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**The succession of fauna
in the Białowieża primeval pine forest**

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Abstract. Multidirectional hypothesis of the secondary succession of fauna is considered. It contains five types of succession: creative, stabilising, rise-and-fall, regressive and restorative. The verification of these hypotheses during pine forest development is based on changes in the number of species, their abundance, the structure of the taxocoenes, actual and potential species diversity. 27 taxons (families or orders) with 1247 species occurring in Białowieża primeval pine forest served as a material for comparisons. They represent all main trophic types of the fauna: phytophages, predators, parasites and saprophages among invertebrates, and also birds and mammals. After the clear cutting of trees, no empty place appears with regard to fauna, which is the richest at this stage. The multidirectional character of the succession of fauna is predominant. Many indices decrease their values in the mature forest. Ecosystem stability is ensured by the better adapted forms while the potential diversity is not fully realised.

1. INTRODUCTION

1.1. Study objectives

The formation of forest ecosystems takes a long time. Depending on the initial state of the environment, the process may follow one of two possible patterns. The first pattern is observed when a forest develops on a formerly unforested site, i.e. when a forest is formed in the area for the first time. Such a process is called primary succession. The other pattern is activated when the forest develops in areas which were previously occupied by a forest ecosystem, so that one may speak of forest reconstruction in that case. It is usually started by planting trees in a clearing formed after forest felling or a forest fire. This process is termed secondary succession.

An example of primary succession is the formation of forest ecosystems in dune areas as a result of the drainage of Lake Chicago and the formation of the shoreline of Lake Michigan in the postglacial period. This object represents a classic example of forest development from the stage of a sandy beach to a maple-beech forest. The sere also includes a pine forest stage (COWLES 1899, SHELFORD 1913). It has helped to construct a theory of ecological succession:

the forming of this ecosystem took about 10,000 years; in the final stage, the vegetation cover attained considerable stability, while there are constant changes in the mineral cycling in the ecosystems (OLSON 1958).

European coniferous forests follow the other pattern – secondary succession. Cultivated, felled and afforested anew for hundreds of years, they become “ecologically mature” as soon as they reach the felling age. For the pine forest, the felling age is 80–150 years. This time span determines the total length of the process of secondary succession because forest felling renders impossible further transformations of both the habitat and the biocenosis, and the ecosystem returns to the initial stage with new cultures being planted.

European and American ecologists usually consider the processes of forest succession from the viewpoint of the climax theory. The theory states that the settling of the former forest habitat is the dominant phenomenon in the first stage of succession. In the second stage, specific subsystems are formed within the biocenosis. In the final stage of succession, after the forest ecosystem has developed, the ecosystem is adapted to the habitat conditions in the area, such as climatic factors. The resulting final and stable stage of succession is called the climatic climax. In some cases, however, the final stage of succession depends on the fertility of the soil habitat, and is termed the edaphic climax.

The process of succession is accompanied by changes in biocenoses and habitat conditions. The direction of habitat transformations is not related to the habitat conditions occurring at the beginning of the process of succession. Most seres develop in a convergent manner, resulting in the same final stage. Under the circumstances of the Polish Lowlands, the final stage is represented by the *Pino-Quercetum* mixed forest (KORNAŚ 1950, PAWŁOWSKI 1959). Thanks to that, primary succession, no matter whether it starts in a shallowed pond, marsh, sand dune or limestone rocks, leads, after numerous ecosystem transformations, to the formation of a mixed forest.

The transformation of the vegetation cover in the course of forest succession is relatively well known (FALIŃSKI 1991). Much less is known about changes in the forest fauna during forest stand development. The data are incomplete, they concern different forests, dissimilar environmental conditions, various time spans and, usually, a small number of animal species. The situation is the same as regards studies of succession in European forests and forests in other continents.

Our understanding of faunal transformations in the course of succession is still much better than the theoretical background of succession processes (ANDERSON 1986). Theoretical assumptions are usually made on the basis of diverse premises, which are usually not sufficiently validated. An additional difficulty for a zoologist is the fact that most concepts of succession are concerned with plant associations, so that the findings, owing to specific traits of the botanical material, cannot be fully applied to faunal studies.

Because of that the theoretical mainstay for a zoologist is still the concept formulated by ODUM (1969). In its terms, the process of ecological succession is:

1. unidirectional and predicable,

2. its pattern and rate are determined by the physical environment which also sets limits to development.

3. the process terminates in a stabilised ecosystem, where maximum biomass is present and functional links between organisms ensure control over the processes taking place and protection against disturbances.

The mechanisms of homeostasis are supported by groups of organisms with similar functional characteristics but different ranges of ecological tolerance (TROJAN 1984). Depending on the internal arrangement of these systems (KIKKAWA 1986) they may be adapted to maintaining short-term or long-term stability.

Puszcza Białowieska is the greatest faunal refugium in the Central European Lowland as can be evidenced by comparing the animals occurring there to the fauna of the Central Polish Lowland. In the best known groups of animals in Puszcza Białowieska, e.g. butterflies or Isopoda, the number of species recorded in the Puszcza well exceeds 80% of those known from the Central Polish Lowland (TROJAN unpublished data). The faunal richness of Puszcza Białowieska is the reason for the concentration of faunal research in the area. As a result, it is possible to analyze the phenomena occurring in the process of secondary succession of fauna. The number of over 30 taxons (orders or families) studied is a representative sample allowing to trace regularities in the process of formation of faunal complexes within the pine forest biocenoses of Puszcza Białowieska. The material included in the present paper is not exhaustive if one considers the species richness of Puszcza Białowieska, but it is the largest faunal sample that has ever been investigated at the same place and stage of the development of fauna of pine forests.

The data on the fauna of Puszcza Białowieska are an irreplaceable source of comparative information. The primeval nature of the forests is much better preserved, and the number of felling cycles much smaller, than in all other European forests. As a result, the data on the fauna of that forest complex serve as a frame of reference for all faunal studies conducted in Polish forests as well as in other countries. The structure of the fauna of Puszcza Białowieska may be used in an exemplary fashion when analysing changes occurring in faunal communities in forests situated in other areas.

Objectives of the study. The following objectives were set for the analysis of the secondary succession of pine forest fauna:

1. Determination of the formula for pine forest zoocenosis structure, and classification of specific groups of animals into functional groups within the forest biocenosis.

2. Comparison of the species composition of the animal groups studied in the various succession stages and assessment of changes in the species composition of the fauna.

3. Estimation of the number of species in each animal group. Comparison of empirical and estimated data and assessment of the degree to which the material collected is representative.

4. Description of the structure of the taxons in each stage of the sere.

5. Determination of actual and potential species diversity of the taxons in the course of succession.

6. Comparison of changes in the structure and diversity of each faunal complex in the course of secondary succession of the pine forests in Puszcza Białowieska.

7. Assessment of the degree of complexity of the zoocenosis in each stage of succession.

The entire analysis of the phenomena occurring in the fauna during pine forest development is based on the concept of functional groups within the biocenosis. The groups are links which form the subsystems of the biocenosis to make up the homoeostatic system (TROJAN 1984), within which the processes of abundance regulation in forest ecosystems occur.

1.2. Review of literature

The course of secondary succession and the underlying mechanisms have been attracting naturalists' attention since the turn of our century. Over the last 15 years, nearly 100 papers concerned with this subject have been mentioned in bibliographical registers. A considerable number of papers is concerned with the theory of succession (about 30 items). Reviews of papers dealing with the theory of succession can be found in ANDERSON (1986) and FALIŃSKA (1991). The development of the theory of succession coincides with ongoing reconsiderations of the concept of the ecosystem, undertaken both by holists and by reductionists. Holistic views have been reflected in papers by MARGALEF (1968), ODUM (1971) and WHITTAKER (1975) where the succession is believed to occur on ecosystem level. Their reductionist opponents, e.g. MACMAHON (1980), GRAY et al. (1987) attach greater importance to population processes. According to them, succession results from the living strategy of species and their interactions with the environment and with one another.

Views on the theory of succession, related notions, characteristic features and mechanisms have been mentioned in many ecology textbooks (TROJAN 1975, STUGREN 1976, ODUM 1977, COLLIER, COX et al. 1978). A number of papers are concerned with various aspects of this phenomenon, concentrating on issues of stability, diversity, bioenergetics as well as mechanisms and mathematical models of succession.

A recent trend has been to treat both concepts as complementary (TROJAN 1984) so that the properties studied when interpreting succession phenomena relate both to individuals of various species and to populations and communities. SHUGART (1984) and PRENTICE (1986) emphasize the hierarchical character of the theory of succession, according to which processes occurring on higher levels stem from processes taking place on lower levels of organisation of the ecological system.

The studies of succession in forest ecosystems are conducted on different levels of organisation of the ecological system, including both soil and vegetation and zoocenoses. The literature on succession in these ecosystems permits to make comparisons in various types of forest stand and to trace transformations

of both vegetation fauna. The studies are based on the theory of edaphic climax. Data on secondary succession in the pine forests in Puszcza Białowieska contain the results of analyses of a number of seres. If the sere develops in a suitable habitat, the rate of succession is usually accelerated. Comparative analyses show that when a forest is grown in an unsuitable habitat, substitute associations emerge and natural succession is delayed.

The structure of faunal systems is a sensitive indicator of changes occurring in the environment. They are manifested as alterations in the species composition, structure and abundance of faunal communities. A comparative analysis of faunal communities carried out in stands of various age may be used for describing and interpreting the processes occurring in the succession in the ecosystem studied. It is usually conducted in spatial seres, but its results can be extrapolated temporally, which makes possible interpretation of changes occurring in the course of succession, while the time of field observation is considerably shortened. A regular cycle of secondary succession in the pine forests of Puszcza Białowieska is completed in 150 years.

The literature on the processes of secondary succession in the pine forests of Puszcza Białowieska is rather poor. The botanical aspects have been dealt with by FALIŃSKI (1989, 1991) and TOLKAČ & DANCEVIČ (1974). Data on faunal succession in these ecosystems are provided in 11 items. With one exception, they are concerned with selected groups of insects. Literature on fauna is exhaustively listed in KARPÍŃSKI and OKOŁÓW (1969) and OKOŁÓW (1976, 1983, 1991).

2. AREA OF STUDY

Puszcza Białowieska is situated in north-eastern Poland. The area is divided by the state border between Poland and Byelorussia. In its contemporary limits, Puszcza Białowieska includes the remains of three forest complexes associated in the north with the forest of Puszcza Knyszyńska. Situated on the border between Poland, Lithuania, and the historical regions of Jaćwierz and Ruś Wołyńska, it was depopulated in the 13th century (WIECKO 1972) to remain uninhabited for about 300 years. Despite the pillage of their resources during World Wars I and II, the forests of Puszcza Białowieska have completed fewer felling rotations than forests situated west of it. Particularly valuable and rich are the deciduous forests characteristic of the temperate climate zone in Europe and undergoing "complete series of secondary and recreative succession" (FALIŃSKI 1989). Taking into consideration the natural values of these forests, it was decided that they would be protected as a Biosphere Reserve.

Apart from the common linden-oak-hornbeam forests and alder forests, Puszcza Białowieska also houses pine forests represented by the ultimate forest associations of *Pino-Quercetum* and *Peucedano-Pinetum* (subcontinental pine forest) (FALIŃSKI 1988). The latter, representing the "fresh" pine forest association type, grow on podzolic soils. The majority of these forests are situated in the south-eastern part of Puszcza Białowieska, in Hajnówka forest inspectorate.

There are about 3739 ha of pine forests in Puszcza Białowieska, accounting for less than 7% of the total forest stand area. The patches of the pine forest are composed of pine (about 76%) and spruce (15%) with a small addition of birch (7%) and scanty contributions from other tree species such as oak or aspen.

Studies of secondary succession of the fauna of the forests of Puszcza Białowieska were carried out in Hajnówka forest inspectorate, more specifically in Starzyna forest district. Three sites were chosen in divisions 538, 667 and 668. Three even-aged coniferous forest stands, several hectares each, were selected within each of the sites for the study. These included mature stands (timber stands: 100–110 years), pole wood, i.e. III age class stands (40–60 years), young stands (15–25 years) and cultures (3–7 years).

In order to collect cambio- and xylophagous beetles, additional catches were carried out in divisions 494 C, 519 D and 539 C.

The location of study sites is shown on the map (Fig. 1).

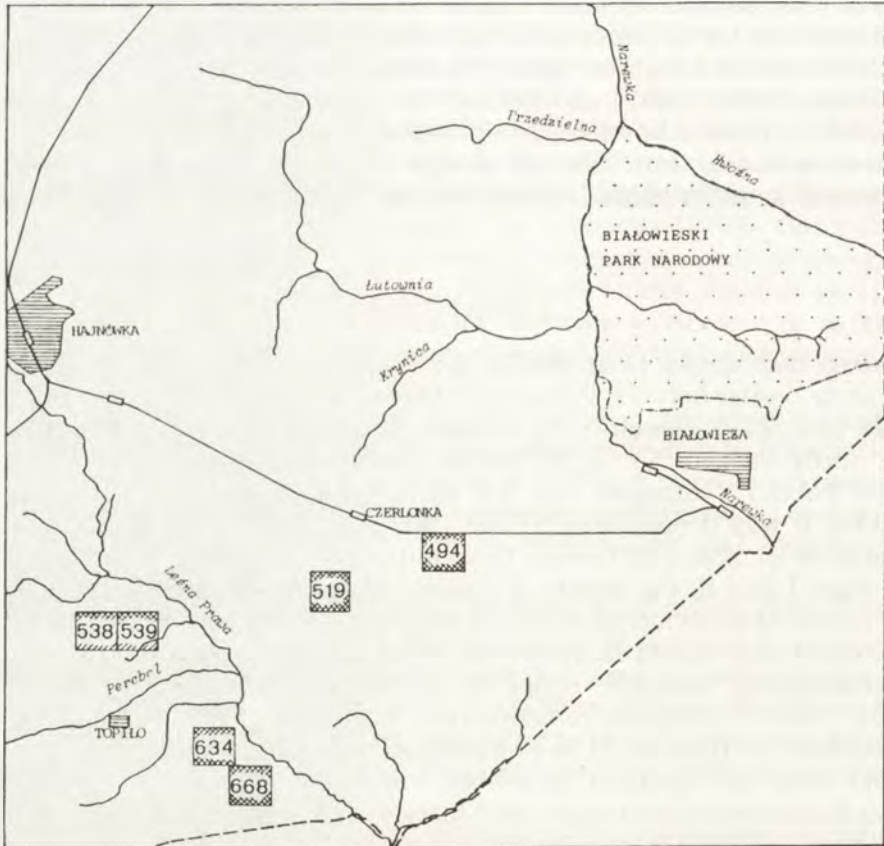


Fig. 1. Location of study stands in the pine forests of Puszcza Białowieska

Prior to collecting faunal materials, studies of plant associations (protocols) and soil analysis (soil profiles) were performed in the areas chosen for the study (MATUSZKIEWICZ et al. 1993).

