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**Effect of age differentiation of the pine forests of Puszcza Białowieska
on faunal resources and diversity**

Abstract. A decrease in the degree of age differentiation of forests stands in Puszcza Białowieska is accompanied by a 50–60% reduction in the number of species of zoophages or sucking and chewing phytophages and a 10–25% reduction in the number of xylo- and cambiohages. The preservation of age differentiation favours the development of useful fauna with an inconsiderable increase in the number of secondary pest species. With the age of the stands becoming uniform (the forest getting older), faunal diversity is usually reduced, while the degree of its utilisation in the organisation of the forest zoocenosis is increased.

The species diversity of the fauna of a given area depends, among other factors, on the patchiness degree of the habitat and the diversification of the plant cover. In systems characterised by a homogeneous habitat and flora, diversity may be determined primarily by the age of the various enclaves forming one phytosociological group. Such situation can be observed in forest complexes, especially those utilised for economic purposes, where the plots contain even-aged stands in various developmental stages from plantings to mature stands.

The aim of the following paper is to examine how the age differentiation of the pine forests of Puszcza Białowieska affects faunal resources and species diversity.

The forests under consideration are characterised by the following:

1. They are located on soils from the class of Spodosol. The forests represent the typical association of *Peucedano-Pinetum* subcontinental pine forest (MATUSZKIEWICZ, DEGÓRSKI, KOZŁOWSKA 1993).

2. The differentiating factor in the forest habitat is the age of the stand. It determines the unique characteristics of the microclimate, the species structure and the vertical structure of the plant cover as well as the amount and quality of the requisites providing a trophic base for the animals.

3. The spatial structure of forest areas with stands of different ages contributes to landscape diversification. The ecosystems forming the landscape are subject to silvicultural practices and renewed by means of planting.

4. The series composed of the forest stands from the planting stage to the mature stage (approximately 150 years in Puszcza Białowieska) functions also as a secondary sere where the structure of the ecosystem is restored and faunal communities are formed.

The last three factors, i.e. the different habitats forming in stands of different ages, their patchy spatial arrangement and the ecological aspect of the time factor expressed as succession-related changes, determine the species diversity of the entire system. That parameter was assessed using the following diversity measures:

1. the empirical number of species (S)

2. Shannon and Weaver's measure. $H' = - \sum_{i=1}^S p_i \log_2 p_i$

3. the derivative measures of H'_{\max} and J (see TROJAN 1992, 1994).

The materials analysed in this paper supplement a broader work on faunal succession in the pine forests of Puszcza Białowieska (TROJAN et al. 1994).

In this paper the degree of age differentiation of the pine forest stands was considered the basic differentiating factor for the faunal material. 4 age classes were distinguished: 1. tree plantings, 2. young stands, 3. pole wood, 4. mature forest. Their time ranges are the same as used in forestry. 4 degrees of age differentiation of the forest were used and defined as follows:

1. mature stands only
2. mature stands and pole wood
3. mature stands, pole wood and young stands
4. mature stands, pole wood, young stands and plantings

The value of species diversity for each degree of differentiation was calculated by combining faunal materials collected in one, two, three or four stand age classes.

The reduction in the number of animal species due to a decrease in age differentiation, i.e. the stands becoming uniform or ageing (Fig. 1), is the most conspicuous unidirectional process observed in the fauna of pine forests. Two types of response are seen:

1. High-degree reduction, when the number of species in the mature stage decreases to about 50–60% of that found for all the age stages of the stands. This type of reduction is most profoundly marked in the group of sucking phytophages and parasitoids, being somewhat less intense in non-specialised predators. The group also includes chewing phytophages and aphidophages, which, however, exhibit a lesser degree of reduction. The number of their species in older stands is nearly half of those occurring in all age classes of the pine forests taken together.

2. Low-degree reduction, when the number of species decreases to 75–90% of the species registered in all the age classes. This group comprises xylophages and cambiohages, among which are found secondary pests of pine, as well as polyphages and soil predators, which are less affected by the ageing of pine forests.

Both types of response indicate that the process of the age uniformity of forest stands, what is usually a result of mature forest being the preferred stage in silvicultural practices and reserve policy, leads to a major impoverishment of the faunal resources of pine forests. The mature forests can accommodate about half of the species associated with the various developmental stages of stands of pine. Another equally well-substantiated conclusion indicates that a rise in the degree of age differentiation of pine forest stands brings about a double increase in the numbers of useful animal species, including parasites of phytophages, predatory insects and aphidophages, while the number of species of secondary pests, including xylo- and cambiohages, will only rise by 10–25% at the most.

