

## Successional trends in the energetics of forest bird communities

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Thirty forest bird communities were studied with regard to the changes in structural indices (number of species, density, biomass, species diversity  $H'$ ) and in energetics (energy flow  $A$ , production  $P$ , ecological efficiency  $P/A$ ) in temporal and spatial gradients. All these characteristics increase during temporal succession; in natural deciduous forest there is a two-peak pattern of the increase, with the maximum in 15-20 yr old forest ('time ecotone':  $A = 692.9$  Megajoules  $ha^{-1}$  season $^{-1}$ ,  $H' = 4.2$  bits). In artificially managed pine forest these indices rise monotonically, reaching a maximum in sub-climax ( $A = 426.2$  MJ  $ha^{-1}$  season $^{-1}$ ,  $H' = 4.2$  bits). In a deciduous forest a tendency exists to decrease the ecological efficiency (from 3% to 2%), while in a coniferous stand this variable remains low (2%) and almost constant during succession. In a spatial gradient, the highest values of energy flow and species diversity occur in forest stands with moderate soil/water regime and of ecotonal character ( $A = 851.2$  MJ  $ha^{-1}$  season $^{-1}$ ,  $H' = 4.5$  bits). All mature forest bird communities show similar values of diversity (4.2-4.5 bits) and ecological efficiency (appr. 2%), though they differ in the rate of energy flow. The relation of these findings to the current concepts of ecological succession are discussed.

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### 1. Introduction

Studies of bird communities that consider energetics are a relatively recent development (Uramoto 1961, Holmes and Sturges 1973, 1976, West and DeWolfe 1974, Weiner and Glowaciński 1975, Wiens and Nussbaum 1975, Wiens and Scott 1975, Wiens 1977, Alatalo 1978, Furness 1978, Smith and MacMahon 1981). Comprehensive evaluations of the productivity and energetics of bird communities during vegetational succession have apparently been made only for the birds of lowland forests in Poland (Glowaciński and Weiner 1977, 1980) and montane habitats in the western USA (Smith and MacMahon 1981), although several other

studies have considered changes in some functional parameters of bird communities along successional gradients (Karr 1968, Ferry and Frochot 1970, Väisänen and Järvinen 1977). Inclusion of the energetical variables to the description of the process of ecological succession has opened some new possibilities for analysis and interpretation of this process.

In this paper we intend to: (1) evaluate the energetics of breeding bird populations during central European forest succession based on recent surveys of 30 different communities; (2) determine relations between some energetic and structural indices of the bird communities; and (3) relate the patterns of these characteristics to current concepts of ecological succession.

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## 2. Methods

### 2.1. Study area

Our investigations were made in the Niepolomice Forest (20°12'–20°27' E, 50°01'–50°08' N) in southern Poland, east of Cracow. Niepolomice Forest is a typical, relatively large lowland forest of 11000 ha, situated in the shallow Vistula River Valley. South of the valley a system of older terraces ascend toward the foothills of the Carpathian mountains.

The tectonic, glacial, and fluvio-glacial processes of the Quaternary have resulted in the origin of the two main river terraces: higher (185–215 m elevation), of Pleistocene origin and lower (180–190 m), which is a result of erosion and silt accumulation from the Holocene Vistula River (Bzowski 1973).

This complex geological origin produces a large variety of habitats and ecosystems. In accordance with local water and soil conditions, various forest types have developed in this area. The low Holocene terrace is covered with wet and moist deciduous forests, chiefly oak-hornbeam stands and alderwoods (Denisiuk and Medwecka-Kornaś 1976). These forest associations are to a large extent natural. The more extensive and older Pleistocene terrace as well as the alluvial cone of the Raba River are occupied almost entirely by acidiphilous pine and oak-pine forests. This part of the Niepolomice Forest contains semi-natural and anthropogenic forest communities (Denisiuk and Dziewolski unpubl.). The lower (and younger) terraces are carved with the system of old river-beds of various age. The majority of them are already overgrown by swamp, meadow or even forest associations. The successions of river-beds constitute typical hydroseres of a primeval character. They are often accompanied, however, by secondary successions resulting from the influence of human activities (Dubiel 1973, Denisiuk 1976, Denisiuk and Medwecka-Kornaś 1976).

The general climate of the Niepolomice Forest is influenced by overlapping masses of oceanic and continental air, but local water conditions produce major variations on this general theme. Shallow water-sheds provide favorable conditions for swamps, which in the narrow confines of old river beds and of the Vistula and Raba rivers produces an increase in humidity and often fog. As a consequence the thermal regime of the Niepolomice Forest is distinctly less variable than in surrounding areas (Klein 1978). The mean annual temperature is 8°C, with extreme monthly average of 17.9°C (July), and of -4.8°C (January). The growing season lasts on the average 220 d (1 Apr–6 Oct), and the breeding season of birds lasts for approximately 150 d. The precipitation is relatively high and amounts roughly to 700 mm. Banasik (1978) provides a complete bibliography of detailed physiographic studies in the Niepolomice Forest.

### 2.2. Description of successional stands

Succession in the Niepolomice Forest is of two sorts: (1) short-term successions of secondary communities toward the potential natural types as determined by the actual habitat conditions ("autogenic series"), and (2) long-lasting successions toward a climatic-climax community which are related to the changes in soil/water conditions ("allogenic series": Denisiuk and Medwecka-Kornaś 1976).