As regards soil and phytosociology, all the areas included in the field study are homogeneous and represent the subboreal variety of the subcontinental (*Peucedano-Pinetum*) pine forest. The variety is characterised by a substantial contribution of spruce in the stand and understorey. The phytosociological analysis carried out in the stands revealed relatively insignificant differences in floristic composition between various age classes, even between stages as different as a mature forest and a clearing with young plantings. Unlike deciduous forests, the associations forming in the culture and young growth stage do not differ phytosociologically. The associations, however, are poorer in the number of species in comparison to a mature pine forest, at the same time comprising some species from sandy greens.

In terms of soil typology, in all the areas under study, the soils belong to the class of podzols and are characterised by acidic reaction and low acid-base sorption.

The study was carried out in patches of pine forest subject to normal silvicultural practices. The area undergoes clear felling with a cutting width of 60–80 m. The restoration of the stand is accomplished by planting a culture in a specially prepared felling site composed of pine (80%), spruce (10%) and birch and oak (10%).

3. FAUNA SAMPLING METHODS AND MATERIAL

The programme of studies encompassed 30 groups of invertebrates and 2 groups of vertebrates. They represent diverse life styles and a wide range of trophic and environmental relationships. Due to that, sampling methods were adjusted to the bionomic peculiarities of the various groups of animals. The methods can be divided into two groups: qualitative sampling techniques and standard quantitative methods.

The qualitative sampling techniques were designed specifically for the particular animal groups studied. They are described in separate papers concerned with individual taxons. The most common qualitative methods included "stalking" with a net, using decoys to attract insects and browsing through substrates associated with a particular faunal group.

The standard quantitative methods suited the vertical structure of the forest and activity patterns of the animals under study. Winged insects occurring in the canopy layer were collected using Moericke's pitfall traps (MOERICKE 1950) attached to top branches of trees by means of special pegs. The pegs enabled the containers to be hauled down at regular intervals in order to take out the specimens collected. Since the canopy layer starts to form only in grown up plantations, this sampling technique was used in pine stands of three age classes: young growth, pole wood (age class III) and mature forest. Three sampling sites were selected and 5 pitfall traps installed in each age class.

resulting in a total of 45 traps. The specimens collected were taken out every fortnight, starting from the withdrawal of the snow cover until late November.

The material collected using this method in the years 1986-1987 contained more than 500,000 of arachnid and insect specimens (Tab. I). After the material had been sorted and species and their abundance determined by experts in the respective taxonomic groups, it was subjected to analyses described below.

Table I. List of materials collected using Moericke's pitfall traps in the pine forests of Puszcza Białowieska in the years 1986-87

| Taxon | Numbers of specimens | | | Total | Average | % |
|---------------------|----------------------|-----------|---------------|--------|---------|--------|
| | young stands | pole wood | mature stands | | | |
| <i>Psocoptera</i> | 451 | 695 | 566 | 1712 | 0.11 | 0.32 |
| <i>Blattodea</i> | 97 | 32 | 10 | 139 | 0.01 | 0.03 |
| <i>Thysanoptera</i> | 48582 | 83437 | 131262 | 263281 | 16.89 | 49.84 |
| <i>Homoptera</i> | 2871 | 5333 | 3998 | 12202 | 0.78 | 2.30 |
| <i>Heteroptera</i> | 265 | 660 | 1243 | 2168 | 0.14 | 0.41 |
| <i>Coleoptera</i> | 3629 | 2767 | 2281 | 8677 | 0.56 | 1.65 |
| <i>Neuroptera</i> | 1060 | 548 | 794 | 2402 | 0.15 | 0.44 |
| <i>Lepidoptera</i> | 1308 | 890 | 889 | 3087 | 0.20 | 0.59 |
| <i>Hymenoptera:</i> | | | | | | 0.00 |
| <i>Aculeata</i> | 3660 | 1028 | 1244 | 5932 | 0.38 | 1.12 |
| <i>Parasitica</i> | 10618 | 9384 | 80963 | 28965 | 1.86 | 5.49 |
| <i>Symphyla</i> | 615 | 581 | 653 | 1849 | 0.12 | 0.35 |
| <i>Diptera</i> | | | | | | 0.00 |
| <i>Nematocera</i> | 30026 | 29555 | 20726 | 80307 | 5.15 | 15.20 |
| <i>Brachycera</i> | 63478 | 30581 | 20889 | 114948 | 7.38 | 21.78 |
| <i>Aranei</i> | 113 | 689 | 672 | 2474 | 0.16 | 0.47 |
| Total | 167773 | 166180 | 194190 | 528143 | 33.89 | 100.00 |

In order to determine the species composition of the herb layer fauna, a sweeping net was used (10 samples of 25 sweeps each in each area).

To collect animals linked with tree stems and branches, such as *Buprestidae*, *Cerambycidae* or *Scolytidae*, stems and branches were scanned and foil window-traps were used.

Estimation of the species composition and abundance of epigeic animals was performed using the square plot methods (1 sq.m., 10 sq.m. and 100 sq.m.). This method was used mostly in the case of ant communities. Rodents were caught into jars and traps placed on the surface of soil.

Soil mesofauna was assessed in the spring and autumn peaks. A standard steel corer with an area of 20 sq. cm. was used for obtaining samples. 10 samples were taken at each site in each period. Additional 25 samples were taken at three sites in mature forests in selected microhabitats represented by patches of bilberry, moss, fern, litter and heather. The samples were then extracted in Tullgren funnels. Special extraction methods were employed for nematodes (BRZESKI et al. 1976). The animals were then conserved in 4% formalin solution.

Enchytraeids were extracted in O'Connor's apparatus (O'CONNOR 1971).

4. METHODS FOR PROCESSING DATA

The data collected, usually quantitative, fulfilled the criteria for application in statistical analysis. This allowed to study the structure of individual taxocoenes and determine their quantitative characteristics.

The formula for the structure of various communities is obtained on the basis of models of five distributions, which are most extensively used in faunal studies nowadays (TROJAN 1992). The following models of structure were used:

1. A geometric series wherein an assumption is made that environmental resources are used successively in an l th part by each species forming the community, in accordance with the following series:

$$l, l(1-l), (1-l)^2, \dots, l(1-l)^{S-1}$$

Thus, the anticipated abundance of individual species assumes values according to the formula:

$$n_i = \eta N l (1-l)^{i-1}$$

where l and η – equation constants calculated from sample parameters

N – the total number of individuals in the sample

i – the rank of species in order of diminishing abundance.

2. Broken stick distribution wherein it is assumed that environmental resources are utilised in a random manner by individual species forming the community; the anticipated share of the species in the community is determined from the formula:

$$E\left(\frac{n_j}{N}\right) = \frac{1}{S} \sum_{j=1}^{S-1} \frac{1}{S+1-j}$$

where i – the species' rank (from the least to the most abundant)

n_j – the number of individuals in the sample belonging to the species of j

N – the total number of individuals in the sample

S – the number of species in the sample

3. A logarithmic series wherein the distribution of the number of species, according to abundance increasing discretely, assumes the form of a series:

$$\alpha v, \frac{\alpha v^2}{2}, \frac{\alpha v^3}{3}, \dots, \frac{\alpha v^r}{r}$$

where r – is the highest abundance of individuals within the species, and the series parameters α and v are calculated theoretically relative to the number of species S and sample abundance N :

4. A lognormal distribution based on the assumption that species abundances, corresponding to the amounts of environmental resources used, present a normal distribution, with the greatest number of moderately abundant species, and small numbers of rare and most abundant species; in a logarithmic scale of increasing classes of abundance, called "octaves", in which the number of species (S_R) determined in accordance with the lognormal distribution equation, is defined by the function:

$$S_R = S_0 e^{-(\varepsilon R)^2}$$

where S_0 – number of species in a modal octave
 ε – equation parameter obtained from empirical distribution
 R – ordinal number of abundance class

5. A negative binomial distribution based on the assumption that the probability of catching a given number of individuals belonging to a particular species is very low, corresponding to Poisson's distribution with the λ parameter; if a certain variability of this parameter is assumed, the anticipated shares of species in the sample represented by a given number of individuals $P(X = r)$, the following form is assumed for the negative binomial distribution:

$$P(X = r) = \frac{\Gamma(v + r)}{r! \Gamma(v)} p^r q^r$$

where v, p, q are distribution parameters determined from the sample;

The computation of distributions was carried out in accordance with descriptions contained in a paper by TROJAN (1992) using a computer programme of the Museum and Institute of Zoology PAS. When the results were similar to the models used, data on quantitative characteristics determining the structure of the model were utilised. The similarity of empirical to theoretical distributions was verified on the basis of the χ^2 test.

Actual species diversity in individual communities was measured with Shannon and Weaver's diversity index:

$$H' = - \sum_{i=1}^S \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

where n_i – the abundance of the i th species
 N – abundance of a given community composed of a total number of S species.

Potential species diversity of various communities is expressed as the border values of Shannon and Weaver's index (TROJAN 1994). Because of that, the degree of realisation of the potential, expressed as Pielou's index, assumes the form:

$$J = \frac{H'}{\log_2 S^*}$$

where S^* – is the potential number of species in the habitat.

Assessment of **similarity of species composition** of individual communities was made according to the “percentage” modification of Sørensen’s formula (SØERENSEN 1948):

$$So = 2 \frac{w}{a + b} 100\%$$

where a and b refer to the number of species in the communities compared and w to the number of species common to both communities.

5. ANALYSIS OF SECONDARY SUCCESSION OF THE PINE FORESTS OF PUSZCZA BIAŁOWIESKA

5.1. A model of the structure of pine forest zoocenosis and the course of secondary succession.

Animal communities inhabiting forest ecosystems form functional systems characterised by close linkage between their components. Puszcza Białowieska is the first natural forest in Poland, for which a model was constructed to determine the ecological structure of the ecosystem (KARPIŃSKI 1949). According to the model “the functional groups of the florotone and the zootone and forest habitats of certain types correlating with one another form a forest biocenosis of a specific type”. Karpiński distinguished 5 functional groups in the zootone, each with a different role to fulfil in the life of the forest.

Nowadays the organisation of forest ecosystems is viewed as a hierarchical system comprising 4 types of structural units (TROJAN 1984).

1. The subsystem, which is characterised by a specific input substrate that supplies this system, and contributes to regulating the whole ecosystem. There are five subsystems within each ecosystem: the biotope, the producers, and three subsystems forming the zoocenosis (or zootone, according to Karpiński): 1) saprotrophs, 2) biotrophs, 3) macrotophs.

2. The trophic (food) chain is the basic organisational unit of the subsystem. Individual chains differ with regard to the type of food (input link) consumed and the manner in which the food is captured. (One host plant may give rise to several trophic chains of biotrophes). Each chain consists of links corresponding to trophic levels (LINDEMANN 1942).

3. The competitive association (guild) encompasses species forming a single link of the trophic chain. The species inhabit identical or similar ecological niches, understood as common food resources utilised by the entire guild and a common group of predatory and parasitic species exploiting the guild.

4. The population is an internal organisation unit of the guild based on competitive relations.

The structure of zoocenoses based on the above four types of units is reproducible and universal. This means that similar organisational structures are found both in forest ecosystems and in meadow or field ones, or even in urbiceneses. Differences between them concern the shares of individual organisational units in a particular ecosystem. The differences are recognised and defined and the degree of uniqueness is determined by comparative faunistical analyses.

The organisation of forest biocenoses exhibits a high degree of complexity (SZUJECKI 1980). It can be seen both in conditions imposed by forest stand development, its spatial structure, seasonal and diurnal rhythms of animals and relationships between individual components of the environment. Any attempt to systematise these relationships is faced with the need to make simplifications and to assume that certain factors are central to regulating the system organisation. In the present paper the central role is performed by the trophic factor. The structure presented is thus equivalent to the trophic organisation of the zoocenosis. The paratrophic factor is given minor importance. Owing to this, for example, parasitic insects have been classified after phytophages, in which their larvae develop. The parasites play an additional role as mellitophages, feeding on honey-dew and nectar and pollen of flowers, which are pollinated in this way. This system of feedback relations has not been reflected, however, in the above outline of the organisation of the pine forest zoocenosis of Puszcza Białowieska.

The pine forest zoocenosis, like other forest ecosystems of this climatic zone, is composed of three subsystems: biotrophic, saprotrophic and macrotrophic. The present paper gives most consideration to the biotrophic subsystem because of the character of the materials collected and analysed and the ability of domestic experts to analyze individual animal groups.