It is only on the background of the general fall in the number of species which is observed as pine forest stands become uniform and grow older that one can assess species diversity changes observed in particular faunal groups. The

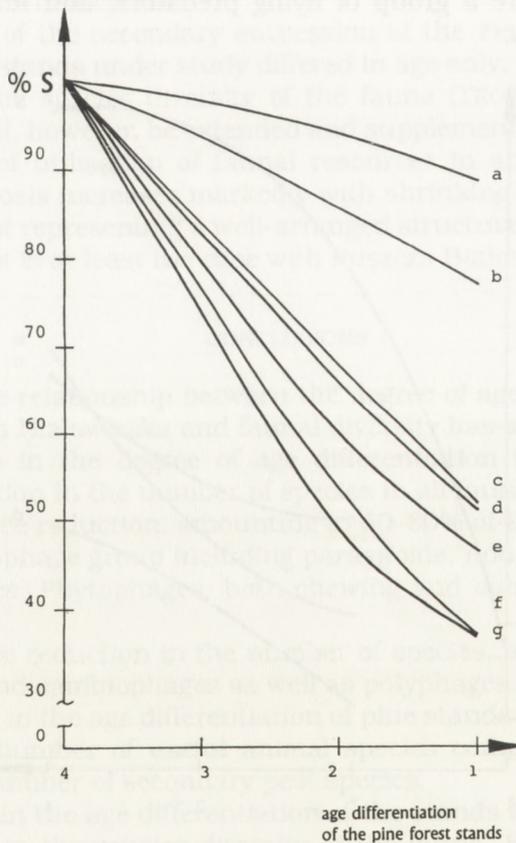


Fig. 1 Reduction in the number of species in various phagous groups of insects with decreasing age differentiation of the stand in the *Peucedano-Pinetum* pine forests: a - xylo and cambiohages, b - polyphages and soil predators, c - aphidophages, d - chewing phytophages, e - non-specialised predators, f - parasitoids, g - sucking phytophages; Extrapolation for S_4 : $S_4 = S_3 \frac{S_3 - S_1}{2}$

trends in actual diversity parallel those seen in the number of species. 16 out of 22 taxons studied register a decrease in diversity as the faunal resources of the group become smaller. It is known, however, that actual diversity is not a mere cumulation of the species diversity values observed in communities inhabiting different age classes of the forests. It is actually related to diversity observed both within the communities and between them (WHITTAKER 1972, BLONDEL 1979). Where the degrees of diversity of the niches are similar and the extent of species replacement limited, a reverse process may take place. An increase of diversity with the falling number of species was observed in 4 cases (Fig. 2). The 4 cases represent insect groups differing in feeding relations, namely, a group of sucking phytophages – leafhoppers (*Auchenorrhyncha*), the xylophagous buprestid beetles (*Buprestidae*), non-specialised flying predators – robber flies (*Asilidae*) and the aphidophagous ladybirds (*Coccinellidae*). A fall in actual diversity preceded by an initial rise was observed in 2 taxons: digger wasps (*Sphecidae*), which are a group of flying predators, and *Rhagionidae*, representing soil predators.

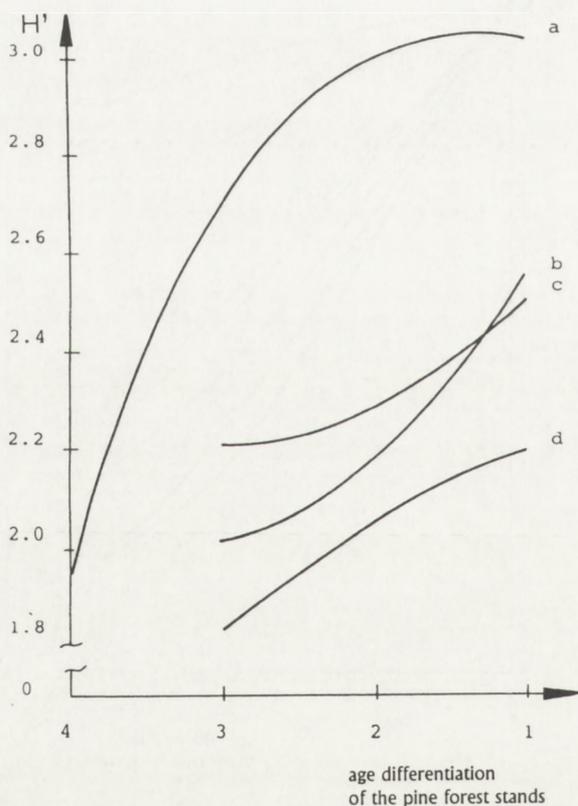


Fig. 2 Increase in the species diversity of insect with decreasing age differentiation of the *Peucedano-Pinetum* pine forest: a – buprestid beetles (*Buprestidae*), b – leafhoppers (*Auchenorrhyncha*), c – robber flies (*Asilidae*), d – ladybirds (*Coccinellidae*)