The successional development of bird communities was studied in two secondary autogenic series (Głowaciński 1981a, Głowaciński and Weiner unpubl.), proceeding from moist alderwood to arid pine forest (Denisiuk and Medwecka-Kornaś 1976, Medwecka-Kornaś, Denisiuk and Dziewolski unpubl.).

(1) The autogenic series of a deciduous forest of the Quercu-Carpinetum association ("AUT-I") which develops under limited forest management; Głowaciński and Weiner (1977) described 16 stages of this series, from a clear cut to the local climax.

(2) The autogenic series in a pine forest ("AUT-II"), an association showing intermediate characteristics between a mixed Pino-Quercetum forest and a dry pine forest of the Vaccinio myrtilli-Pinetum association. It consists of five stages, from a clear cut to a near-mature forest (subclimax). The forest regeneration in this series is semi-natural, and intensively managed (Głowaciński and Weiner 1980).

(3) The allogenic series ("ALL") consisted of the following stages: (1) moist alder wood *Circaeo alnetum*, a typical form of the forest association; → (2) alder wood × oak-hornbeam forest (intermediate association); → (3) oak-hornbeam forest Quercu-Carpinetum (typical); → (4) oak-hornbeam × oak-pine forest (intermediate); → (5) oak-pine forest Pino-Quercetum (typical); → (6) pine forest with oak and birch (intermediate); → (7) dry pine forest Vaccinio myrtilli-Pinetum (typical). A detailed description of this successional series is presented elsewhere (Głowaciński 1981a, Głowaciński and Weiner unpubl.). All the stages of allogenic series considered here are presented by mature forests of about 100 yr old.

In addition, two bird communities of mature forests were studied: a climax oak-pine forest (stage 4') and a subclimax oak-pine forest with an admixture of artificially planted spruce *Picea excelsa* (stage 4''). All of these succession gradients occur in a relatively small geographical area of Niepolomice Forest.

The secondary succession AUT-I was studied in a lower part of the terrain, while the AUT-II series was examined on the upper terrace of the Vistula River; the succession occurring on a moisture gradient (ALL) was described basing on the most representative forest associations in the area (Denisiuk et al. 1977, Denisiuk and Dziewolski unpubl.), as extended on a meridional cross-section of the Niepolomice Forest (see Głowaciński 1981a, 1981b).

### 2.3. Field studies and the structural indices of bird communities

The successional series were traced back, from pedological and botanical surveys. The series AUT-I was studied most carefully; in this case the comparative method was complemented with the direct observations of several stages during consecutive years (see Glowaciński and Weiner 1977). The allogenic series was described by contemporary comparisons of typical stages as well as of some transitory ones. In this paper the ALL series and the communities 4' and 4'' are used only as a complement to the comparison of autogenic series.

Only breeding bird communities were studied. The series AUT-I was studied during 1967–1975; AUT-II in 1975, and ALL during 1967–1977. Breeding bird density ( $N$ ) was estimated using the mapping method with corrections improving its efficiency (Glowaciński 1975a). The number of "pairs" of the cuckoo *Cuculus canorus* was roughly estimated as a half of the average number of individuals recorded in all censuses. Field methods and census data were presented elsewhere (Glowaciński 1975b, Glowaciński and Weiner 1977, 1980). The study plots were of 5–10 ha for early stages of succession (brush and thicket), and usually over 10 ha for mature forests.

Species diversity ( $H'$ ) was estimated using the Shannon's formula:

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

where  $S$  = number of species in the community and  $p_i$  = the fraction of individuals belonging to the  $i$ :th species. Evenness ( $J'$ ) of bird communities was estimated according to Pielou's (1966) formula:  $J' = H'/\log_2 S$ .

The indices  $H'$  and  $J'$  were also estimated in terms of standing crop biomass ( $H'_{sc}$  and  $J'_{sc}$ ), energy assimilation ( $H'_a$  and  $J'_a$ ) and production ( $H'_p$  and  $J'_p$ ), where  $p_i$  was substituted with the proportion of total standing crop, assimilation, and production of the  $i$ :th species, respectively.

### 2.4. Energetic calculations

The estimates of energy flow are based on computer simulations. The model used has been described previously (Glowaciński and Weiner 1977, 1980) and it is comparable with that of Wiens and Innis (1974). Population dynamics of adults and juveniles were simulated according to the breeding density, phenology, mortality rate and breeding success as estimated in the field. Energy computations followed the general functions of Kendeigh et al. (1977). The energy requirements for maintenance were estimated as functions of body weight and temperature. The appropriate corrections

for the free living activity, activity increase during nest building and nestlings' care period were added to the maintenance expenditures (Kendeigh et al. 1977, Glowaciński and Weiner 1980). The energy costs of egg production and growth of nestlings were also included. The energy demands of a population were then distributed in time according to the phenology of the species. The model included 21 parameters: 3 local population-specific parameters derived from the field studies (maximum breeding density, date of the arrival or onset of breeding for residents, ambient temperatures), 10 species-specific parameters taken mostly from the literature and supplemented with the author's own field data (body weight, egg weight, clutch size, 5 phenological parameters, breeding success, proportion of the population taking part in each brood), and 8 model-specific literature-based parameters (mortality rates of adults and fledglings, caloric values of the body and eggs, all parameters of metabolic functions). The lack of appropriate field data prevented us from specifying biological parameters separately for bird populations from various habitats. This simplification, however, is of a minor significance when compared with other rough assumptions unavoidable in such modelling and taking into account the great number of species considered. The simulations covered only the breeding season (15 Mar–15 Aug), so it does not include the period of intense dispersion and departure of migrants. The seasonal dynamics and seasonal sums of energetic variables (respiration, production, assimilation, consumption) for each species as well as for the whole community were given as model outputs. The results are expressed in Joules (J) or Joules per hectare per season ( $J \text{ ha}^{-1} \text{ season}^{-1}$ ) and derived units (kJ, MJ).