The biotrophic subsystem comprises two groups of trophic chains. The chains are initiated by first-level consumers (C1) i.e. chewing phytophages and sucking phytophages (Fig. 2). Particularly important is the chewing phytophage link, which comprises lepidopterans (*Lepidoptera*) and sawflies (*Symphyla*) – the most dangerous pine foliophages which periodically invade some regions of Poland causing severe damage to pine stands. Similar functions are also fulfilled by weevils (*Curculionidae*) and leaf beetles (*Chrysomelidae*). Only the former pose a significant threat to forests as pests of pine. The next group of phytophages is composed of species sucking leaves and young sprouts. It includes aphids represented by the specialised family of *Lachnidae* associated with coniferous trees. Parallel chains are formed by homopterans (*Homoptera*, *Auchenorrhyncha*) and heteropteran bugs (*Heteroptera*). This group may be defined as phytophages undermining the forest stand by sucking substantial amounts of assimilates out of leaves and sprouts. A particular role in forest ecosystems is played by xylophages and cambiophages. This group occurs characteristically in forest ecosystems. In the present study, it is represented by three beetle families:

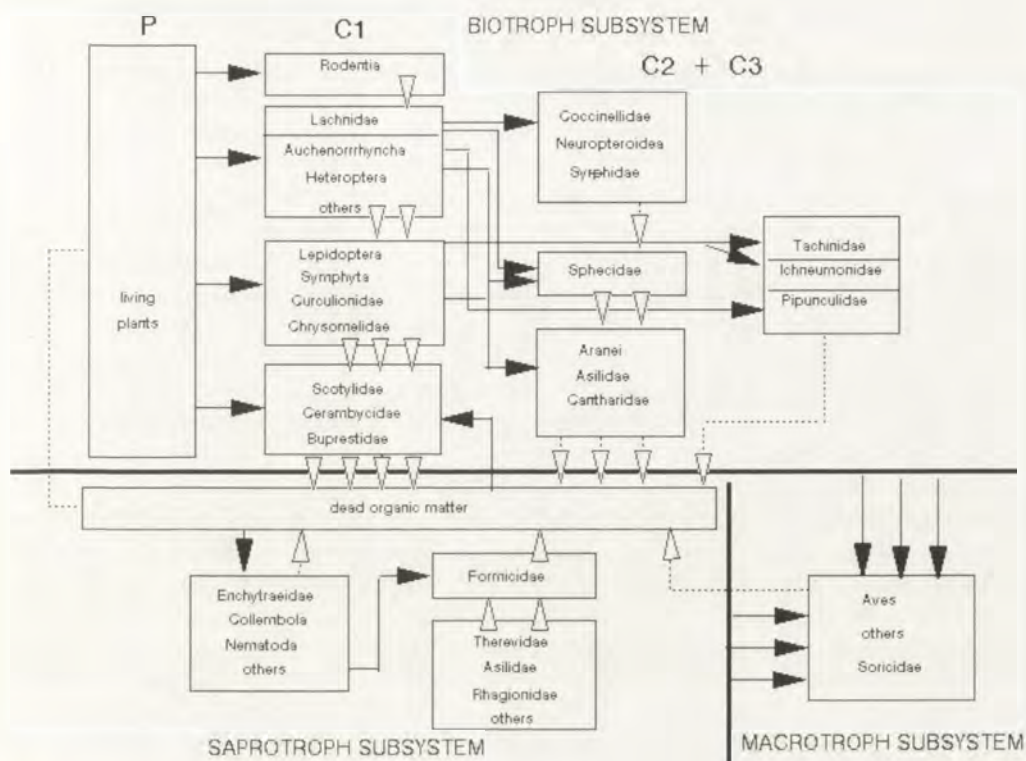


Fig. 2. Zoocenosis organisation in the pine forests of Puszcza Białowieńska

buprestids (*Buprestidae*), cerambycids (*Cerambycidae*) and bark beetles (*Scolytidae*).

Zoophages include parasitic and predatory forms specifically associated with certain groups of phytophages. In this paper special attention is given to distinguishing parasitoids that reduce the abundance of foliophages, i.e. tachinid flies (*Tachinidae*) and ichneumon flies (*Ichneumonidae*). Groups of species reducing the abundance of sucking phytophages, i.e. predatory aphidophages and parasites of *Homopterans*, are also well represented. All these animal groups are second-level consumers (C2). Two subsequent links are formed by predatory forms (C3) hunting in flight or on the surface of plants and soil robber-flies (*Asilidae*) and digger wasps (*Sphecidae*) as well as spiders (*Aranei*) hunting in their webs.

The saprotrophic subsystem in the pine forest is well-developed both as regards detritophages, polyphages and zoophages. Not all of the groups of soil fauna can be analysed at present with accuracy required for faunal studies. The relationships occurring in animal communities of this subsystem have been described on the basis of model animal groups such as nematodes (*Nematoda*).

enchytraeids (*Enchytraeidae*) and springtails (*Collembola*). Polyphages are represented by ants (*Formicidae*), which are most effective in controlling forest ecosystems. *Therevidae* served as an example of soil predators.

The macrotrophic subsystem, which controls both the biotrophic and the saprotrophic subsystems, is represented by birds and small mammals.

Ecological succession is one of the more important processes occurring in ecosystems. It is a reflection of dynamic processes that take place in every ecosystem. The studies of the forests of Puszcza Białowieska have provided a basis for the development of the dynamic concept of vegetation cover (PACZOSKI 1951). The idea has also been developed by KARPÍŃSKI (1949), who distinguished fluctuation and succession processes. He also drew attention to the relative stability of climax systems bustling with continuous processes of change, which are, however, not directional. These concepts have recently been developed by FALIŃSKI (1989), also on the basis of Puszcza Białowieska. Faliński distinguished three types of processes occurring in ecosystems: directional, fluctuating and cyclical. Of the three types, only the directional processes of succession and regression are important from the viewpoint of the present analysis. The separation of the two processes is, however, difficult. The task is all the more complicated because regression processes, like succession processes, consist of multiple stages and result in the system adapting to the altered environmental conditions. Particularly unclear is the problem of finding measures for the progress resulting from succession. FALIŃSKI (1989: 105) lists among such measures "a conventional dynamics index", the state of the biomass, energetic relations between the components, etc. All of these measures are incremental so that non-growth processes are not regarded as elements of the notion of succession. In zoocenology, such a reasoning has an implicit assumption of growth of the biomass, diversity, abundance and the number of species. Such a course of succession is, however, very poorly evidenced for.

In the present paper, the assumption is made that succession (primary as well as secondary) leads to relative stability of the system. The stability is expressed, among other things, by the fact that the growth processes in the system are slowed down or stopped, and the entire energy gain is utilised in internal regulatory processes, i.e.

$$B \approx \text{const.}$$

$$\Delta B = R$$

where B – biomass and R – respiration. All regulatory processes are thus accomplished at the expense of energy, which, in the ecosystem's final account, is used to compensate for the costs of maintenance and activity, i.e. the metabolism of the components forming the biocenosis.

It is not easy to resolve the issues in question on theoretical grounds. The nature of material collected for the purpose of the study still permits verification of the views on secondary succession by determining which of the 5 variants of succession presented below (Fig. 3) is actually observed in the course of development of the pine forest of Puszcza Białowieska.

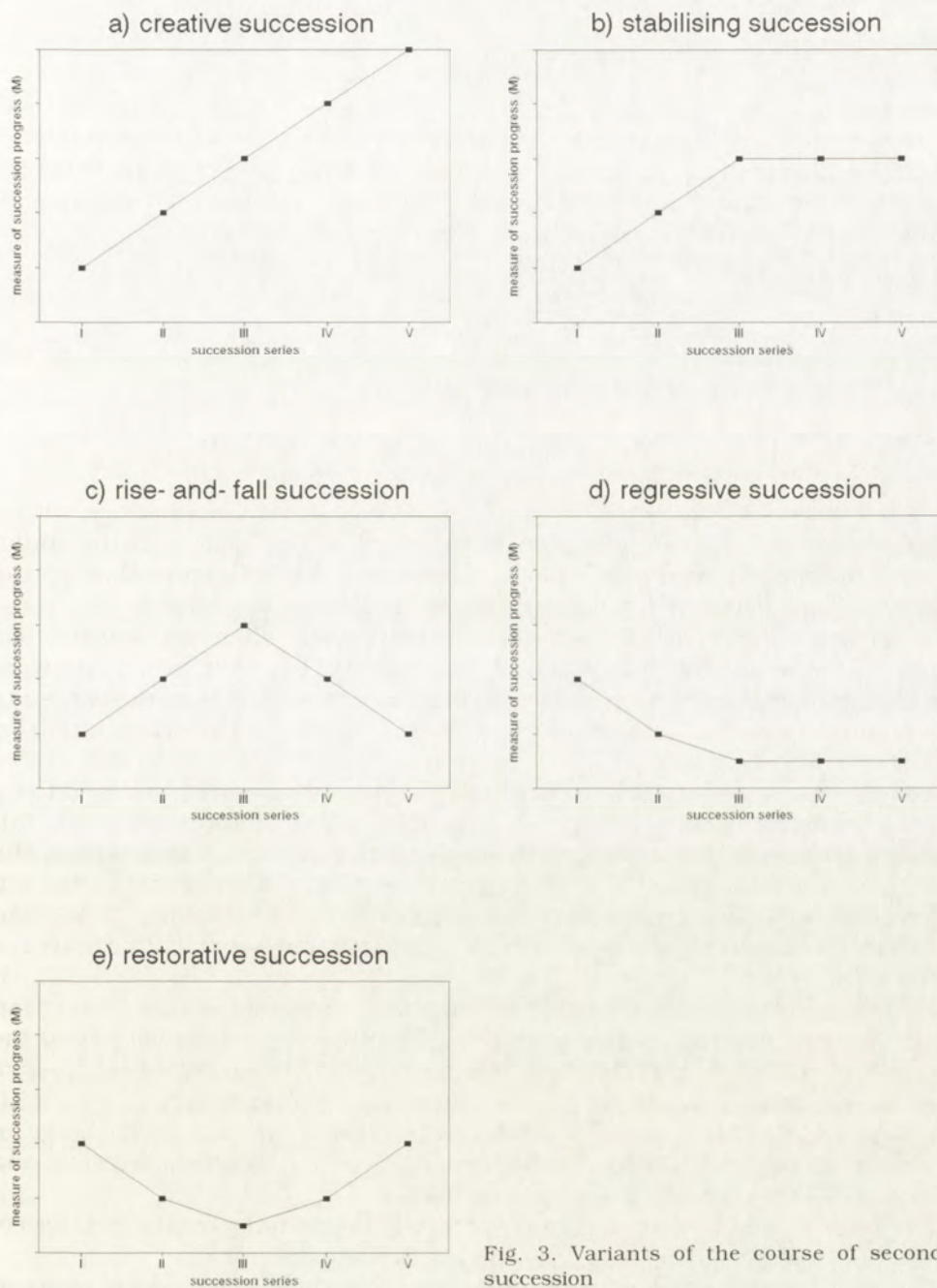


Fig. 3. Variants of the course of secondary succession

Creative succession (a) is observed when the measure of succession progress of a community in the consecutive stages of the sere is higher than the preceding one

$$M_0 < M_1 < M_2 \dots < M_n$$

The system where such a series of values is registered develops infinitely.

Stabilising succession (b) is seen when the measure of succession progress increases in the initial period to subsequently stabilise, irrespective of development or growth processes observed in other components

$$M_0 < M_1 < M_2 = M_3 \dots = M_n$$

Rise-and-fall succession (c) is characterised by an initial increase in the measure of succession progress followed by a fall

$$M_0 < M_1 < M_2 \dots < M_{\max} > \dots M_{n-2} > M_{n-1} > M_n$$

Such a series of values will be characteristic of those communities within zocoenoses which contribute to the development of the system in the initial stages of the sere. They are often pioneer species or pioneer groups that set the stage for groups better adapted to living in an organised biocenosis.

Regressive succession (d) is observed in situations when a group reaches maximum values in the first stage of succession where the system is least organised. The increase in the degree of organisation of the biocenosis results in a gradual reduction of the function of this group and its elimination or substantial decline.

Restorative succession (e) is an attribute of communities which survived fairly well the catastrophe connected with the destruction of the ecosystem, but witness a decrease in the measure of succession progress in the first stages. The value increases only after the target level of ecosystem organisation is attained.

A number of simple measures of the progress of succession may be used in assessing the progress of succession of a given taxon representing either a certain faunal complex or a certain guild:

1. Abundance, when assessed with comparable methods; it may be referred to area or volume; or be relative in character, expressing animal activity or the action of a hunting tool. Abundance is a measure of the ecological success of the taxon studied – if it increases, or a regression – if it decreases.

2. The number of species inhabiting the ecosystem in a given stage of succession reflects community development or recession. Both empirical (S) and estimated (S*) number of species may be used.

3. Actual (H') and potential (Hmax) species diversity indicates the richness of a given taxocoene and the degree to which it fills the habitat.

4. The index of dominance determining quantitative relationships between species forming a guild. Interpretation of the value of this index is not clear, especially when a sere is concerned.

5.2 Succession in the subsystem of biotrophs

5.2.1. Phytophages

As regards the mode of feeding and the quality of the food they take in, phytophagous insects may be divided into three biotic groups. The first group is composed of ecotrophs or chewing phytophages, which feed on the green parts of plants. The second group is that of endotrophs with a stinging-sucking mouth apparatus designed to absorb substances produced by plants without damaging the assimilating apparatus. The third group comprises xylophages and cambiohages trophically associated with woody plants. Chewing phytophages include caterpillars of butterflies (*Lepidoptera*), larvae of sawflies (*Hymenoptera*, *Symphyla*) as well as numerous families of beetles, such as leaf beetles (*Chrysomelidae*) or weevils (*Curculionidae*). Sucking phytophages embrace, above all else, hymenopterans such as aphids (*Aphidoidea*) and leafhoppers (*Auchenorrhyncha*) together with phytophagous heteropteran bugs (*Heteroptera*).