The utilisation of the potential for the formation of diversified ecological structures, where the potential is based on the current state of the fauna in a mature forest ecosystem, may be estimated with Pielou's index (J). In the study material, that index provides the most diversified representation of the progress of changes occurring as the stands of pine become more uniform. As the forest stand approximates the mature stage, there is a rise in the intensity of the process of increased utilisation of the shrinking species resources in a given taxocoene in order to build the inner diversity of the community. The values of (J) rise in nearly a third of the cases. The process is observed in both sucking and chewing phytophages as well as in predators. In a similar number of taxons an initial decrease in the value of (J) is transformed into a rise or at least checked. The period of decrease is always associated with the first degree of reduction in the age differentiation of pine forest: 4 to 3 or 3 to 2. If the age differentiation is further decreased, the degree of realisation of potential diversity becomes stabilised or begins to increase.

In the course of the secondary succession of the *Peucedano-Pinetum* pine forest, where the stands under study differed in age only, the dominant process is reduction of the species diversity of the fauna (TROJAN et al. 1994). This conclusion should, however, be extended and supplemented with the statement that the degree of utilisation of faunal resources in an attempt to form an organised zoocenosis increases markedly with shrinking faunal resources in a mature pine forest representing a well-arranged structure in terms of ecological organisation. This is at least the case with Puszcza Białowieska.

CONCLUSIONS

Analysis of the relationship between the degree of age differentiation of the stands in Puszcza Białowieska and faunal diversity has shown that:

1. A decrease in the degree of age differentiation is accompanied by a significant reduction in the number of species in all faunal groups.

2. A high-degree reduction, amounting to 50–60% of the number of species, is seen in the zoophage group including parasitoids, non-specialised predators and aphidophages. Phytophages, both chewing and sucking, follow a similar pattern.

3. A low-degree reduction in the number of species, amounting to 10–25%, occurs in xylo- and cambiohages as well as polyphages and soil predators.

4. An increase in the age differentiation of pine stands brings about a double increase in the number of useful animal species compared to only a slight increase in the number of secondary pest species.

5. A decrease in the age differentiation of the stands is not accompanied by a uniform trend in the species diversity of the fauna. However, the response consisting in a decrease in actual diversity may be considered to prevail.

6. As the pine forest stands in a *Peucedano-Pinetum* forest grow older (acquire a more uniform age structure) the resources of the invertebrate fauna shrink,

while a rise is observed in the degree of utilisation of the fauna in order to set up the structures of a mature and stable zoocenosis.

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STRESZCZENIE

[Tytuł: Wpływ zróżnicowania wiekowego borów sosnowych Puszczy Białowieskiej na zasoby i różnorodność fauny]

W przypadku jednorodnego pod względem siedliskowym i fitosocjologicznym boru sosnowego świeżego na glebach bielicoziemnych, reprezentującego zespół *Peucedano-Pinetum*, czynnikiem różnicującym warunki środowiskowe jest wiek drzewostanów.

Wpływa on na zasoby i różnorodność fauny, przy czym wraz ze spadkiem stopnia różnorodności wiekowej drzewostanów sosnowych ma miejsce wyraźna redukcja liczby gatunków wszystkich grup fauny. Przy tym redukcja wysoka (50–60%) obejmuje wszystkie grupy zoofagów oraz fitofagi zgryzające i ssące. Redukcja niska (10–25%) dotyczy ksylo- i kambiofagów. Tym samym wzrost zróżnicowania wiekowego drzewostanów w krajobrazie powoduje dwukrotny wzrost zasobów faunistycznych, przede wszystkim gatunków pożytecznych.

Spadkowi różnorodności wiekowej towarzyszą niejednakowe reakcje różnorodności gatunkowej fauny, jednak decydujące znaczenie ma jej redukcja. Tym malejącym tendencjom towarzyszy jednak zwiększony stopień wykorzystania uszczuplonych zasobów, które zostają wbudowane w struktury dojrzałej biocenozy leśnej.