## 3. Results and discussion

### 3.1. Community structure and standing crop

In both of the successional autogenic series studied basic avian community structural attributes (number of species  $S$ , density  $N$ , species diversity  $H'$ ) increase discontinuously to a peak in late succession (Figs 1, 2, 3). In the more natural series AUT-I, the values of  $S$ ,  $N$  and  $H'$  increase very rapidly during the first 15 yr of succession, later on all these indices decrease by almost 25% in a 25–30 yr old forest, and rise again towards final stages.

The curves characterizing these indices thus had two peaks with maxima in concluding stages ( $S$ ) and in young forests ( $N$  and  $H'$ ). In the semi-natural series AUT-II the general trend was similar although the peaks are not as distinct in early stages. The extent to which a smaller number of sample sites influence this difference is not known.

Such trends in species number and diversity, as well as a distinct peak of density in early stages of different forest types and a decrease of these indices in a 25–30

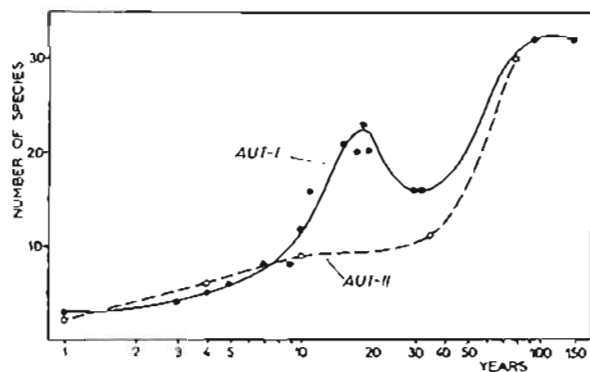


Fig. 1. Changes in the number of species ( $S$ ) of bird communities during autogenic successions AUT-I (solid circles, solid line) and AUT-II (open circles, broken line). Logarithmic time scale.

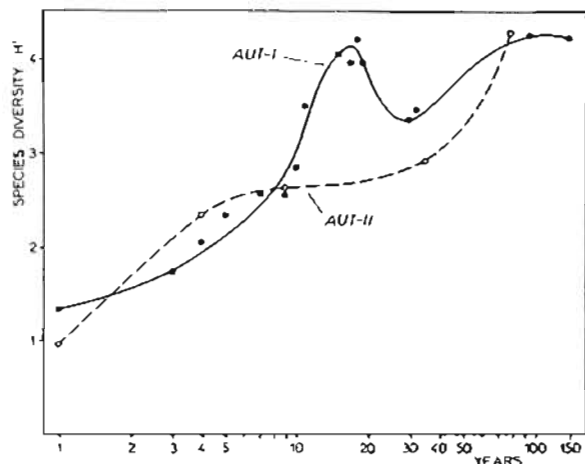


Fig. 2. Changes of the bird species diversity ( $H'$ ) during succession. Symbols as on Fig. 1.

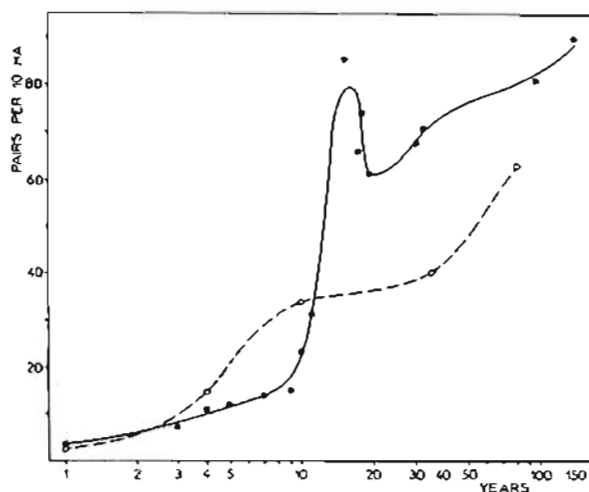


Fig. 3. Changes in the bird density ( $N$ ) during succession. Symbols as on Fig. 1.

yr old forests have also been observed by other authors. The pattern occurs in silvicultures (Lack 1939, Pospelov 1957, Dierschke 1973) as well as in forests regenerating without human interference (Haapanen 1965, Johnston and Odum 1965, Pikula 1967, Ferry and Frochot 1970). The rate of structural change in the avifauna is higher by 10–30 times during the early phases than in concluding stages (Głowaciński and Järvinen 1975). This may be related to the higher turnover rate of the biotic habitat, to the selectional pressure favouring rapidly growing species ("r-selection"), and/or to the relatively high productivity of the forest ecosystems during early development stages (see Odum 1971: 251–275). Birds respond rapidly and in a complex manner to changes in habitat characteristics (Hildén 1965, and others).

Several studies have shown a strong correlation between vegetation physiognomy or habitat structure (e.g. foliage height diversity), and the basic features of bird communities (Recher and Cody 1966, Karr and Roth 1971). In our study, bird densities (and consequently, the ecological indices) are strikingly higher in the respective successional stages of a deciduous forest than in the coniferous one. These differences increase during forest development and reach the maximum (ca 30%) in the avifauna of old forests. In the mature stages, on the other hand, the number of species and species diversity of both autogenic series are more convergent. Climax bird communities consist of approximately 35 species which results in a diversity index of about 4.0; in comparison with allogenic series, this corresponds with the values for moderately humid mature habitats.