Another important phytophagous group in forest ecosystems is formed of xylophages and cambiohages biologically associated with trees.

Sucking phytophages

7 species of aphids of the family *Lachnidae*, 23 species of leafhoppers and 39 species of phytophagous Heteroptera (KOŁODZIEJAK in press, CHUDZICKA unpublished data, CMOLUCHOWA, LECHOWSKI 1993) were recorded in the canopies of pine forest stands in Puszcza Białowieska in all the forest stand age classes studied (young growth, pole wood, mature forest). In each of the above groups, a similar number of species was registered in every age class of the forest stand, with the greatest number of aphid species recorded in the pole wood, and of leafhoppers and heteropteran bugs, in mature stands (Fig. 4).

The species composition of all the communities of sucking phytophages collected in canopies of pine was similar (Sørensen's similarity indices ranked from 62% to 99%). The highest similarity of species composition was recorded for communities of aphids: in each age class of the forest stands these communities were solely composed of monophages feeding on one or a number of pine species. Similarity indices of species composition of aphid communities occurring in canopies of pines in the stands studied in Puszcza Białowieska ranged between 80%–99%.

It should be added that the species composition of each of the chewing phytophage communities studied in the canopies of trees in the pine forests of Puszcza Białowieska was considerably similar to the species composition of communities inhabiting canopies (So) of pines in other Polish forest complexes (KOŁODZIEJAK in press, CHUDZICKA unpublished data, CMOLUCHOWA, LECHOWSKI 1993).

In the pine forest sere changes in abundance and dominance structure occur in all the communities of sucking phytophages under study. In aphid and leafhopper communities the indices of relative abundance decrease with the

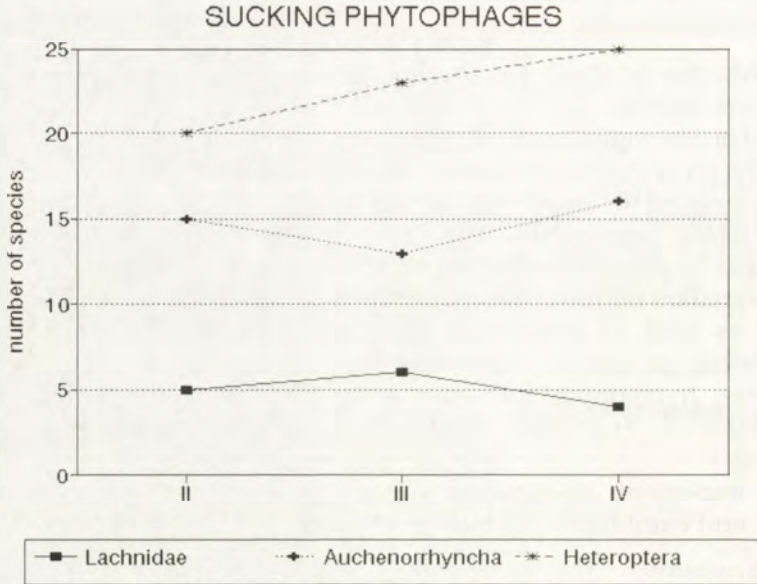


Fig. 4. Changes in the number of species of sucking phytophages in pine forests (3 age classes of the forest stand)

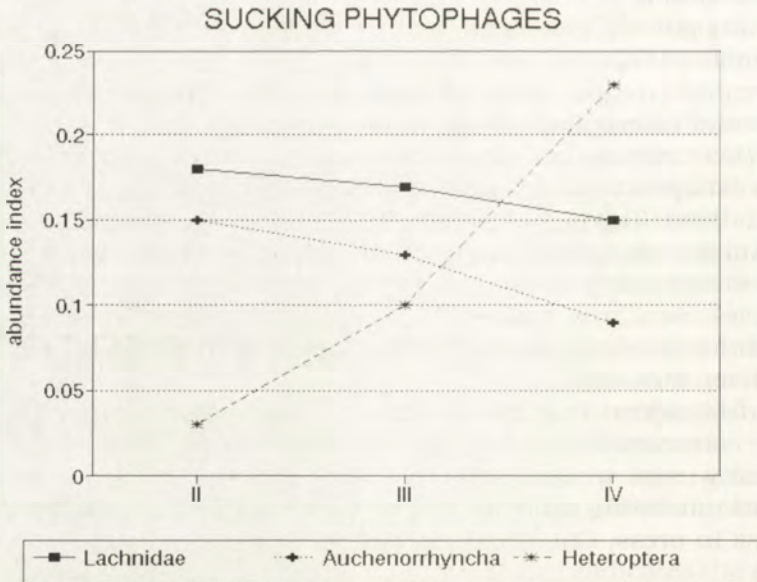


Fig. 5. Changes in the abundance of sucking phytophages in pine forests (3 age classes of the forest stand)

growing age of the stand, while communities of phytophagous heteropteran bugs exhibit the reverse (Fig. 5).

Changes in the structure of dominance of the phytophagous insect communities under study consisted predominantly in shifts of positions, or ranks, of the dominant species. On the other hand, differences in the composition of the dominant species group were not observed in any community studied (Fig. 6–8).

A significant transformation of the dominance structure in communities of aphids took place between the young growth and pole wood stages. Compared to the young growth community, the pole wood community is characterised by a diminished rank of *Schizolachnus pineti*, a species which forms compact colonies on tops of sprouts and feeds predominantly on young needles. On the other hand, there is an increase in the proportion of *Eulachnus agilis*, a species which does not form colonies and feeds on 2–3-year-old needles of pine (Fig. 6).

In the leafhopper communities studied in the sere, there is an increase in the rank of two pine monophages, namely *Wagneripteryx germari* and *Grypotes puncticollis*. On the other hand there was a reduction in both abundance and proportion of *Speudotettix subfuscus*, a polytope settling in various forest habitats (Fig. 7). In the leafhopper communities, a considerable transformation of the dominance structure occurred between the pole wood and mature stages.

In the case of heteropteran bugs, changes in the structure of dominance occurring in the sere consisted predominantly in an increase of the proportion of *Plesiodema pinetellum*, a monophage of pine, in older stands. The species

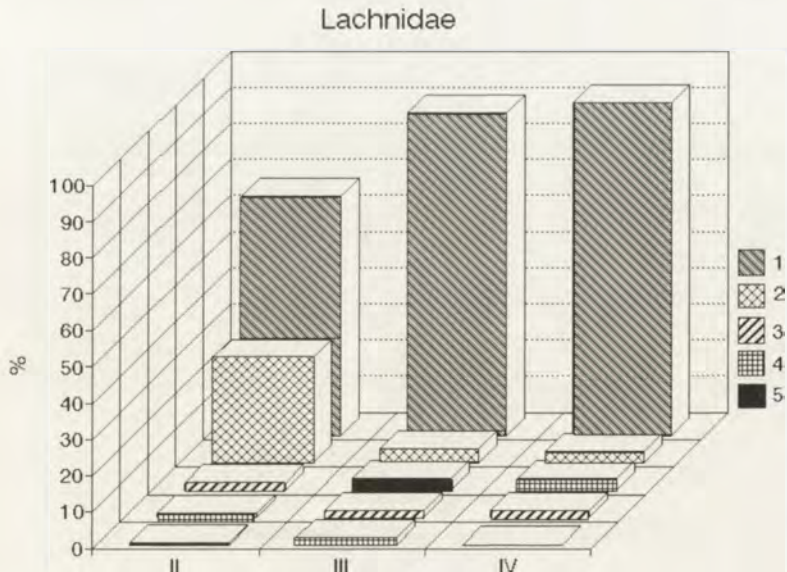


Fig. 6. Dominance structure of communities of aphids (*Aphidoidea*, *Lachnidae*) in canopies of pine in forest stands of various ages in Puszcza Białowieska: 1 – *Eulachnus agilis*, 2 – *Schizolachnus pineti*, 3 – *Cinara pinea*, 4 – *C. pilosa*, 5 – *C. pini*

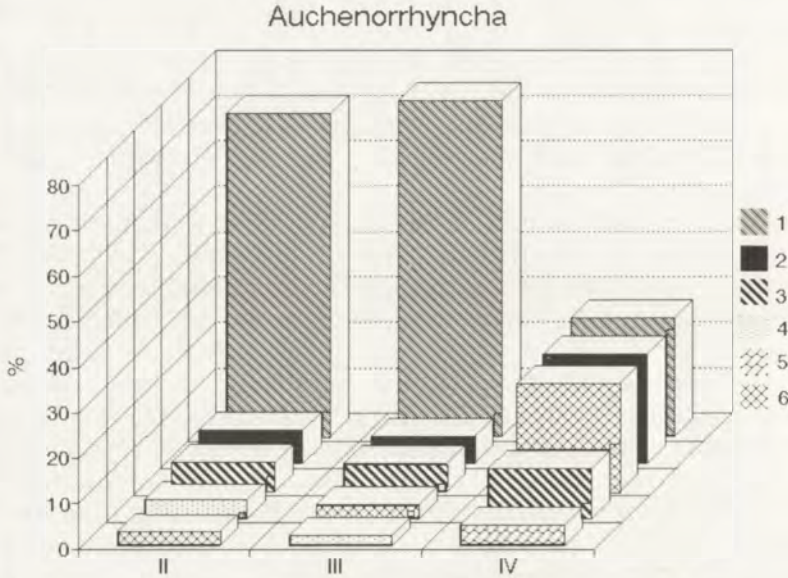


Fig. 7. Dominance structure of communities of cicadas (*Homoptera*, *Auchenorrhyncha*) in canopies of pine in forest stands of various ages in Puszcza Białowieńska; 1 – *Speudotettix subfuscus*, 2 – *Wagneripteryx germari*, 3 – *Oncopsis flavicollis*, 4 – *Hesium domino*, 5 – *Grypotes puncticollis*, 6 – *Allygus mixtus*

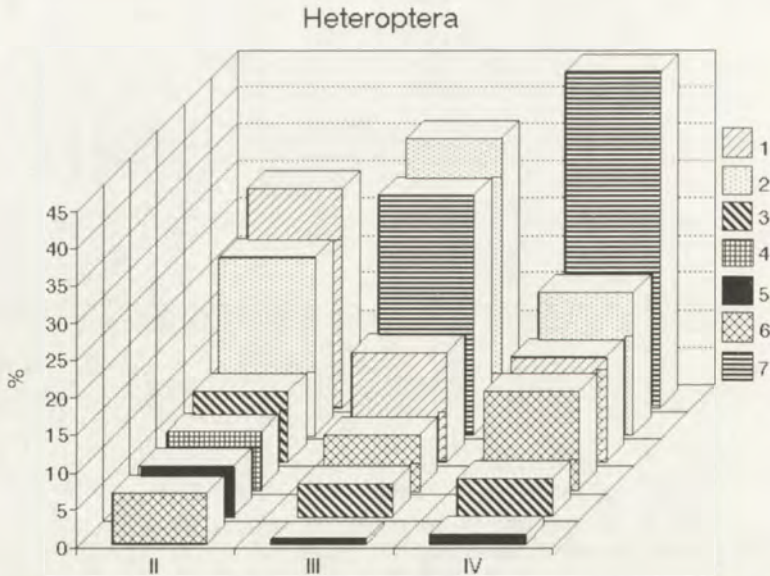


Fig. 8. Dominance structure of communities of heteropterans (*Heteroptera*) in canopies of pine in forest stands of various ages in Puszcza Białowieńska; 1 – *Phytocoris intricatus*, 2 – *Phoenicocoris obscurellus*, 3 – *Camptozygum aequale*, 4 – *Phytocoris intricatus*, 5 – *Alloetomus germanicus*, 6 – *Phoenicocoris modestus*, 7 – *Plesiodesma pinetellum*

attained peak abundance and proportion in the mature forests of Puszcza Białowieska (Fig. 8). Its abundance in pole wood was nearly four times lower, and in young stands, a hundred times lower, than in mature stands. Moreover, in older stands a decrease was observed in the proportion of two species not so narrowly specialised as monophages, namely *Phytocoris intricatus* and *P. pini*, both of which are tropically associated with various coniferous tree species.

