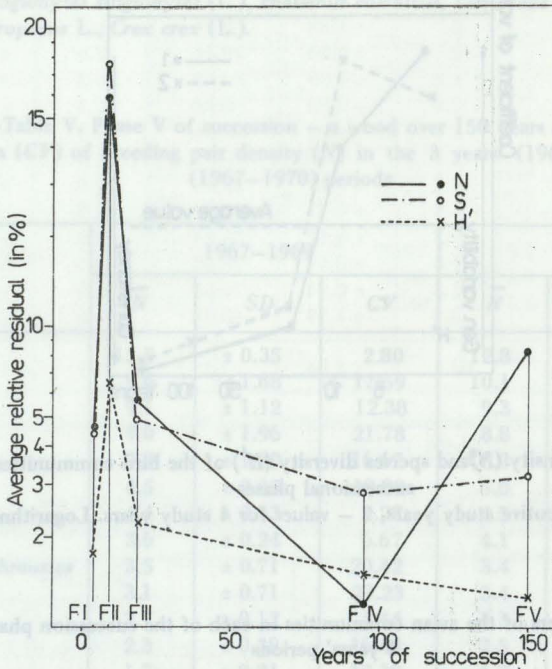


Fig. 6. Random variability (average relative residual) of density ( $N$ ), number of species ( $S$ ) and species diversity ( $H'$ ) of the birds in consecutive successional phases FI–FV

The description of phase IV is based on one successional stage less than the descriptions of the remainder of the phases (see Tables IV, VI and VIII), for this reason the values of  $N$ ,  $S$  and  $H'$  are slightly lowered.

Logarithmic time scale

#### 4.3. VARIABILITY OF THE SPECIES DIVERSITY OF AVIFAUNA

The coefficient of variation of the  $H'$  index of the avifauna in both the 3 years' and 4 years' observation series in general showed a tendency to fall, from the initial phases (phases I and II) to the last, the climax phase (phase V, Fig. 5). A similar tendency of changes was also indicated by the  $DIV_{\text{diff}}$  index. Over the 3 years' cycle of studies phase I was characte-

alized by a slightly lower variation than phase II. It must be stressed, however, that in that cycle the first two most dynamic years of succession were left out.

Because in the 4 years' study cycle the first year of succession was taken into account, the trends of changes in the values of  $CV_{H'}$  and  $DIV_{diff}$  became clearer, indicating a stabilized diversity of the avifauna with the maturing of the forest (Table VIII). This process coincided with an increase in species richness ( $S$ : 8, 17, 26, 33 and 36) and species diversity ( $H'$ ) of the birds in the consecutive phases of succession (Table VIII).

Considered separately, the course of the random variability of the species diversity ( $H'$ ) of the bird communities during the succession was as shown in Table IX.

Table VIII. Coefficient of variation ( $CV$ ) of species diversity ( $H'$ ) and between-year component of diversity ( $DIV_{diff}$ ) of the avian communities in individual succession phases during 3 and 4 years

| Phases of succession | 1967-1969* and 1973-1975** |        |       |            |              | 1967-1970* and 1971-1975** |        |       |            |              |
|----------------------|----------------------------|--------|-------|------------|--------------|----------------------------|--------|-------|------------|--------------|
|                      | $\bar{H}'$                 | $SD$   | $CV$  | $H'_{TOT}$ | $DIV_{diff}$ | $\bar{H}'$                 | $SD$   | $CV$  | $H'_{TOT}$ | $DIV_{diff}$ |
| I                    | 2.06                       | ± 0.24 | 11.65 | 2.33       | 0.27         | 1.88                       | ± 0.37 | 19.68 | 2.40       | 0.52         |
| II                   | 3.03                       | ± 0.40 | 13.20 | 3.41       | 0.38         | 2.91                       | ± 0.41 | 14.09 | 3.33       | 0.42         |
| III                  | 4.04                       | ± 0.11 | 2.72  | 4.28       | 0.24         | 4.04                       | ± 0.11 | 2.72  | 4.28       | 0.24         |
| IV                   | 4.13                       | ± 0.05 | 1.20  | 4.16       | 0.03         | —                          | —      | —     | —          | —            |
| V                    | 4.13                       | ± 0.02 | 0.48  | 4.16       | 0.03         | 4.15                       | ± 0.03 | 0.70  | 4.19       | 0.04         |

\* Years of study of phases IV and V. \*\*Years of study of phases I-III.