The bird communities of extremely humid (series ALL, stage 1), and extremely dry (series ALL, stage 7) habitats have fewer species ( $S = 25-26$ ); and lower diversity ( $H'$  about 4.0), while the transitory (2 and 4), and climax stages (3' and 4') are the richest ( $S =$  over 35 species,  $H' =$  above 4.5). Community standing crop (SC) in the series AUT-I reaches a peak in the 15 yr forest ( $1332 \text{ g ha}^{-1} = 106 \text{ MJ ha}^{-1}$ ). At this stage the community SC is 40% higher than in the 150 yr climax forest. A similar pattern of SC changes occurs in the series AUT-II, but the maximum apparently falls at the stage of mature forests (Fig. 4). The distinct peak of standing crop in the young and climax forests occurs as a consequence of a high bird density and/or the occurrence of relatively large species. In the series AUT-I in early successional stages the pheasant *Phasianus colchicus* plays an important role. This species was introduced to Poland very long ago. Till the stage of a 20-yr old forest, the occurrence of the pheasant causes almost a two-fold increase community biomass in until forest reach 20 yr of age (Fig. 4), affecting also other community characteristics. The inclusion or exclusion of pheasant to the community may substantially change the above interpretation as well as further results. If this species is included a general (though unsteady) increase of SC toward the later suc-

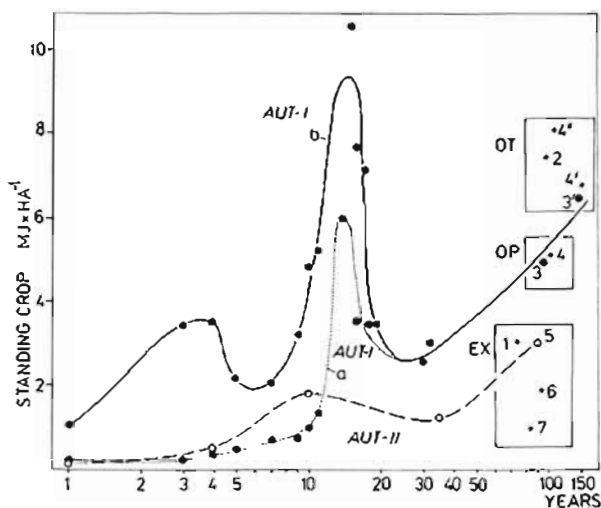


Fig. 4. Changes in bird community standing crop (SC) during succession. AUT-I (solid circles, a - dotted line: excluding pheasant; b - solid line: including pheasant), and AUT-II (open circles, broken line). OT - bird communities of mature and transitory forest associations; OP - bird communities of optimal forest stands; EX - bird communities of the forests with the extreme soil and water conditions. Logarithmic time scale.

cessional stages is apparent. On the other hand, the pheasant has replaced other gallinaceous bird species (e.g. black grouse *Lyrurus tetrix*) which formerly inhabited the area, and probably influenced the bird community properties in a similar manner.

The bird communities of mature autogenic series (3, 3', 4', 5) together with the communities of ALL series (which includes stages 3 and 5 of series AUT-I and AUT-II, and 4''), can be divided into three gradient groups: (1) extreme habitat communities (EX) with a very low standing crop, (2) the communities of mesic habitats (OP), and (3) a group of the climax or intermediate communities (OT), with relatively high SC (Fig. 4).

### 3.2. Average body size

Changes in the average biomass of individuals (SC/INDIV) in the series AUT-I and AUT-II do not show a clear pattern during succession. If the pheasant is excluded, a slight two-peak pattern is apparent in both series (Fig. 5). This seems to support weakly the thesis that the species adapted to the more mature stages tend to have larger body sizes. This is consistent with the observations of Karr (1968) and Ferry and Frochot (1970), but contrasts with those of Bock and Lynch (1970) and Smith and MacMahon (1981). Also the results for the series AUT-I remain in contradiction with this postulate, when the pheasant is included into the community (Fig. 5).

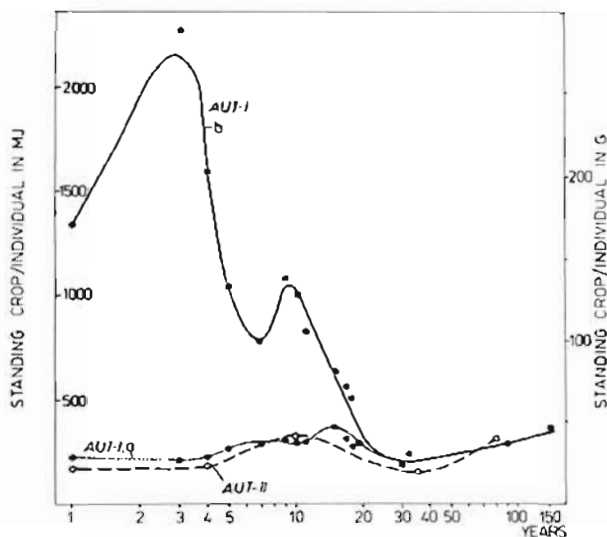


Fig. 5. Changes in average bird size (standing crop per individual) in bird communities during succession. Symbols as on Fig. 4.