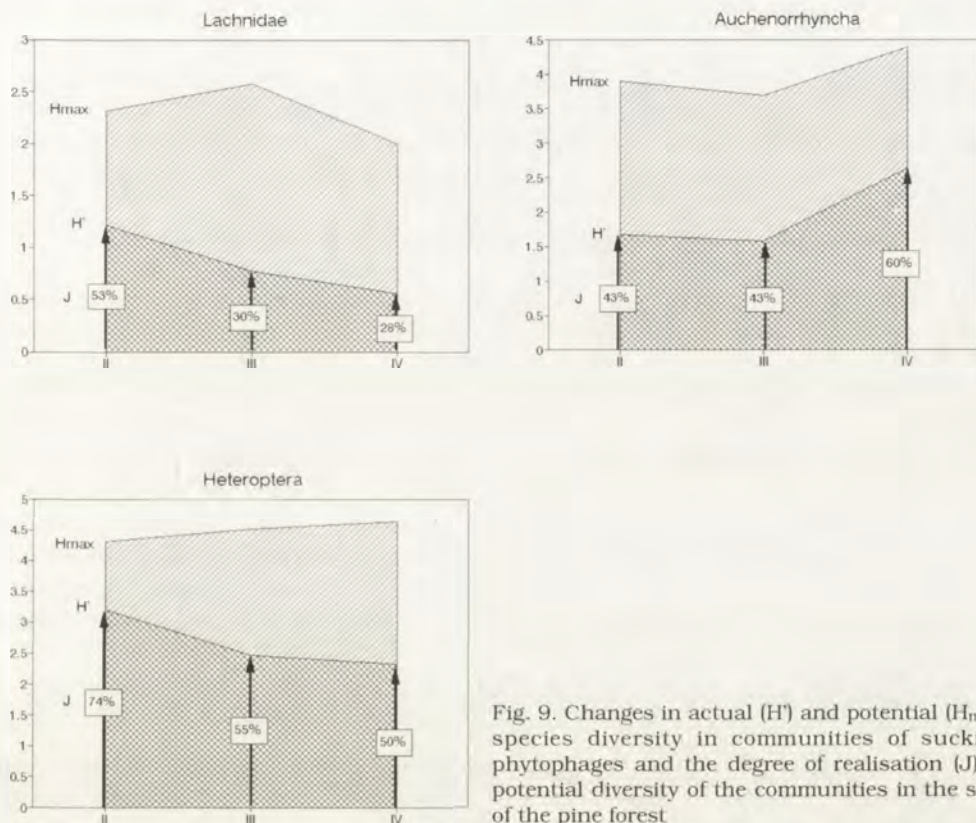


Fig. 9. Changes in actual (H') and potential (H_{max}) species diversity in communities of sucking phytophages and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

The similarity of species composition in all the sucking phytophage communities occurring in stands of all age classes in Puszcza Białowieska, as well as the differences in abundance and community structure described above substantially affected species diversity measured with Shannon and Weaver's index (Fig. 9). In the sere under investigation, species diversity of both aphid and heteropteran communities decreased with greater species diversity differences noted in both communities between young growth and older stands (pole wood, mature forest) than between the latter two. Cicadas exhibited a different response to the process of succession, reflected in an increase in species diversity with the growing age of the forest stand. In that case the mature forest is a stage of greater potential species diversity than the younger stages: young stand and the pole wood. In the pine forest sere studied in Puszcza Białowieska,

the degree to which species diversity approximated the potential of the faunal system varied from community to community. In aphid and heteropteran communities, the degree of realisation of diversity (measured with Pielou's index) is highest in young stands, while in the case of leafhoppers the highest values were registered in mature stands (Fig. 9). As the forest stand grows older, differences are also noted in the distribution of individual species' shares in their communities. Decreases in the degree of uniformity of individual species distribution were recorded in aphid and heteropteran communities, while increases in species proportions' uniformity with the growing age of the stand were seen in communities of leafhoppers.

Analysis of structures of the communities of sucking phytophages showed that they do not fit any of the five distribution models formed so far i.e. the geometric series, broken stick distribution model, logarithmic series, lognormal distribution and negative binomial distribution.

The process of formation of the unique sucking phytophage fauna of the canopies of trees in pine forests starts in young stands (or possibly even earlier, in the culture stage), as is indicated by the remarkably high similarity of species composition of communities occurring in different age classes of the pine forests of Puszcza Białowieska. The transition between consecutive succession stages of the pine forest is marked by changes (although their rate and direction differ from group to group) in abundance and dominance structure of all the sucking phytophage communities studied. Generally, as the forest stand grows older, both the abundance and proportions of species associated with pine tend to increase, while the abundance and proportion of poly- and oligotrophic species are reduced. The formation of a dominance structure characteristic of pine canopies is nearly completed in 50-year-old forest stands (aphids, heteropteran bugs). In leafhoppers the process is slower, concluding in stands older than 50 years.

Chewing phytophages

115 species of sawflies (*Hymenoptera, Symphyta*), 23 species of leaf beetles (*Coleoptera, Chrysomelidae*) 46 species of weevils (*Coleoptera, Curculionidae*) and 122 species of butterflies (*Lepidoptera*) (HUFLEJT unpublished data, WASOWSKA unpublished data, WIŚNIEWSKA unpublished data, BUSZKO and WINIARSKA unpublished data) were recorded in the canopies of pine forest stands in Puszcza Białowieska in all the forest stand age classes studied (young stand, pole wood, mature forest). In the majority of the groups of chewing phytophages under study, the number of species forming the communities tended to decrease as the forest stand grew older. The reason for the decrease in the number of species was the same for all communities. In younger stands (particularly in young stands), there was a significant number of species associated trophically, often only in the larval stage, with plants occurring in the ground cover of the pine forest studied in Puszcza Białowieska: 30 such species were recorded in the community of sawflies in young stands, 26 in the pole wood and 20 in mature stands. The respective figures for the Curculionid community were 12 species

in young stands, 6 in the pole wood and 7 in mature stands. On the other hand, the number of species of butterflies grows steadily as the stand develops with 70 species recorded in young stands, 91 in the pole wood and 100 in mature stands (Fig. 10).

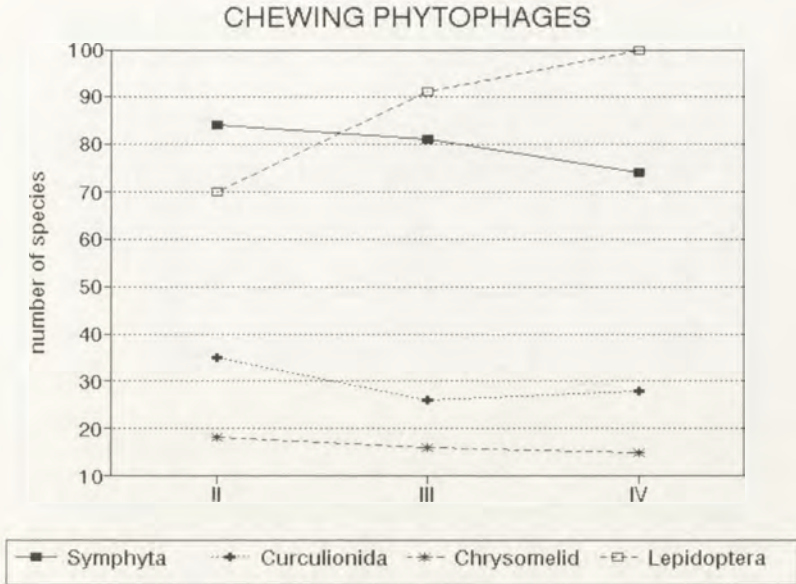


Fig. 10. Changes in the number of species of chewing phytophages in pine forests of three age classes of the forest stand

The species composition was similar in all the communities of biting phytophages studied. The highest similarity of species composition was recorded for communities of butterflies and sawflies with Sørensen's similarity indices ranged from 68% to 79% for individual communities, while the lowest values were obtained for communities of *Chrysomelidae* (47%–58%). The values of similarity indices (S_o) of individual communities inhabiting canopies of pines were largely dependent on local differences in the species composition of the ground cover and the understorey vegetation. It was particularly evident in the case of insect species of high trophic specificity. For example, *Hypera nigrostris* (*Curculionidae*), a species feeding on clover, was registered in young and mature stands (in the latter it was even a dominant species), but did not occur in the pole wood. Of three species associated with cruciferous plants and recorded in young stands, only one was found in the pole wood and none in the mature forest. In leaf beetle communities, virtually all the species caught in canopies of trees in the pine forests feed on leaves of either herbaceous plants or deciduous trees (only 1 out of 27 species found in Puszcza Białowieska feeds on pine). As a result, the species composition of communities of beetles of this family was

much more dependent on local species richness of the ground cover and on the presence of various tree species and deciduous shrubs in the understory.

Communities found in older stands (pole wood, mature forest) exhibited conspicuous similarity both in species composition (similarity indices ranged from 58% for leaf beetle communities to 77% for sawflies) and the structure of dominance of individual communities.

On the other hand, abundance of the sawfly, leaf beetle and weevil communities studied did not exhibit significant differences related to the age of the stand (Fig. 11).

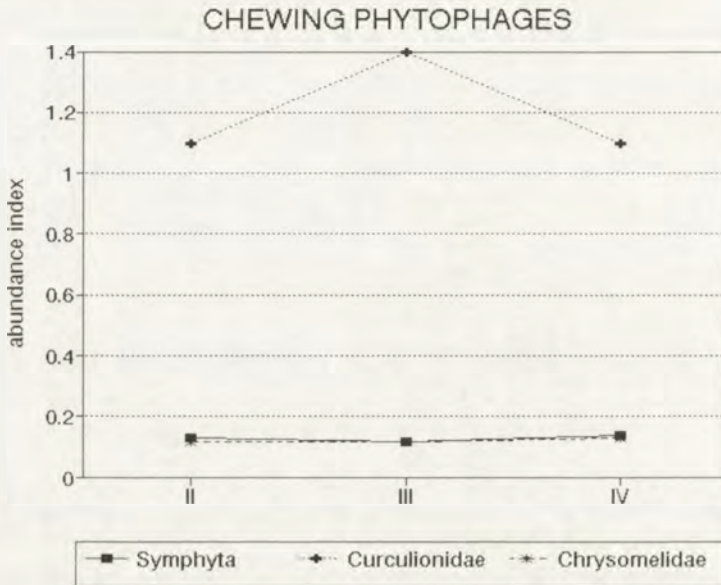


Fig. 11. Changes in the abundance of chewing phytophages in pine forests of three age classes of the forest stand

In the sere studied changes in dominance structure occurred in all the communities of chewing phytophages under study. They consisted predominantly in shifts in the rank of the dominant species.

In sawfly communities, the proportion of the monophage of pine *Xyela julii* (larvae feed on male efflorescence) rose with the growing age of the stand (from 2% in young stands to 16% in mature stands), while the reverse phenomenon was observed for *Athalia rosae* (from 33% in young stands to about 10% in mature forests). *A. rosae* is a very common species occurring in various habitats (Fig. 12). The proportion of *Pristiphora abietina*, the larvae of which feed on needles of spruce, remained fairly constant in all the age classes of the forest stand.

A significant transformation of the dominance structure in communities of beetles of the family *Curculionidae* could be seen between the young growth and

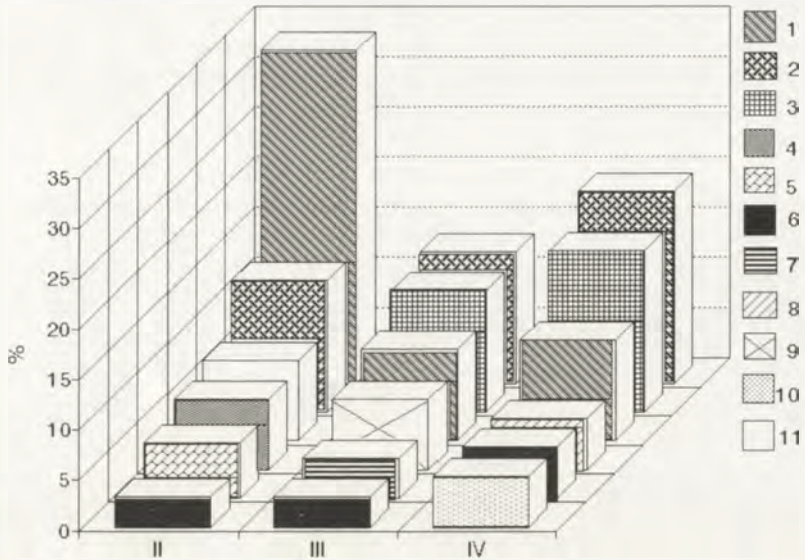


Fig. 12. Dominance structure of communities of sawflies (*Hymenoptera, Symphyta*) in canopies of pine in forest stands of various ages in Puszcza Białowieska; 1 - *Athalia rosae*, 2 - *Pristiphora abietina*, 3 - *Xyela juli*, 4 - *Rhogogaster picta*, 5 - *Athalia bicolor*, 6 - *Pristiphora pseudodecipiens*, 7 - *Nematus dispar*, 8 - *Dineura viridorsata*, 9 - *Shaliphora parva*, 10 - *Fenusa pusilla*, 11 - *Athalia circularis*

Curculionidae

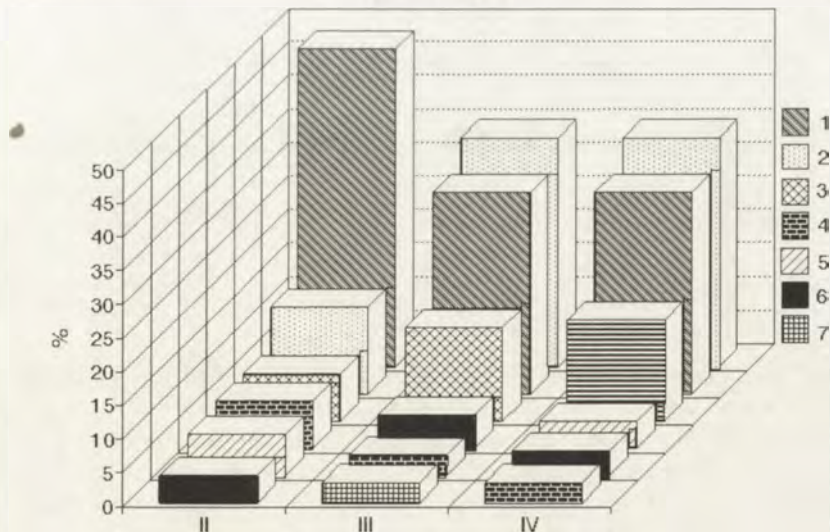


Fig. 13. Dominance structure of communities of xxx (*Coleoptera, Curculionidae*) in canopies of pine in forest stands of various ages in Puszcza Białowieska; 1 - *Brachonyx pineti*, 2 - *Rhinomacer attelaboides*, 3 - *Anthonomus phyllocola*, 4 - *Attelabus nitens*, 5 - *Magdalis linearis*, 6 - *Straphosoma capitatum*, 7 - *Daydrhynchus austriacus*, 8 - *Hypera nigrirostris*

pole wood stages. It consisted in a decrease in the rank of *Brachonyx pineti*, a species feeding on pine needles, for the benefit of *Rhinomacer attelaboides*, which develops in male efflorescence of coniferous trees. In young stands, *B. pineti* was the eudominant with a proportion of 47.4%, and was followed by *R. attelaboides* (13%) (Fig. 13). In older stands (pole wood, mature stands) both species were co-dominant.