Table IX. Fluctuant variability of species diversity  $H'$  of the avifauna in consecutive successional phases I-V  
 $Y_{exp}$  - expected dependent variable

| Phases of succession | Average relative residual (percentage) | Equations of regressions      |
|----------------------|--|-------------------------------|
| I                    | 1.5                                    | $Y_{expI} = 1.05 + 0.253 X$   |
| II                   | 6.3                                    | $Y_{expII} = 0.73 + 0.236 X$  |
| III                  | 2.2                                    | $Y_{expIII} = 3.95 + 0.005 X$ |
| IV                   | 1.1                                    | $Y_{expIV} = 7.01 - 0.030 X$  |
| V                    | 0.5                                    | $Y_{expV} = 1.88 + 0.015 X$   |

The summary in the table (Table IX) and the curve (Fig. 6) indicate that the random variability of bird species diversity was very low in phase I, being the highest in phase II then falling to reach its minimum in phase V. The course of variability of this type with regard to the value of  $S$  was similar (Fig. 6).

#### 4.4. CORRELATIONS BETWEEN TOTAL VARIABILITY AND ABUNDANCE, DIVERSITY AND NUMBER OF SPECIES

The course of the relationships between the parameters  $N$ ,  $H'$  and  $\bar{N}$ , and the coefficients of variations of density ( $CV_N$ ), diversity ( $CV_{H'}$ ) and the between-year component of diversity in

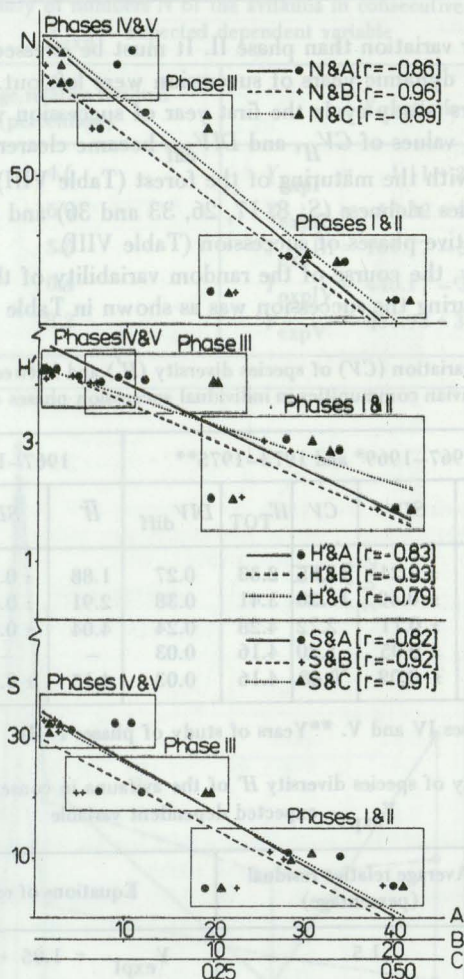


Fig. 7. Correlations between the density of individuals ( $N$ ), species diversity ( $H'$ ) and number of species ( $S$ ), and the determinants of the total variability:  $CV_N$  (denoted as A),  $CV_{H'}$  (B) and  $DIV_{diff}$  (C). For  $CV_N$  and  $S$ :  $0.01 > P > 0.001$ ; for  $CV_N$  and  $N$ :  $0.005 > P > 0.001$ ; for  $CV_N$  and  $H'$ :  $P \approx 0.005$ , for  $DIV_{diff}$  and  $H'$ :  $0.1 > P > 0.005$ ; for the remainder:  $P < 0.001$ ;  $d.f. = 7$ .

communities ( $DIV_{diff}$ ) has been presented in Figure 7. The correlation between these indices are negative and highly significant ( $r \geq -0.8$ ). A strong correlation occurs particularly between  $S$ ,  $N$ ,  $H'$  and  $CV_{H'}$  ( $r > -0.9$ ).