### 3.3. Energy flow and production

The energy flow (assimilation; Fig. 6) increases rapidly but unevenly in the series AUT-I, from 44.0 MJ ha<sup>-1</sup> season<sup>-1</sup> in the initial stage to as much as 692.9 MJ ha<sup>-1</sup> season<sup>-1</sup> in 15 yr forest. In the later stages, particularly in the 20–30 yr forest, a rapid decrease of community assimilation occurs (393.6–410.3 MJ ha<sup>-1</sup> season<sup>-1</sup>). Thereafter the rate of energy flow rises again, reaching the maximum in a climax forest (734.8 MJ ha<sup>-1</sup> season<sup>-1</sup>).

Changes in production follow a similar pattern, although at much lower energetic level (production con-

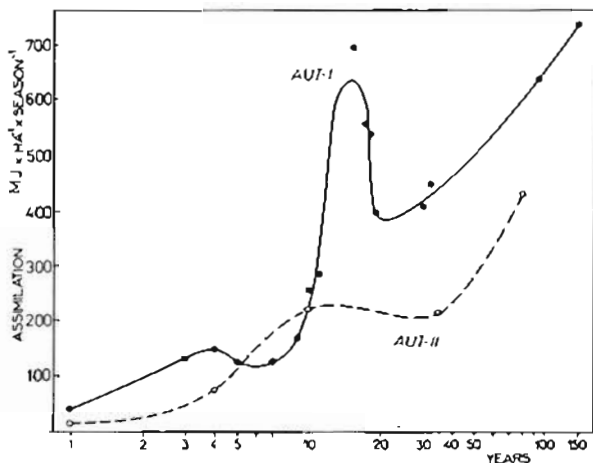


Fig. 6. Changes in energy assimilation (A) of the bird communities during succession. Symbols as on Fig. 1.

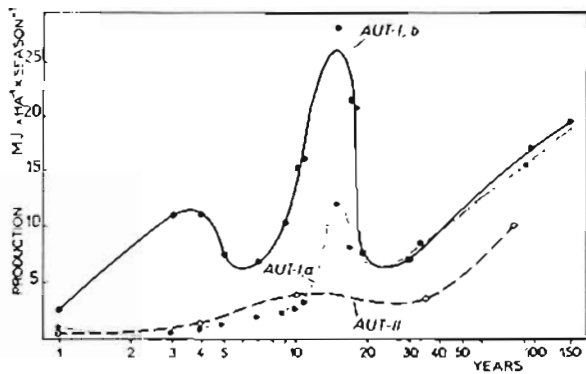


Fig. 7. Production (P) of the bird communities during succession. Symbols as on Fig. 4.

sists of 1.7–8.4% of assimilation, Fig. 7). Assimilation (Fig. 6) and production (Fig. 7) of birds in the successional series AUT-II increase almost monotonically, but the increase is also markedly higher at the stage of young forest (e.g.  $A = 219.0 \text{ MJ ha}^{-1} \text{ season}^{-1}$ ), and mature forest ( $A = 426.2 \text{ MJ ha}^{-1} \text{ season}^{-1}$ ). The two-peak pattern characteristic of AUT-I is absent in AUT-II. The rate of energy flow and production in the bird communities of semi-natural coniferous forest are lower by 20–75% than in the respective stages of deciduous forest (Figs 6, 7).

The productivity of the avifauna is distinctly higher in forests with moderate and transitory habitat regimes (alder-oak, oak-hornbeam, and oak-pine forests) than in forests of extreme habitats (moist alder wood, and dry pine wood). Among the mature woods of the Niepolomice Forest, the energy flow is highest in the mixed alder-oak forest ( $A = 851.2 \text{ MJ ha}^{-1} \text{ season}^{-1}$ ), while in a dry pine forest it is 5 times lower (Głowaciński and Weiner unpubl.). A comparison of the avian communities of the series AUT-I and AUT-II reveals analogous differences between the forest types at different stages of secondary succession.

The share of birds in the ecosystem energy flow is small and it hardly reaches 0.5% of primary production. This amount however may represent 2 to 10% of insect production (Głowaciński et al. in print).

### 3.4. Turnover and ecological efficiency

Biomass turnover ( $P/SC$ ) in bird communities of both series remains approximately equal (3.0). The fluctuations of this coefficient are slightly higher in AUT-II (2.17–3.62) than in AUT-I (2.51–3.23). In the autogenic series of a deciduous forest up to the stage of young forest the turnover ratio slightly exceeds 3.0, while in older formations it is usually lower than 3.0. In mature forests the turnover fluctuates between 2.49 and 3.64 (Głowaciński and Weiner unpubl.). In the allogenic series, which includes the final stages of au-

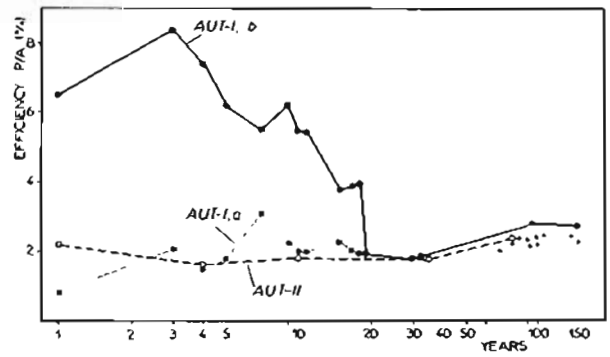


Fig. 8. Changes in the ecological efficiency (P/A) of bird communities during succession. Mature stands (ALL) not included in autogenic series are marked with crosses. Other symbols as on Fig. 4.

togenic series AUT-I and AUT-II, the turnover ratio is higher in extreme habitats (well above 3.0) than in the intermediate ones (usually below 3).