In the *Chrysomelidae* beetle communities the proportion of *Galerucella lineola* increased as the stand grew older. The imagines of this species feed on deciduous trees and shrubs. On the other hand, there was a reduction in the share of *Aptona euphorbiae*, a species associated with the ground cover vegetation (Fig. 14).

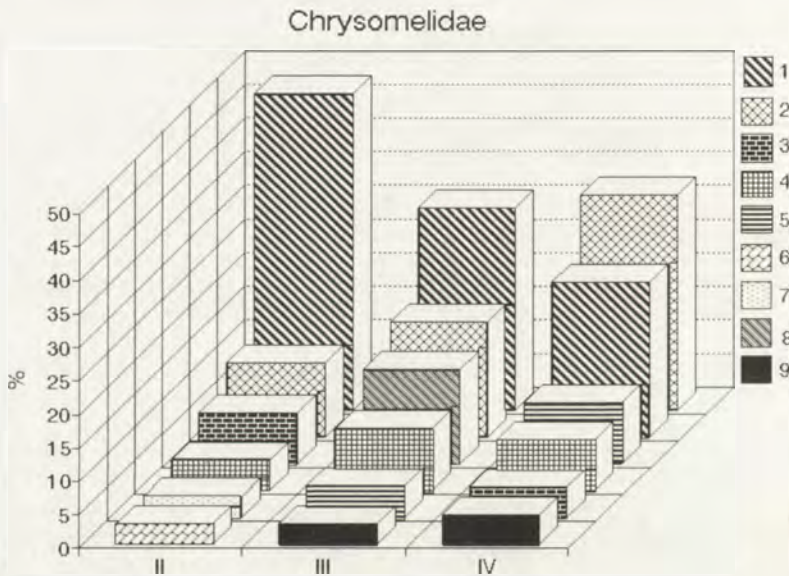


Fig. 14. Dominance structure of communities of leaf beetles (Coleoptera, Chrysomelidae) in canopies of pine in forest stands of various ages in Puszcza Białowiecka; 1 - *Aptona euphorbiae*, 2 - *Galerucella lineola*, 3 - *Longitarsus parvulus*, 4 - *Crytocephalus parvulus*, 5 - *Crytocephalus flavipes*, 6 - *Longitarsus longisetus*, 7 - *Phyllotreta nemorum*, 8 - *Phratora laticollis*, 9 - *Crytocephalus saliceti*.

In *Lepidoptera* communities the pine monophage, *Olethreutes bifasciana* is the dominant species in all succession stages. There is also a high proportion of species associated with the ground cover or even deciduous trees (*Rhopobota naevana*, *Apotomis betuletana*, *Alcis repandata*). *A. betuletana* is only found in mature stands, while *R. naevana* and *A. repandata* belong to the dominant group in all age classes. Characteristic is an extremely low proportion of species recognised as primary pine foliophages (*Lymantria monacha* and *Bupalus piniarius*).

The values of Shannon and Weaver's index corresponding to total species diversity of individual communities of chewing phytophages display relatively

insignificant differences in relation to the age of the stand (Fig. 15). Despite the small differences, the highest species diversity in all the communities of chewing phytophages was recorded in younger stands: young stands (*Curculionidae*) or the pole wood (*Symphyta*, *Chrysomelidae*)

In the sere of the pine forest of Puszcza Białowieska potential species diversity (measured with Pielou's index) ranged from 72–82% for sawfly communities, and 76–85% for leaf beetle communities. Somewhat lower values of potential species diversity were obtained for *Curculionidae* communities, but even in this case, the values of Pielou's index were similar in all stand age classes (Fig. 15).

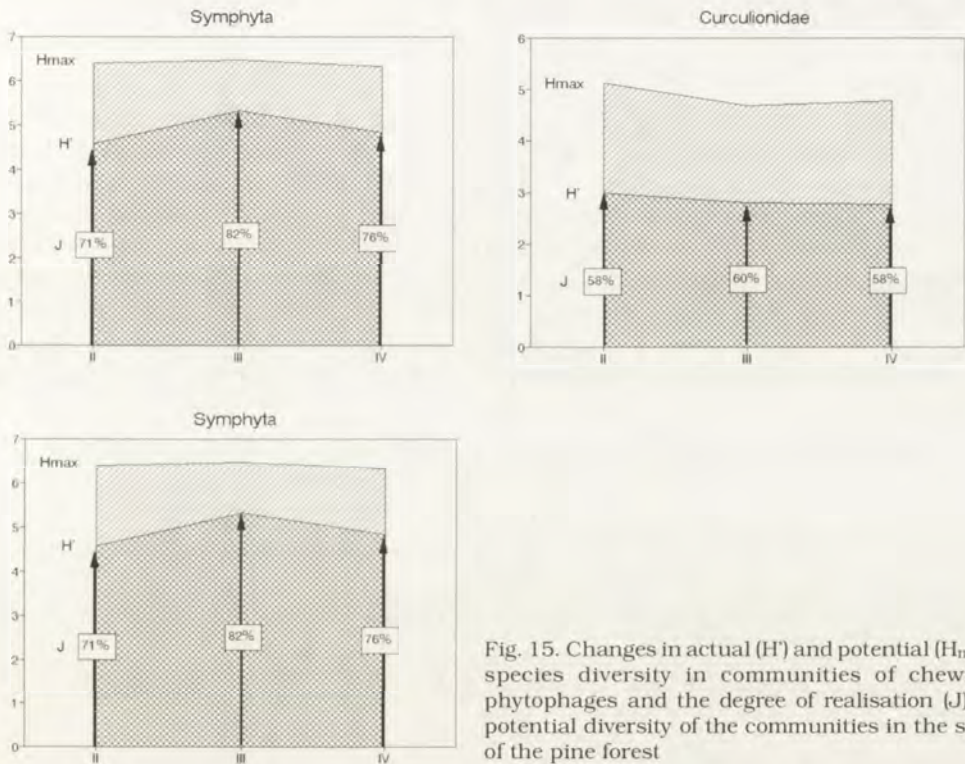


Fig. 15. Changes in actual (H') and potential (H_{max}) species diversity in communities of chewing phytophages and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

Analysis of structures of the communities of chewing phytophages showed that they do not fit any of the five models of abundance distribution among individual species i.e. the geometric series broken stick distribution series, logarithmic, lognormal distribution and negative binomial distribution.

The process of formation of the chewing phytophage fauna specific to the pine forests of Puszcza Białowieska takes place in the pole wood stage, as is indicated by the considerable similarity of species composition and dominance structures in communities occurring in the pole wood and mature stands.

In all the chewing phytophages communities studied transitions between consecutive stages of the pine forest sere are marked by changes in abundance

and dominance structure. The changes in the dominance structure consist predominantly in shifts in the position, or rank, of species predominating in a given community. In weevil and sawfly communities older stands witness an increase in the proportions of species whose larvae feed on male efflorescence of pine; in the leaf beetles community there is a decrease in the proportion of the species feeding on deciduous tree leaves. As the stand grows older, a decrease is observed in the number of species trophically associated (often only in the larval stage) with herbaceous plants that only penetrate canopies of pines. This holds true both for many species of sawflies, the majority of adult forms of which are mellitophagous, and many species of beetles, which are phytophagous both in the larval and adult stages.

Xylophages and cambioptages

The consecutive stages of the pine forest sere create different conditions for the development of xylophages and cambioptages, which develop in or under the bark, or in the wood of various species of trees and shrubs. Individual species of these beetles are associated with specific plant species, inhabiting different layers from roots, stems, branches to thin twigs. They also settle in decaying stumps, damaged during forest felling and clearance, and in wood remaining after the felling. Various species of these insects show preference for certain phases of bark decomposition. Injuries to the foot of a tree, which weaken the entire organism, increase in severity as the stand grows, promoting the development of xylo- and cambioptages.

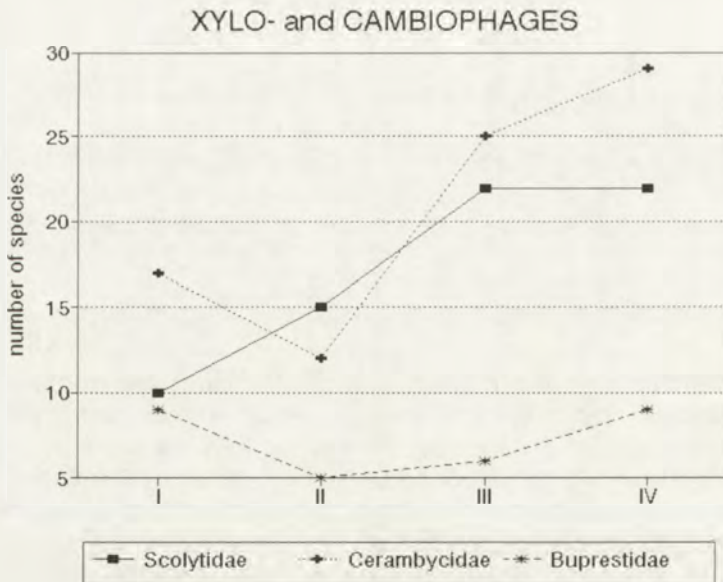


Fig. 16. Changes in the number of species of xylophages and cambioptages in pine forests of three age classes of the forest stand

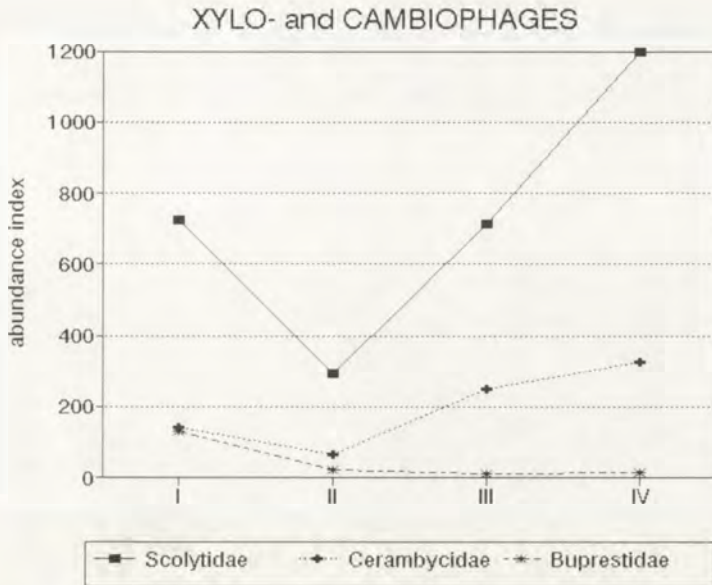


Fig. 17. Changes in the abundance of xylophages and cambiohages in pine forests of three age classes of the forest stand

Bark beetles (*Scolytidae*)

Bark beetle communities are characterised by a steady rise in the number of species throughout the sere (Fig. 16). The lowest number of species – 10 – was recorded in the culture stage. Those species show an affinity for habitats forming immediately after felling and are more apt to inhabit fresh stumps (*Hylurgos palliatus*, *Hylastes ater*, *H. opacus* and *Hylurgos ligniper*). Some of them prefer the underground part of the stump due to higher moisture (*Hylastes ater* and *H. opacus*), others inhabit the whole of the stump (Mokrzycki, oral information). The species damage the bark and may occur in considerable abundance in 3–5-year-old cultures. In the young stand stage, the species composition of the bark beetle community is even richer: all the species occurring in the culture are still present, there appear species settling on trunks, such as *Pityogenes quadridens*, or characteristic of older stands, e.g. *Ips sexdentatus*. In older stands the species composition of the communities becomes richer still, owing to, among other factors, an influx of species settling on branches. The communities most similar in species composition are those inhabiting pole wood and mature stands (Sørensen's similarity index ranged among 81 to 100%). The lowest abundance is noted for communities in young stands. In older stands, the abundance increases steadily, achieving a maximum in the mature stage (Fig. 17). Analysis of the structure of dominance reveals that the structure of the community is transformed in the course of succession since different species are dominant in the consecutive age classes (Fig. 18). The similarity of dominance structures of *Scolytidae* communities inhabiting older stands (pole

wood, mature stands) is high. In younger stands (culture, young stands) on the other hand, community structures differ both from one another and from communities of older stands. It is therefore suggested that the communities become stable after the stand reaches the pole wood stage (MOKRZYCKI unpublished data).