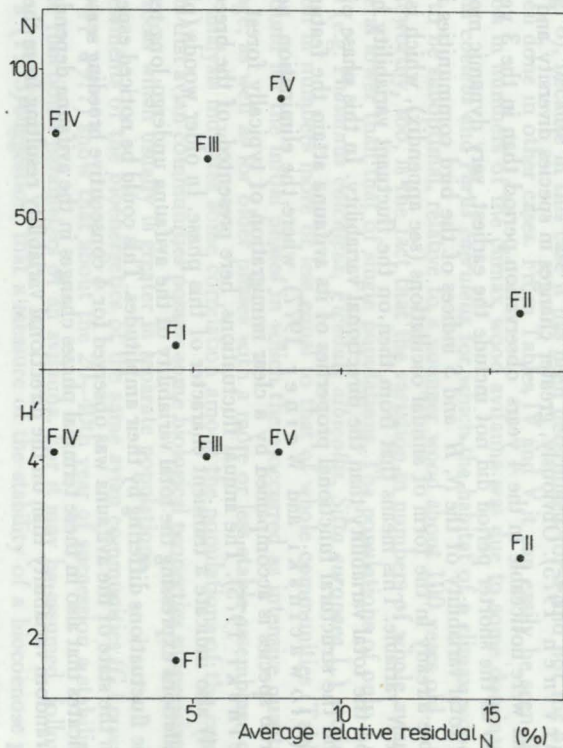


Fig. 8. Relationship between random variability of density index (av. rel. resid.  $N$ ) and the numbers ( $N$ ) and species diversity ( $H'$ ) of the bird communities in succession phases FI–FV

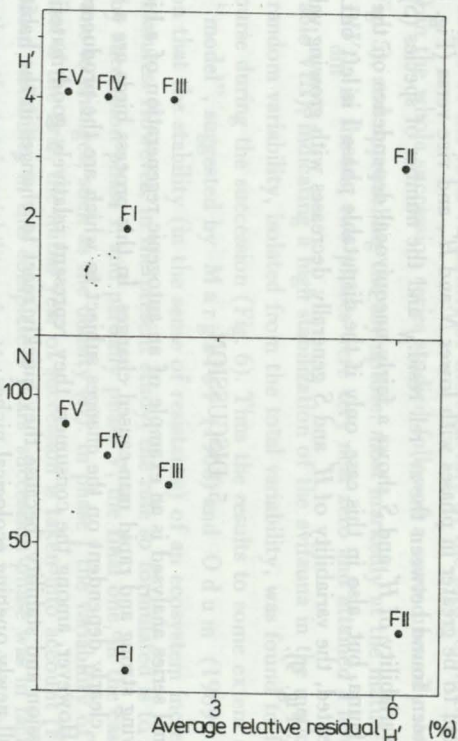


Fig. 9. Relationship between random variability of species diversity index (av. rel. resid.  $H'$ ) and the numbers ( $N$ ) and species diversity ( $H'$ ) of the bird communities in succession phases FI–FV

#### 4.5. RELATIONSHIP BETWEEN RANDOM VARIABILITY AND ABUNDANCE, DIVERSITY AND NUMBER OF SPECIES

Because of the position of phase I, the random variability does not show any close correlation with abundance ( $N$ ) and species diversity ( $H'$ ) of the avifauna. If phase I is left out, this variability is found to be greater in phases with lower  $N$  and  $H'$ , and vice versa (Fig. 8). No correlation has been found between the av. rel. resid. $_N$  and the number of species ( $S$ ).

The random variability of  $H'$  and  $S$  shows a fairly unequivocal dependence on the  $N$ ,  $H'$  and  $S$  of the avifauna, but, also in this case, only if the disputable phase I is left out. If this condition is accepted, the variability of  $H'$  and  $S$  generally decreases with growing values of  $N$ ,  $H'$  and  $S$  (e.g. Fig. 9).

### 5. DISCUSSION

The successional series analysed is an example of an autogenic regeneration of a biocoenotic system following strong and rapid man-caused changes. In this process birds are a secondary component, clearly dependent on the changes subject to which are the producers, especially the stand. However, among the consumers they represent relatively good material for testing the succession and stability, because they quickly react to changes in the habitat, and fairly easily fill all newly opening ecological niches.