The ecological efficiency ( $P/A$ ) is almost constant throughout the series, oscillating around a value of 2%. On the other hand, in the more natural series AUT-I this index decreases from approximately 8% to 2% during the first 30 yr of succession, stabilizing at a level of 3%. The exclusion of pheasant, however, brings the two patterns of AUT-I and AUT-II back together (Fig. 8). In mature forests of allogenic series ALL, efficiency is 2.0–2.6% (Fig. 8, Głowaciński and Weiner unpubl.).

The two autogenic series differ most markedly in ecological efficiency. While the changes in  $P/A$  in the series AUT-I do agree with the generally predicted trends in succession, the efficiency is low and stable in the whole series AUT-II. It is, however, possible that this series does not represent a true successional series, but merely a combination of causal avian aggregations occupying semi-artificial forest cultures.

### 3.5. Energy flow and species diversity

The rate of energy flow ( $A$ ) through bird communities of both autogenic series seems to correlate exponentially with species diversity ( $H'$ ; Fig. 9), and the communities of the allogenic series also follow this pattern. It is difficult, however, to understand the meaning of this relationship, as both of these variables are related to  $S$  and  $N$  by definition. In some theoretical considerations (Margalef 1968) it is argued that energy flow reflects the "energetic costs of accumulation of information". These verbal considerations are still lacking any straightforward meaning. On the other hand the greater variability (more energy channels) may provide better stability and energetic efficiency of animal communities (MacArthur 1955).

The relationship between species diversity ( $H'$ ) and production ( $P$ ) in birds is not as clear. The communities

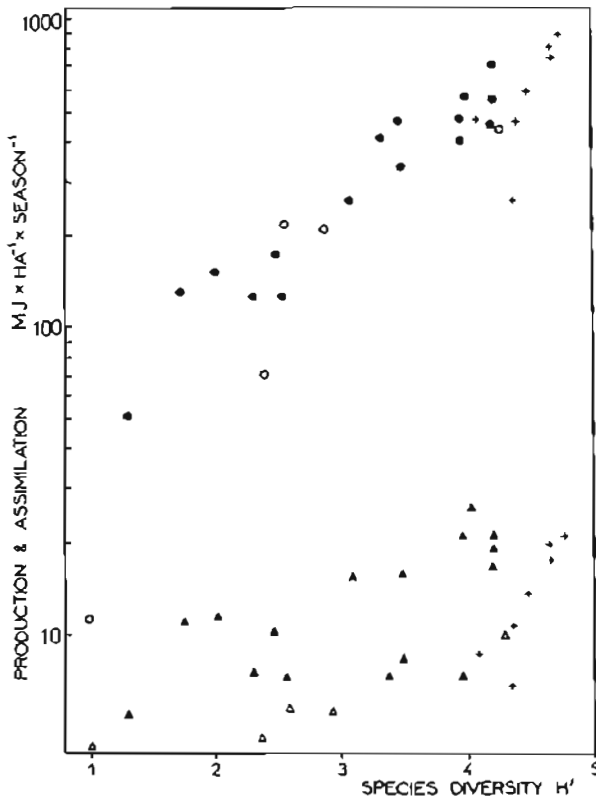


Fig. 9. Correlation between species diversity ( $H'$ ) and assimilation (A) – circles; and between species diversity ( $H'$ ) and production (P) – triangles. Solid symbols: AUT-I; open symbols: AUT-II. Other communities marked with crosses. Logarithmic scale for P and A.

of the series AUT-II and ALL show an exponential relationship, but this relationship does not occur in AUT-I. If all of the communities are considered jointly, the pattern of this relationship remains unclear (Fig. 9). This suggests that the productivity of bird communities is not related simply to their density. Whittaker (1965, 1966) has shown that diversity and productivity are weakly related also in the communities of vascular plants (Drury and Nisbet 1973).

### 3.6. Ecological efficiency and species diversity

The correlation between ecological efficiency ( $P/A$ ) and species diversity ( $H'$ ) is more interesting (Fig. 10). In the successional series AUT-I a distinct negative correlation exists, and in the course of time this relationship proceeds from high efficiency (6–8%) and low diversity (1.0–2.5), toward low efficiency (1.5–2.5%) and high diversity (ca 4.0). This effect is caused by the occurrence of pheasant which affects strongly the value of  $P/A$ , and only slightly that of  $H'$ . In the series AUT-II the efficiency is low (ca 2%) and almost con-

stant, while diversity increases toward mature stages. Both successions converge in the phase space ( $P/A = 1.5$ –2.5%,  $H' = 4.0$ –4.8). This is also true for the bird communities of various old forests that develop under different soil and water conditions (Fig. 10).

### 3.7. Diversity and equitability of energy flow

Species diversity calculated from the numbers of individuals ( $H'_n$ ) and from the distribution of assimilation energy ( $H'_s$ ), production ( $H'_p$ ) and standing crop ( $H'_c$ ), follow different patterns in the autogenic series. In the more natural series AUT-I these parameters differ during the first 20 yr of succession and reach almost equal values. In general,  $H'_n$ ,  $H'_s$ ,  $H'_p$  and  $H'_c$  increase during the first 20 yr, reaching the level of approximately 4.0, and then stabilize after a slight depression in intermediate stages (Fig. 11a). In the series AUT-II the patterns of changes in all diversity estimates are parallel increasing continuously from the initial stages (Fig. 11a). The two stages of diversity change apparent in the series AUT-I, are absent in AUT-II.