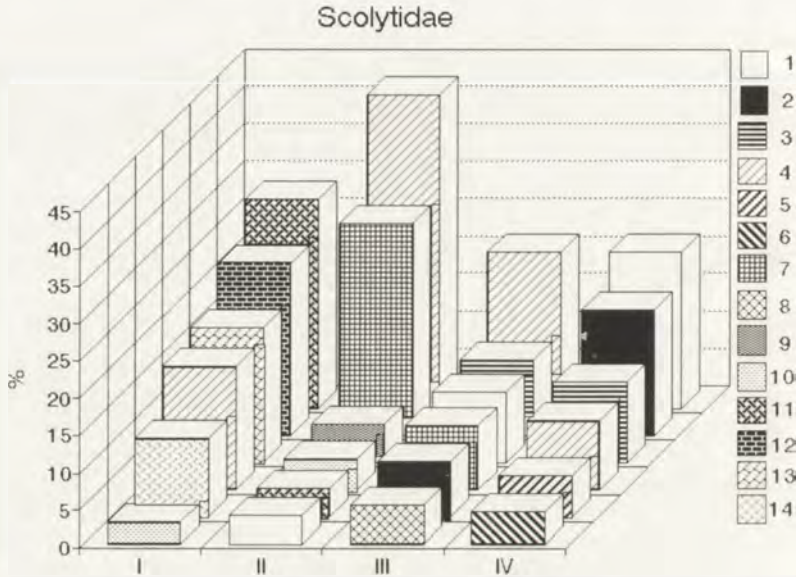


Fig. 18. Dominance structure of communities of bark beetles (*Scolytidae*) in forest stands of various ages in Puszcza Białowiecka: 1 - *Crypturgus hispidulus*, 2 - *Crypturgus cinereus*, 3 - *Trypodendron lineatum*, 4 - *Tomicus piniperda*, 5 - *Ips acuminatus*, 6 - *Ips sexdentatus*, 7 - *Pityogenes bidentatus*, 8 - *Orthomicus suturalis*, 9 - *Pityogenes quadridens*, 10 - *Hylastes opacus*, 11 - *Orthomicus laricis*, 12 - *Hylurgops palliatus*, 13 - *Hylastes ater*, 14 - *Hylurgus lignipetra*

Longicorns (*Cerambycidae*)

Longicorns communities are characterised by an increase in the number of species in the pole wood and mature forest stage as compared to young stands (Fig. 16). A similar number of species in every age class of pine forest (young stand, pole wood, mature stand) was recorded only in the case of tree canopies. The culture stage is characterised by a relatively rich *Cerambycidae* taxocoene, which is associated with the taxon settling stumps and what has remained after clearfelling. The species composition in the young stand stage is the poorest and most different in comparison to communities occurring in older stands. In the pole wood, the Longicorn beetle community is similar in species composition to the community inhabiting natural mature stands (Sørensen's index is 67%) (GUTOWSKI unpublished data). In the sere under study, the abundance of *Cerambycidae* reaches the lowest values in young stands, and increases in the pole wood and mature stands (Fig. 17). In the *Cerambycidae* communities under

investigation, *Asemum striatum* is dominant in the culture stage (16.5%), *Pogonocherus decoratus* in young stands (32.8%), *Corymbia rubra* in the pole wood (15.0%) and *Rhagium inquisitor* in the mature stand (17.7%) (Fig. 19).

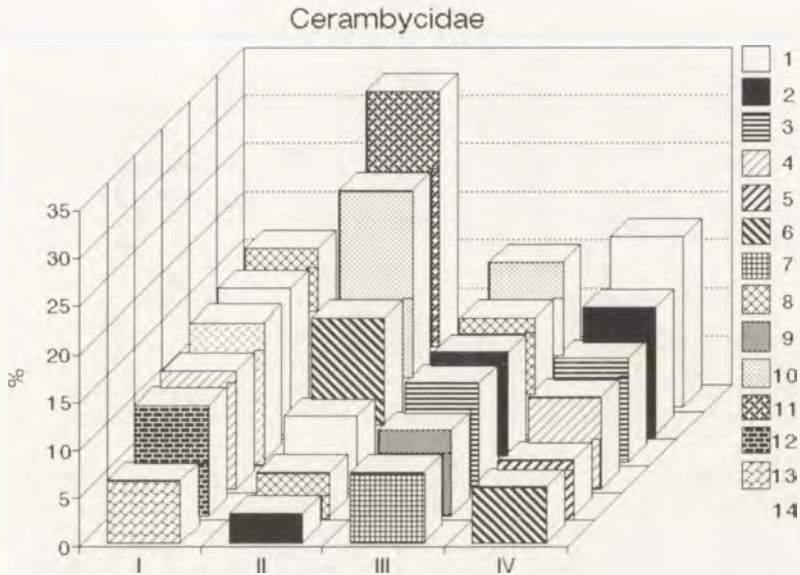


Fig. 19. Dominance structure of communities of *Cerambycidae* in forest stands of various ages in Puszcza Białowieńska; 1 – *Rhagium inquisitor*, 2 – *Stenurella melanura*, 3 – *Molorchus minor*, 4 – *Arhopalus rusticus*, 5 – *Tetropium castaneum*, 6 – *Pogonocherus fasciculatus*, 7 – *Acanthocinus griseus*, 8 – *Asemum striatum*, 9 – *Callidium coriaceum*, 10 – *Corymbia rubra*, 11 – *Pogonocherus decoratus*, 12 – *Spondylis buprestoides*, 13 – *Callidium violaceum*

Buprestids (*Buprestidae*)

The highest number of species is recorded in buprestid communities from pine cultures and significantly thinned mature forests (Fig. 16). The highest similarity of species composition was noted for communities of cultures, pole wood and mature stands (Sørensen's similarity index ranged among 67 to 70%). The abundance of *Buprestidae* community is the highest in the culture stage (Fig. 17). The same species, namely *Anthaxia quadripunctata*, is dominant in all the age classes of the pine forest sere and the communities inhabiting consecutive stages of forest stand development are characterised by relatively high similarity of dominance structures (Fig. 20). The most similar in this respect are communities occupying cultures and young stands, while the greatest differences in dominance structures were recorded for the culture and mature stand communities (GUTOWSKI unpublished data).

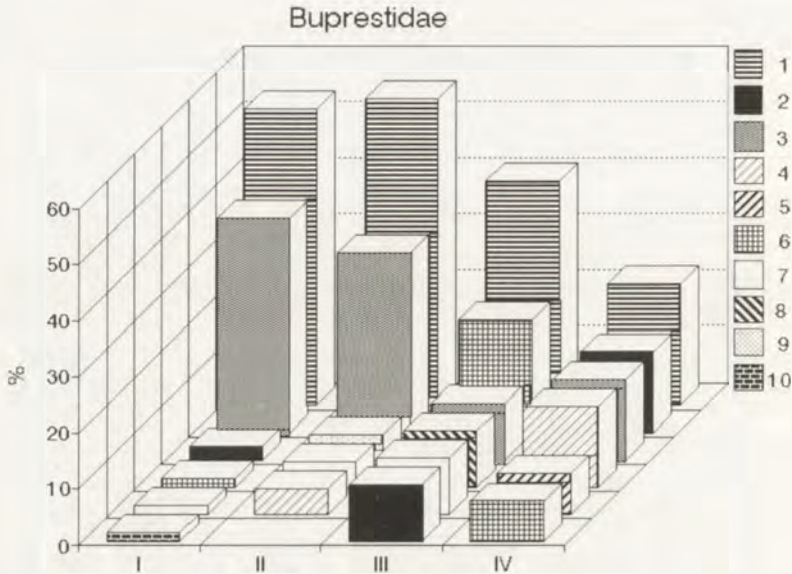


Fig. 20. Dominance structure of communities of buprestids (*Buprestidae*) in forest stands of various ages in Puszcza Białowieska; 1 – *Anthaxia quadripunctata*, 2 – *Chalcophora mariana*, 3 – *Buprestis rustica*, 4 – *Anthaxia submontana*, 5 – *Buprestis haemorrhoidalis*, 6 – *Agrilus sulcicollis*, 7 – *Trachys minuta*, 8 – *Phaenops cyanea*, 9 – *Buprestis octoguttata*, 10 – *Agrilus angustulus*

Analysis of changes in xylo- and cambioophage communities in the course of succession

Transformations of the communities of the xylo- and cambioophage groups studied are a little different in each group. The greatest number of species is noted for the xylo- and cambioophage communities occurring in mature stands (Fig. 16). *Buprestidae* and *Cerambycidae* are characterised by relatively high species richness in the culture stage as well, but *Scolytidae* are represented by the lowest number of species at this stage. Young stands are home to the lowest numbers of species of *Buprestidae* and *Cerambycidae*. The abundance of *Scolytidae* and *Cerambycidae* increases towards more mature stands, and it is only the markedly xerophilous *Buprestidae* that are most abundant in the culture stage. In the sere under investigation, the dominant species group of *Scolytidae* and *Cerambycidae* undergoes substantial transformation. Other species are dominant in younger stands than prevail in older ones, although the former dominant group is not completely supplanted. *Buprestidae* are the only taxon where one species (*Anthaxia quadripunctata*) is dominant in all the communities studied. In *Scolytidae*, *Cerambycidae* and *Buprestidae*, the group of dominants is composed of a number of species in every age class.

Analysis of similarity of empirical xylo- and cambioophage communities with the five theoretical statistical distributions showed that the distribution of

species in the communities examined is closest to the negative binomial distribution (*Scolytidae* and *Cerambycidae*). In the case of *Cerambycidae* it is also similar to the logarithmic series (communities of cultures, pole wood and mature forest) and to the geometric series (young stands). In some instances, the estimated number of species is higher than the one actually recorded (*Cerambycidae*) which suggests the presence of higher species capacity of the habitat. In *Scolytidae* the estimated number of species corresponds to the actual one.

Species diversity, measured with Shannon and Weaver's index, is highest in mature stages (*Scolytidae* – pole wood, *Buprestidae* and *Cerambycidae* – mature stands) (Fig. 21). The degree of realisation of potential species diversity (H_{max}) increases in general for the course of the groups studied in each succession stage.

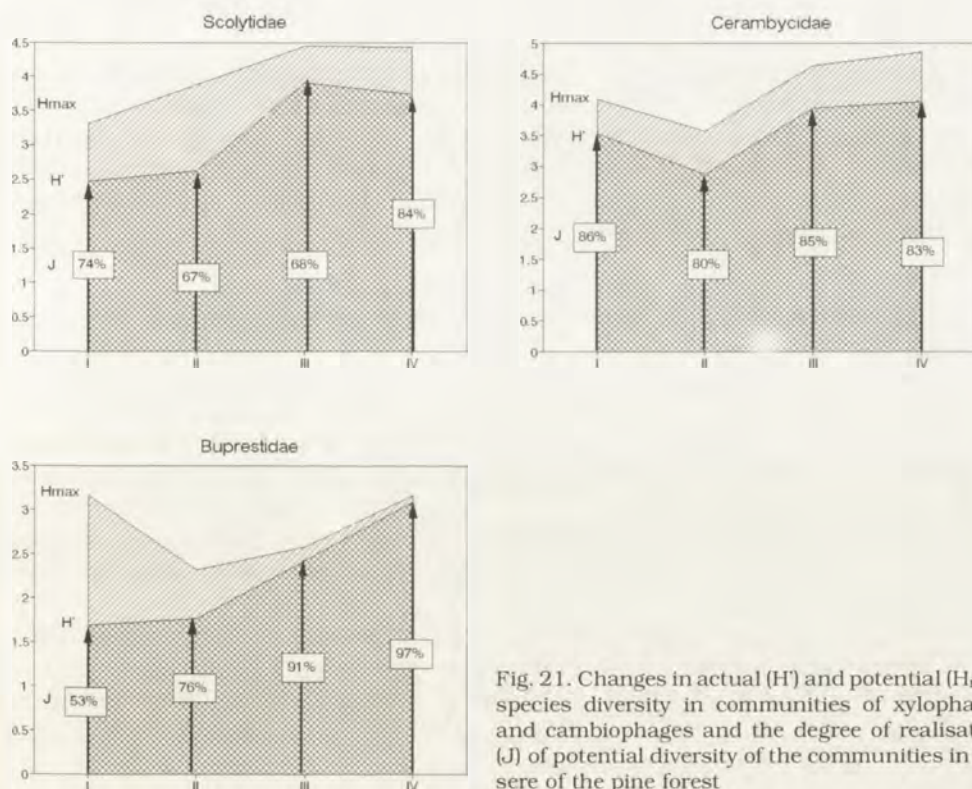


Fig. 21. Changes in actual (H') and potential (H_{max}) species diversity in communities of xylophages and cambioptophages and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

Analysis of structures of the communities of selected xylo- and cambioptophages permits a fuller description of the changes taking place in the succession stages studied in the pine forest sere.

The culture stage creates most favourable conditions for *Buprestidae* to reach a high abundance and a number of species similar to that of the mature forest. *Cerambycidae* are also characterised by relatively rich fauna at this stage. This

is related to the possibility of settling in stumps, clearfelling remains and to high insolation which, is particularly crucial for the appearance of *Buprestidae*.

The young stands harbour the lowest numbers of *Cerambycidae* and *Buprestidae* species. The decaying stumps in young stands are no longer a suitable habitat for most species of *Cerambycidae* and *Buprestidae*, and the thin stems and branches combined with low exposure to sunlight do not provide a good feeding basis for a wider range of species. The situation may change if deadwood appears in younger age classes. Cambio- and xylophagous species of both groups may then increase their numbers. Bark beetle communities have richer species composition at this stage. The species composition of bark beetle communities becomes steadily richer as the forest grows older. Species characteristic of the subsequent stages start to appear while the species occurring in younger age classes do not retreat, but only change their positions in the structure of dominance.

The pole wood stage is a preparatory phase for the formation of communities characteristic of natural mature pine forests. Especially important for the development of xylophages and cambiophages is the appearance of litter, dead trees, development of the herb layer and an increase in insolation at this stage.

The analysis of the selected groups of xylo- and cambiophages revealed that the beetle groups studied become stabilised in older stands (pole wood). The xylo- and cambiophage fauna occurring at this stage most closely resembles the fauna of a natural mature forest.