**Stability and succession.** In the successional sequence studied the greatest structural changes in the avifauna occurred during the first 10 years of regeneration of the wood, shortly after a strong biocoenotic "shock" caused by the cutting down of the tree stand. In the first two phases, directional, growth changes clearly dominated. As a result, even in cases of strong fluctuant changes of some parameters at the beginning of succession (Fig. 6), the total variability was then also clearly directional (Tables I and II and appendix). The high total variability (instability) of communities, relative to the average values for these phases, fairly coincided with the rate of avian succession, for it is in the initial period of regeneration of forest ecosystems that it is the highest and then it drops almost hyperbolically (Głowaciński and Järvinen 1975). Obviously, greater changes in species diversity and numbers of the avifauna were noticeable in the 4 years' observation period than in the 3 years' period, the more so as the shorter period did not include the earliest, very dynamic moment of succession. The total variability of the  $N$ ,  $H'$  and  $S$  indices of the bird communities in phase III was noticeable already in the form of annual oscillations (see appendix), which is best exemplified by the  $N$  variable. This means that from then on the fluctuant variability had a greater influence on the total variability than the directional variability. In this phase of succession, a forest and the structural functional properties of its avifauna attain the features of a "time ecotone" (Głowaciński and Weiner 1977), where the elimination, not great as yet, of shrub species is accompanied by a clear immigration of typically forest bird species (Głowaciński 1975). The annual fluctuations, here presented, of the breeding avifauna (Figs. 2–4) also indicate a transient character of this phase. In older woods (phases IV and V), the oscillations expressing the total variability of the avifauna undergo long-term (many years') cyclic fluctuations differing by their amplitudes. This could be noticed especially in phase V in which the state of the avifauna was observed for 4 consecutive breeding seasons (Table V). This indicates that also in these terminal phases changes in the avifauna depended much more on the random variability than on the directional variability resulting from the trend of succession.



Of the characteristics studied, subject to the strongest changes was density ( $N$ ). Changes in the number of species ( $S$ ), and especially in the species diversity ( $H'$ ), which is logarithmic in nature, were milder (Tables VI, VIII). Similar observations result from the data reported by Järvinen and Väisänen (1976) concerning avian communities of mature woods.

The course of the total variability of the structure of the bird communities ( $CV_N$ ,  $CV_{H'}$ ,  $DIV_{diff}$ ) in the whole succession series studied followed a curve unevenly sloping over time scale (Fig. 5), and approaching the asymptote, most markedly at the mature stages. The values of  $DIV_{diff}$  in the last two phases were very near zero and attained a level exceptionally even (Table VIII), indicating a high stabilization of the avifauna in the mature woods.

The random variability, isolated from the total variability, was found to follow a fairly similar course during the succession (Fig. 6). Thus the results to some extent support the succession "model", suggested by Margalef (1968) and Odum (1969), based on the assumption that the stability (in the sense of resistance) of an ecosystem increases as the ecosystem matures. However, in the present study, the rule so formulated is to some extent disturbed by succession phase I, and partially phase V, the final one, in the case of parameters most prone to changes, such as the density ( $N$ ). In phase I the variability of avifauna is not the highest if the first, the initial year of succession is taken into account (Figs. 5 and 6). The random variability in this complete 4 years' succession phase was in fact very small (Fig. 6); then the total variability of avifauna was relatively greater (Fig. 5), this being determined by the higher, relatively, rate of changes in the avian communities at the beginning of the succession (cf. Głowaciński and Järvinen 1975).

Interesting, too, is the fact that the amplitudes of changes in the value of  $N$  were slightly smaller in a wood about 100 years old ( $CV_N = 3.8$ ) than in an older, a climax one ( $CV_N = 8.8$ ). This applies also, and primarily, to the random variability of  $N$ , because at a very low and even rate of succession from the subclimax to the climax it is the random variability that determines the total variability of an avifauna. It must be pointed at once that the value of the random variability in the subclimax phase (FIV), relative to other phases, has been lowered (Fig. 6), because in this case it has been determined for 3 and not for 4 years of study, as has been done in other cases. From Tables IV and V it can easily be seen that the stronger variation in numbers of the climax wood avifauna was due to some dominant species such as *Fringilla coelebs* and *Parus caeruleus* for which the habitat of a climax wood 150 years old seems to be suboptimal, relative to a younger wood about 100 years old.