The community equitability as calculated using the numbers of individuals ( $J'_n$ ), maintaining a consistently and high level of ca 0.85 in the whole series AUT-I (Głowaciński and Weiner 1977). The analogous coeffi-

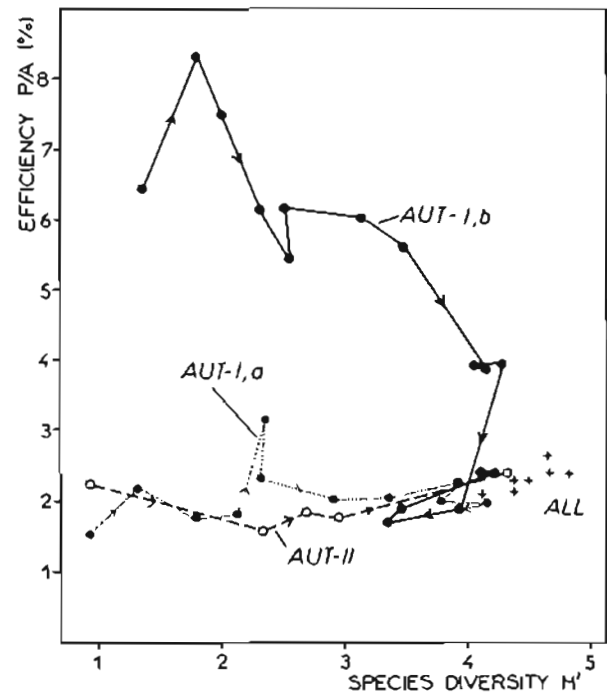


Fig. 10. Correlation between species diversity ( $H'$ ) and ecological efficiency ( $P/A$ ). Time array marked with lines (solid: AUT-I; dotted: AUT-I without pheasant; broken: AUT-II). Crosses denote bird communities of mature forest making up the ALL series.

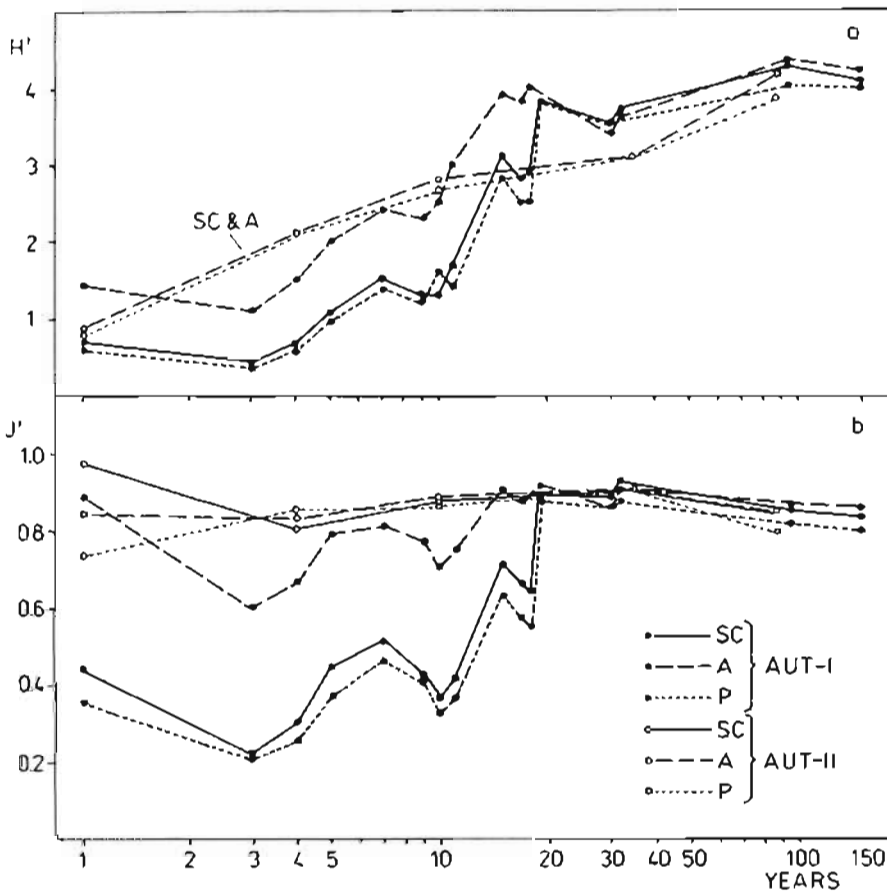


Fig. 11. a: diversity ( $H'$ ) and b: equitability ( $J'$ ) changes in energy distribution in bird communities during succession. Logarithmic time scale.

coefficients estimated on the basis of the distribution of assimilation energy ( $J'_a$ ), production ( $J'_p$ ) and standing crop ( $J'_c$ ) during the first 20 yr of succession are generally lower than  $J'_n$ .  $J'_a$  has an exceptionally high value of 0.9 at the initial stage. The equitability of assimilation distribution among the species ( $J'_a$ ) during the stages of clear cuts and young forests is higher than those of  $J'_p$  and  $J'_c$ . Following the 20 yr forest, all the equitability estimates stabilize at nearly maximum level (Fig. 11b). It means, that in early succession various species contribute in an unequal manner to the community assimilation, production and standing crop, despite of the apparently high equitability of species population numbers. In a semi-natural series of coniferous forest (AUT-II) all estimates of  $J'$  are similar, at the level of 0.8–0.9 (Fig. 11b; Głowaciński and Weiner 1980), although at the initial stage the variability of these parameters is somewhat greater ( $J'_p = 0.74$ ,  $J'_n = 0.99$ ).  $J'_n$  has a similar pattern in both series compared, but the marked difference in the other equitability coefficients suggests that the processes of avifauna development follow different ways in the two series.