Noteworthy, too, is the fact that the variation in numbers of whole avian communities was in general lower than that of single populations. The populations of only a small number of species (e.g. *Phasianus colchicus*, *Ficedula albicollis*, *Sitta europaea* L.) attained a degree of variation in numbers more or less equal to that of whole communities (Tables I–V). This has been found for the initial phases in which there occurred as intensive qualitative-quantitative exchange, as well as for older phases with a more or less stable assemblage of species. The statistical analysis indicates some correlation among the populations of the communities, and suggests that avian communities possess some biological properties suppressing the variation in numbers which usually is greater in separate populations.

Assessments of the bioenergetics of the same avian communities (Głowaciński and Weiner 1977) show that about the 20–40th year of succession a stabilization also occurs of some functional parameters of an avifauna. For it may be assumed, following MacArthur's (1955) suggestion, that a measure of the stability of a biocoenose may be the  $H'$  in-

dex derived from the information theory (section 3), where  $n$ , the number of individuals, would be replaced with  $e$ , the appropriate energetic equivalent for each trophic chain  $i$  separately, and  $T$ , that is, jointly all the trophic chains in a community, or biocoenose. Since a direct measurement of energy flow along food chains is impossible for practical reasons, it may be assumed that the same formula is useful if  $T$  is replaced with  $S$ , that is, the energetics of all species in a set (Collier et al. 1978). Thus the index may be defined as follows:

$$H'_e = - \sum_{i=1}^S pe_i \log_2 pe_i$$

where  $S$  = number of species in a community,  $pe_i$  = a fraction of the total energy flow through all individuals of the  $i$ -th species. It is, therefore, possible to calculate also the equitability of energy ( $J'_e$ ), by using the formula:  $J'_e = H'_e : \log_2 S$ , where  $H'_e$  and  $S$  are as above. The indices, thus calculated, of assimilation diversity ( $H'_A$ ), production ( $H'_P$ ), or standing crop energy ( $H'_{SC}$ ), as well as the coefficients of even energy distribution among species in communities ( $J'_A, J'_P, J'_{SC}$ ) become even already at the pole stages, that is to say, several dozen years after the initiation of succession (Fig. 10). These data, as well as the structural indices prove that the avifauna clearly stabilized at the stage of the formation of typical forest formations, and it attained its full steady state, that is, dynamic stability, in woods about 100, or more, years old.

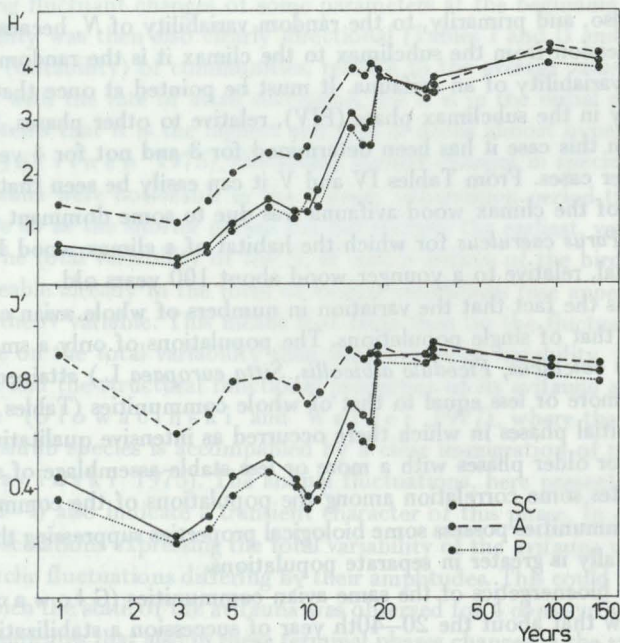


Fig. 10. Energetic indices of  $H'$  and  $J'$  in the bird communities in different stages of the successional series studied (after Głowaciński and Weiner 1977)

SC — standing crop, A — assimilation, P — production. Logarithmic time scale

**Stability and diversity.** A strong negative correlation between the total variability and the  $H'$  index (Fig. 7) indicates a close positive relationship between the stability (as the reverse of total variability) and the species diversity of avian communities. Relationships of this type between diversity and stability have been proved and suggested also by many other ecologists (Pimental 1961, Loucks 1970, Boesch 1975) therein also for birds (Brewer 1963). This regularity has been accepted in Odum's (1969) "strategy of ecosystem development", where the author describes "low diversity developmental stages" of succession as having poor stability (in the sense of resistance), and high diversity "mature stages" as having good stability. MacArthur (1955) explains in a model that the greater the diversity and the greater the number of alternative food (energetic) webs, which may control the populations in a system, the greater the possibilities for that system to maintain a state of equilibrium. In his further speculations the above author suggests a relationship between the stability of a system and its species and abundance structure (see Collier et al. 1978). Watt (1965) does not confirm this hypothesis, but he supports it by a conclusion which says that in a community a growth in number of species competing for food increases stability. Moreover, on the basis of experiments McNoughton (1977) states as follows: "species diversity stabilizes ecosystem functional properties". MacArthur's (1955) view, partially supported by experiments carried out by other ecologists, implies the statement that "diversity makes stability". To put it in other words, the stability of a community should be the function of its diversity (Trojan 1978). This view is contradicted by May (1973) whose mathematical models of trophically complex food webs are less stable than those for trophically simple ones. Mathematical models representing the relationships between diversity and stability are very distant from reality (May 1973, Maynard Smith 1974). Some empirical studies also suggest that the relationship between diversity and stability may be negative (e.g. Hurd et al. 1971, Witkowski 1973). Finally, there are papers indicating that there is no relationship between these parameters (e.g. Järvinen and Väisänen 1976). Łomnicki (1978) presents a model of population density control based on differences between individuals in single populations, and suggests that between stability and diversity a correlation may occur, but it is impossible to sensibly speak about a cause-result relationship in any direction of this system. He relates stability to spatial heterogeneity, at the same time assuming the existence of a correlation between diversity and habitat heterogeneity.

The paper indicates a close positive correlation between the stability and diversity of birds, although it does not state whether there exists any direct causal relationship between these parameters. There is a strong positive correlation between stability and the number of bird species (Fig. 7). It is also indicated by the data reported by Brewer (1963) concerning a series of bird communities of American woods diversified in respect of humidity. The finding of a greater stability of systems richer in species, and more diverse, speaks in favour of the diversity-stability conception represented by MacArthur (1955).

If diversity is compared with the relative variability which informs more about stability conceived as a community resistance, the relationship between these characteristics will not be unequivocal (Fig. 8). When compared with species diversity, the random variability seems to be the greater, the lower the diversity of an avifauna. However, this regularity can only be accepted on condition that phase I of succession, which disturbs this rule, is considered to be of a lower value, because it comprises a biocoenotic system that is very poor in species and too much disturbed.

**Stability and density.** The total variability of avian species during succession in a clearing is also strongly negatively correlated with the abundance of birds ( $r \approx -0.9$ ). This indicates a positive relationship between the stability and density of avifauna (Fig. 7), but it is difficult to define the nature of the links between these parameters. The dependence of the random variability on density is in general not clear. It is noticeable only in certain cases (e.g. rel. resid.<sub>N</sub> and  $N$ , av. rel. resid.<sub>H'</sub> and  $N$ ), and even in this case only conditionally if phase I is not taken into consideration.

**Stability and selection strategy.** In ecology the opinion prevails that in stable systems the percentage increases of species which are subject to  $K$  type selection (Wilson and Bosset 1971), that is to say, more specialized species. Specialization leads to a growth of the number of species and their diversity (MacArthur and Wilson 1967). A decreased stability of a system increases the chance to survive for  $r$  type species (Southwood et al. 1974). The increase in the proportion of conventionally defined  $K$ -strategists in relation to conventional  $r$ -strategists during the secondary succession of a wood has not been unequivocally demonstrated for birds (Głowaciński 1979). Therefore there are no noticeable relationships between the type of evolutionary strategy (in the sense of the  $r$  and  $K$ -selection theory) and the stability of avifauna which generally increases with the progress of succession of these animals.

## 6. APPENDIX

The number of species ( $S$ ), diversity ( $H'$ ) and the number of pairs ( $N$ ) in the avian communities of the successional series studied.

Phase I: 1971 -  $S = 3$ ,  $H' = 1.33$ ,  $N = 3.4$ ; 1973 -  $S = 4$ ,  $H' = 1.76$ ,  $N = 7.4$ ; 1974 -  $S = 5$ ,  $H' = 2.07$ ,  $N = 11.0$ ; 1975 -  $S = 6$ ,  $H' = 2.34$ ,  $N = 12.0$ .