### 3.8. Trends in the structural and energetic changes in forest bird communities

Both autogenic developmental series differ in many qualitative (species composition, patterns of changes in  $H'$ ,  $J'$ , energy, and P/A), as well as quantitative characteristics (the values of N, SC, A, P, and others). Some ecological variables are, however, very similar at the final stages of succession. In other words, the development of the forest avifauna may follow different pathways, depending on local conditions, but the maturation leads to a common final pattern. The features of the bird communities at this last phase (quantitative characteristics of diversity and the relations between energy flow, production, and ecological efficiency) are virtually identical for all mature bird communities of the Niepołomic Forest.

The general relations between these communities are shown on the three-dimensional diagram of energy flow (Fig. 12), which clearly shows that the rate of energy flow is distinctly higher in the communities developed in moderate conditions of the habitat gradient and in the transitory communities of ecotonal character (series ALL). The maximum rate of energy flow (stage 2 of



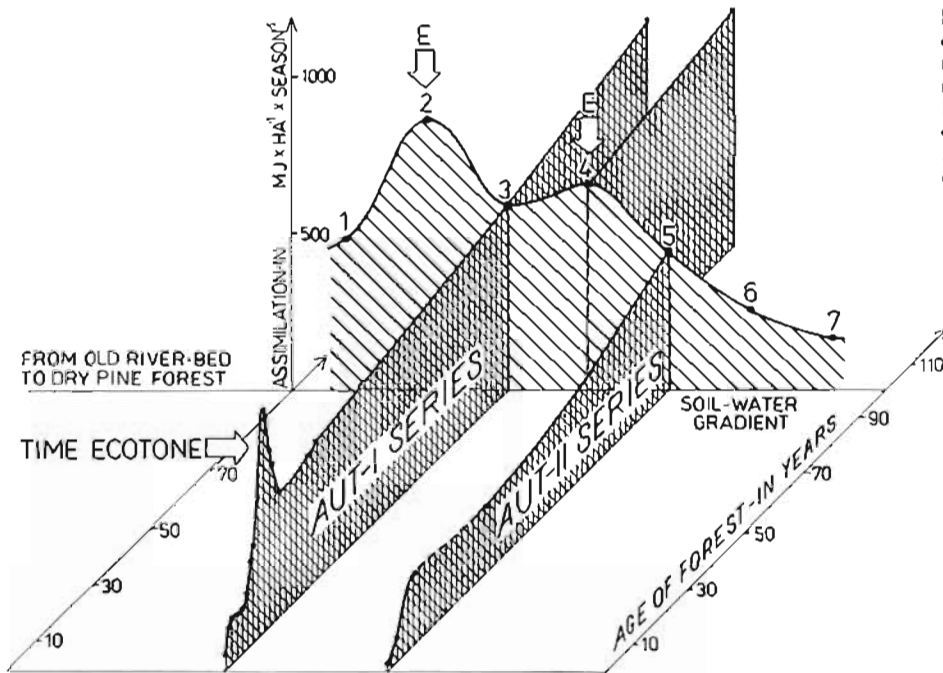


Fig. 12. Three-dimensional diagram of energy flow through various bird communities in the Niepolomice Forest. Communities 1-7 constitute a gradient series ALL. E - communities of ecotonal character.

series ALL) is 5 times higher than the minimal one (stage 7).

This diagram illustrates the previous statement, that the patterns of changes in bird community energetics differ only during the first 15-20 yr of forest development, and later on the changes in energetic parameters are parallel. The distinct peak in energy flow at younger stages of natural succession (AUT-I) is connected with the transition from the younger phase of a brushwood to the older one - a typical forest. We define this effect a "time ecotone", since it resembles the effect of a spatial ecotone (Fig. 12; Głowaciński and Weiner 1977).

#### 4. Processes in bird communities and the recent concepts of succession

Among the various concepts of ecological succession (Clements 1916, Margalef 1968, Odum 1969, 1971, Horn 1974, 1976) the "cybernetic" interpretation of this process (Margalef 1968, Odum 1969, 1971) allows a test of some theoretical assumptions as stated by the authors of this concept (e.g. Odum 1969).

The structural parameters of bird communities developing in clearcuts of the Niepolomice Forest support only partly the successional "rules" defined by Odum (1969) and Margalef (1968) for the whole ecosystems (Głowaciński 1975b, 1981, Głowaciński and Weiner 1977, 1980). The functional and energetic parameters also do not confirm the theoretical predictions.

The tabularized scheme of succession (Odum 1969) postulates, among others, that an increase of produc-

tion, biomass and average size of organisms occurs during the course of ecosystem development. In birds, there is a general increase of A, P, SC, and SC/INDIV, but showing a two-peak pattern, with a maximum at the young forest stage rather than in climax. The Odum-Margalef model is corroborated starting from the medium-age stage of a typical forest. Our findings do not allow us to determine whether the average body size of animals tends to increase in older stages of ecosystem development, although the trend is positive if pheasant is excluded from series AUT-I.

The theoretical model of succession does not predict the phenomenon that we have defined as the "time ecotone".

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