Phase II: 1971 -  $S = 7$ ,  $H' = 2.55$ ,  $N = 14.0$ ; 1973 -  $S = 7$ ,  $H' = 2.51$ ,  $N = 14.7$ ; 1974 -  $S = 11$ ,  $H' = 3.10$ ,  $N = 23.8$ ; 1975 -  $S = 15$ ,  $H' = 3.49$ ,  $N = 31.1$ .

Phase III: 1971 -  $S = 20$ ,  $H' = 4.02$ ,  $N = 84.4$ ; 1973 -  $S = 19$ ,  $H' = 3.95$ ,  $N = 65.0$ ; 1974 -  $S = 22$ ,  $H' = 4.22$ ,  $N = 72.2$ ; 1975 -  $S = 19$ ,  $H' = 3.95$ ,  $N = 60.4$ .

Phase IV: 1967 -  $S = 31$ ,  $H' = 4.13$ ,  $N = 83.7$ ; 1968 -  $S = 32$ ,  $H' = 4.20$ ,  $N = 80.6$ ; 1969 -  $S = 29$ ,  $H' = 4.07$ ,  $N = 76.2$ .

Phase V: 1967 -  $S = 33$ ,  $H' = 4.15$ ,  $N = 96.3$ ; 1968 -  $S = 31$ ,  $H' = 4.11$ ,  $N = 86.8$ ; 1969 -  $S = 30$ ,  $H' = 4.14$ ,  $N = 78.0$ ; 1970 -  $S = 32$ ,  $H' = 4.19$ ,  $N = 103.3$ .

The species composition and numbers of individual avian populations in the communities distinguished have been given in other papers (Głowaciński 1975, 1978, Głowaciński and Weiner 1977).

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## 7. SUMMARY

For five phases of the secondary succession of a deciduous forest in southern Poland (the Niepołomice Forest) the stability (in the sense of constancy and resistance) of the breeding avifauna has been established. Each of the phases was analysed over a period 3-4 years (Tables I-VI and VIII). The object of the

research was primarily the variability (as the reverse of stability) of density ( $N$ ) and species diversity ( $H'$ ) of avian communities. The total variability (i.e., directional variability + random, or fluctuant variability) was calculated, as well as (separately) the random variability, independent of directional changes of succession.

For the assessment of the total variability the coefficient of variation ( $CV$ ) and index of annual changes in species diversity according to Järvinen and Väisänen (1976) ( $DIV_{diff}$ ) were used. The random variability was defined by means of regression equations, calculating for the particular phases the average relative residual between two dependent real variables and expected dependent variables for the appropriate time variables (formulae 1–3, section 3, Fig. 1).

Prevailing in the first 15 years of succession was directional variability of the parameters studied, and in later stages the random, or fluctuant variability became more decisive (Figs. 2–4). The total variability of the avifauna throughout the successional series generally followed a curve unevenly sloping against time, whereas its determinants approached the lower asymptote in the older stages. Certain deviations from this tendency, could, however, be observed: for example, the abundance of birds, very prone to changes, showed stronger variations during the climax phase (FV) than during the pre-climax phase (FIV), this being determined by several dominant species (Tables IV, V, Fig. 5). In the first two phases  $CV_N$  was 4 times,  $CV_{H'}$  – 18 times, and  $DIV_{diff}$  – about 10 times as high as in the last two phases.

At the beginning of the succession the random variability was comparatively low. In the scrub phase (FII) it attained its maximum, whereafter it decreased at a variable rate in the final phases (Fig. 6). The assessment of the total variability and random variability permits the statement that with the progress of succession in a forest clearing the stability of the birds there generally increases, although not in every case is it at its lowest during the initial phase (FI) and not always at its highest in the climax phase (FV). The results in general support the succession "model" presented by Odum (1969) assuming an increasing stability (as resistance) of an ecosystem with its maturation. Variation in numbers among avian communities is on the whole lower than at the level of individual populations (Tables I–V); statistical tests do not rule out the existence in avian communities of biological properties suppressing the populational variability which is usually greater.

Besides, a high correlation ( $\bar{r} \approx -0.90$ ) has been found between the total variability and the value of  $S$  and  $N$  of the communities, as well as between the total variability and species diversity  $H'$  ( $\bar{r} \approx -0.85$ ) (Fig. 7). However, the relationships between the random variability and numbers and diversity of the avifauna are less clear (Figs. 8, 9). The finding of a higher stability in communities that are richer in species and more diverse supports MacArthur's (1955) opinion on the relationship between diversity and stability.

## 8. POLISH SUMMARY

Dla pięciu faz wtórnej sukcesji lasu liściastego w południowej Polsce (Puszcza Niepołomska) określono stabilność (w sensie stałość i odporność) lęgowej awifauny. Każdą z tych faz analizowano w okresie 3–4-letnim (tab. I–VI, VIII). Badano głównie zmienność (jako odwrotność stabilności) zagęszczenia ( $N$ ) i różnorodności gatunkowej ( $H'$ ) zespołów ptaków. Obliczono zmienność całkowitą (tj. zmienność kierunkowa + zmienność losowa, czyli fluktuacyjna) i osobno zmienność losową, niezależną od zmian kierunkowych sukcesji.

Dla oceny zmienności całkowitej stosowano współczynnik zmienności ( $CV$ ) i wskaźnik rocznych zmian różnorodności gatunkowej Järvinena i Väisänen (1976) ( $DIV_{diff}$ ). Zmienność losową określano za pomocą równań regresji, obliczając w poszczególnych fazach średnią względną różnicę między zmiennymi zależnymi rzeczywistymi i zmiennymi zależnymi oczekiwanymi dla odpowiednich zmiennych niezależnych czasu (wzory 1–3, rozdz. 3, rys. 1).

W pierwszych 15 latach sukcesji przeważa zmienność kierunkowa badanych parametrów, w późniejszych stadiach decydującego znaczenia nabiera zmienność losowa, fluktuacyjna (rys. 2–4). Zmienność całkowita awifauny w całej serii sukcesyjnej kształtuje się ogólnie według krzywej nierównomiernie opadającej w stosunku do skali czasu, a jej wyznaczniki zbliżają się do dolnej asymptoty w fazach starszych. Od tej tendencji bywają pewne odstępstwa, np. bardzo podatna na zmiany liczebność ptaków wykazuje silniejsze rozchwianie w fazie klimaksowej (FV) niż w przedklimaksowej (FIV), o czym decyduje kilka gatunków

dominujących (tab. IV–V, rys. 5). W dwóch pierwszych fazach  $CV_N$  jest 4-krotnie,  $CV_H$  – 18-krotnie i  $DIV_{diff}$  ok. 10-krotnie większy niż w dwóch ostatnich.

Zmienność losowa na początku sukcesji jest stosunkowo mała, w fazie zarosłowej (FII) osiąga ona maksimum, po czym w różnym stopniu maleje w fazach finalnych (rys. 6). Ocena zmienności całkowitej i losowej prowadzi do stwierdzenia, że z postępem sukcesji na zrębie leśnym stabilność ptaków ogólnie wzrasta, jakkolwiek nie w każdym przypadku jest ona najniższa w fazie początkowej (FI) i nie zawsze najwyższa w fazie klimaksowej (FV). Wyniki te w ogólnym zarysie wspierają „model” sukcesji O d u m a (1969), zakładający wzrost stabilności (jako odporność) ekosystemu w miarę jego dojrzewania. Zmienność liczebna między zespołami ptaków jest na ogół niższa niż na poziomie pojedynczych populacji (tab. I–V); testy statystyczne nie wykluczają istnienia w ptasich zespołach biologicznych właściwości tłumiących zwykle większą zmienność populacyjną.

Wykazano ponadto wysoką korelację ( $\bar{r} \approx -90$ ) między zmiennością całkowitą a wielkością  $S$  i  $N$  zespołów, jak również między zmiennością całkowitą a różnorodnością  $H'$  ( $\bar{r} \approx -85$ ) (rys. 7). Zależności między zmiennością losową a liczebnością i różnorodnością awifauny są natomiast mniej klarowne (rys. 8–9). Wykazanie większej stabilności w zespołach bogatszych w gatunki i bardziej różnorodnych wspiera pogląd na relację „różnorodność–stabilność” reprezentowany przez M a c a r t h u r a (1955).

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2. Study area

3. Methods

4. Results

5. Discussion

6. Summary

7. Polish summary

8. References

## I. INTRODUCTION

The role of earthworms in organic, fertile soil formation is known since a century ago, when Darwin (1881) has published his book devoted to these problems. In the available

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