5.2.2. Epiphytic predators

Predators preying in the ground cover, shrub and tree canopy layers may be divided into two groups playing different ecological roles of specialised and non-specialised predators. Prime examples of non-specialised predators (or forms with hardly-marked trophic specialisation) abundantly represented in the canopy layer of pine forest stands are spiders (*Aranei*), soldier beetles (*Cantharidae*, *Coleoptera*), robber-flies (*Asilidae*, *Diptera*) and digger wasps (*Sphecidae*, *Hymenoptera*). In specialised predators, one can find groups of aphidophagous species belonging to syrphids (*Syrphidae*, *Diptera*), digger wasps (*Sphecidae*, *Hymenoptera*), neuropterans (*Neuropteroidea*) and ladybirds (*Coccinellidae*, *Coleoptera*).

In pine forests these groups of predators exhibit high species richness, at the same time occurring in high abundances to play a doubtlessly significant role in the functioning of the biocenosis. From among non-specialised predators, large-sized forms may even attack larger animals, and the markedly sclerotised protective layer of their victims' bodies poses no obstacle for them. Adult robber-flies and digger wasps, which are good flyers, penetrate into all vegetation layers while hunting.

Web spiders of pine stands have been studied by ŁUCZAK (1963), spiders of middle-aged stands have been investigated by DZIABASZEWSKI (1976), and spiders living in forest stands of various ages have been analysed by STERZYŃSKA and ŚLEPOWROŃSKI (in press).

Pine forest robber-flies have not been dealt with in a separate paper to date.

The species composition and dominance structure of digger wasp communities of these ecosystems have been analysed in papers devoted to Warsaw environs (SKIBIŃSKA 1981) and older pine stands in Byelorussia (SHLYAKHTENOK in press).

The species composition and dominance structure of syrphid communities have been presented in a paper on the pine forest of Puszcza Kampinoska and Białoleka Dworska (BAŃKOWSKA 1982). To date, there has been only one paper which compares the course of secondary succession of syrphid communities in three age classes of pine forest stands in three different pine forests (BAŃKOWSKA in press).

Ladybirds of older stands of pine have been analysed by HOREGOTT (1960), KLAUSNITZER (1968), KLOMP and TEERINK (1973) and CZECHOWSKA (1981).

Few papers have been devoted to neuropterans of pine forests (CZECHOWSKA 1985) and none of them is concerned with succession.

Spiders (*Aranei*)

75 spider species occur in the pine forest stands studied in all the age classes, with 51 species in young stands, 31 in the pole wood and 39 in mature stands (Fig. 22) (STERZYŃSKA unpublished data). 15 species were found to occur in every succession stage in the pine forest, accounting for about 20% of the spider fauna collected with Moericke's pitfall traps in the study areas. The species composition of spiders in young pine stands is characterised by a much greater uniqueness than the fauna registered in older stands. The degree of species composition similarity (S_o) of the young stand and pole wood communities was 46%, and of

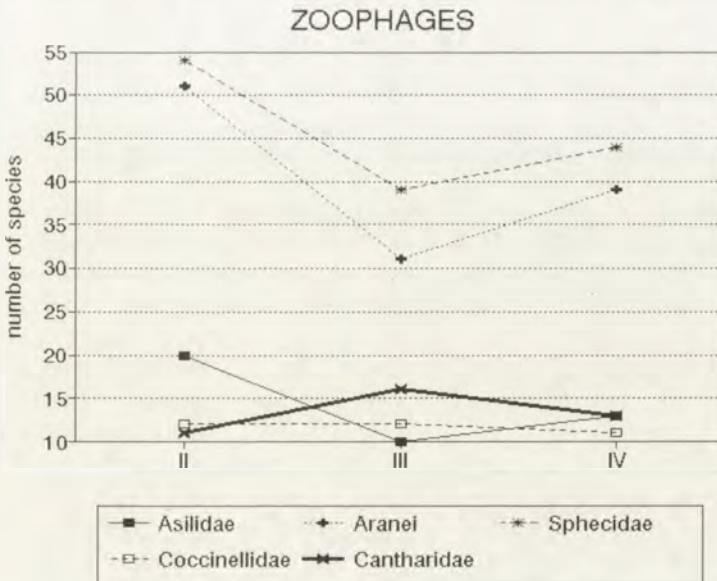


Fig. 22. Changes in the number of species of predators in pine forests of three age classes of the forest stand

spider communities of young and mature stands – 44%, while the figure for the pole wood and mature stands was 60%.

The differences in abundance of spider communities in pine stands of various ages in Puszcza Białowieska were not as significant as differences in the number of species. The most abundant community lived in young stands, while in pole wood the community abundance was lower by about 40% and in mature forests – by 30% (Fig. 23).

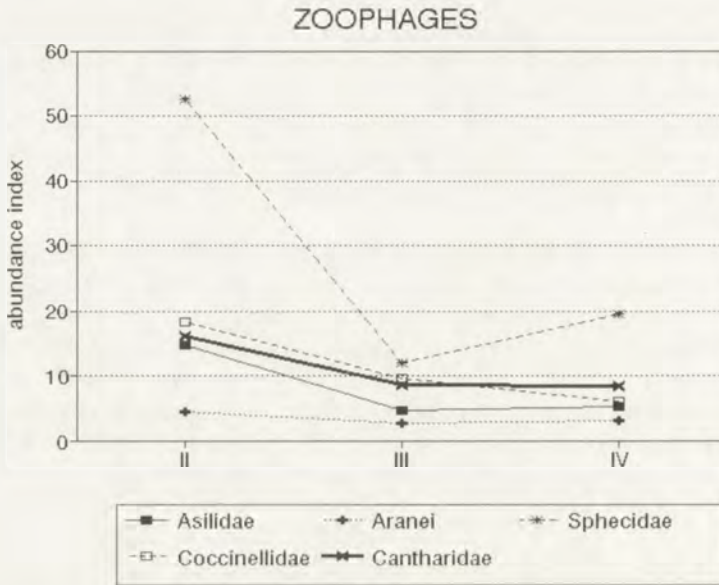


Fig. 23. Changes in the abundance of predators in pine forests of three age classes of the forest stand

The structures of dominance of spider communities were similar in all the succession stages of pine forests (Fig. 24). *Heliophanus dubius* was dominant in young stands and the pole wood, and subdominant in mature stands, where *Diaea dorsata* was the dominant species. From among the 10 most abundant species caught in canopies of pines, as many as 7 belonged to the group of species prevailing in all the forest stands studied. The species included: *Heliophanus dubius*, *Anyphaena accentuata*, *Trematocephalus cristatus*, *Theridion tinctum*, *Diaea dorsata*, *Xysticus cristatus* and *Atea sturmi*. The share of this group was significant in each community exceeding 45% in young stands, reaching nearly 65% in pole wood and about 50% in mature stands. All of the above species are forest polytopes, associated mostly with coniferous forests. Only *T. cristatus* is considered to occur more often in deciduous forests (STERZYŃSKA unpublished data).

As the stands grew older, the abundance of *H. dubius*, *A. accentuata*, *T. cristatus* and *T. tinctum* decreased while the abundance of *D. dorsata* and *A.*

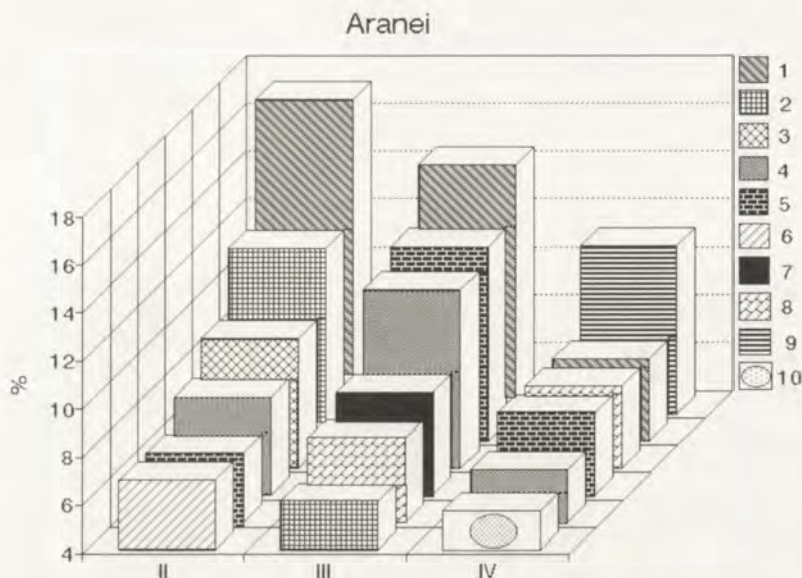


Fig. 24. Dominance structure of communities of spiders (*Aranei*) in forest stands of various ages in Puszcza Białowieńska; 1 – *Heliophanus dubius*, 2 – *Euryclubiona subsultans*, 3 – *Dendryphantès rudis*, 4 – *Annyphaena accentuata*, 5 – *Trematocephalus cristatus*, 6 – *Entelecara congenera*, 7 – *Theridion tinctum*, 8 – *Atea sturmi*, 9 – *Diaea dorsata*, 10 – *Dictyna arundinacea*

sturmi rose together with their ranks in the community as they occupied higher positions in the structure of dominance in older stands. In the case of *X. cristatus* the abundance remained the same in all the pine stands studied, while its share in older stands' communities increased since the total abundance of these communities was lower than the abundance of the young stand spider community.

Soldier beetles (*Cantharidae*)

In the pine forest stands studied in Puszcza Białowieńska soldier beetles were represented by 16 species (CHOBOTÓW 1993), all of which were registered in medium age stands. The community poorest in regard to species composition (11 species), but at the same time the most abundant, was found in young stands (Fig. 22). 11 species were found to be common to all the communities studied, so that soldier beetle communities were characterised by a high degree of species composition similarity. The values of Sørensen's index ranged from 81% to 92%. The composition of the dominant species group in the beetle communities was quite similar in the stands of various ages, but the young stand soldier beetle community was a little more unique than communities of older stands (Fig. 25). The two co-dominant species from young stands, *Cantharis nigricans* and *C. pellucida* functioned as subdominants in older stands; in the pole wood the co-dominants were *C. obscura* (a subdominant in young stands) and

Rhagonycha lignosa, which became a strong dominant in mature forest. A characteristic finding is that polytopic species were dominant in young stands, while other forms predominated in older stands – a forest polytope and coniferous forest oligotope in the pole wood, and a coniferous forest oligotope in the mature forest.

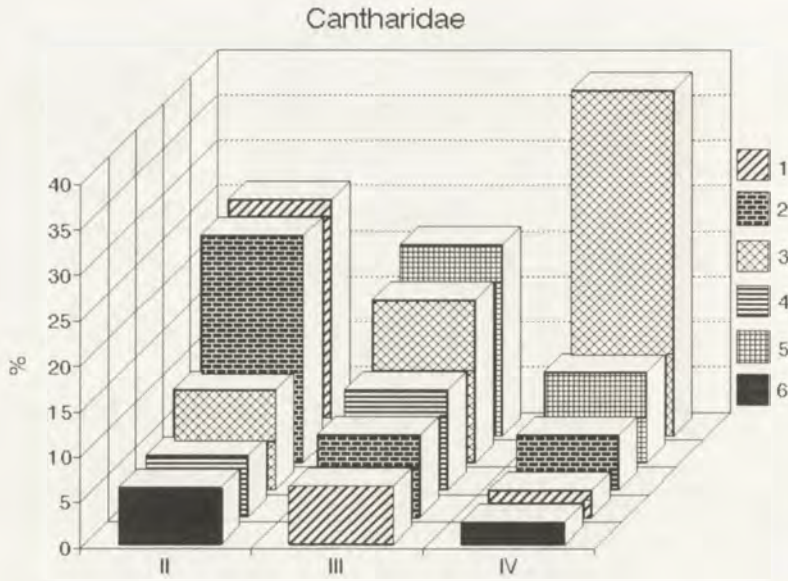


Fig. 25. Dominance structure of communities of cantharides (*Cantharidae*) in forest stands of various ages in Puszcza Białowieska: 1 – *Cantharis nigricans*, 2 – *Cantharis pellucida*, 3 – *Cantharis obscura*, 4 – *Rhagonycha limbata*, 5. *Rhagonycha lignosa*, 6 – *Rhagonycha elongata*

Just like in the case of spiders, robber-flies (*Asilidae*) (TROJAN unpublished data) and digger wasps (*Sphécidae*) (SKIBIŃSKA unpublished data) were also represented by a much higher number of species in young stands (Fig. 22). Those predatory insects were also more abundant in young stands.

Robber-flies (*Asilidae*)

A total of 22 species of *Asilidae* were found in the pine forest stands studied in Puszcza Białowieska, as many as 20 of which were registered in young stands compared to 10 species caught in the pole wood and 13, in mature stands. Most of them were rather common species, with the exception of *Lasiopogon immaculatus*, a species only recently found in Poland and characteristic of Puszcza Białowieska. The species was among the most abundant species in mature forests. 9 species were found to be common to all the stands studied. A high degree of species composition similarity was noted for *Asilidae* communities of older stands, with Sørensen's index equalling 78% for pole wood and mature forest communities.

The abundance of *Asilidae* communities in pole wood and mature forests was similar and nearly three times lower than the abundance of the dipteran community in young stands (Fig. 23).

From the viewpoint of the composition of the most abundant species group, the structure of dominance was similar in all the succession stages of pine forests (Fig. 26) with *Neoitamus cyanurus* functioning as a dominant and *N. socius*, as a subdominant. The abundance of each of the two species was much lower in mature than in young forests. The group of the most abundant species in all the communities studied included also *Tolmerus atricapillus*. The contribution of these species to robber-fly communities was significant and amounted to over 80% in young stands, over 90% in pole wood and almost 70% in mature stands.

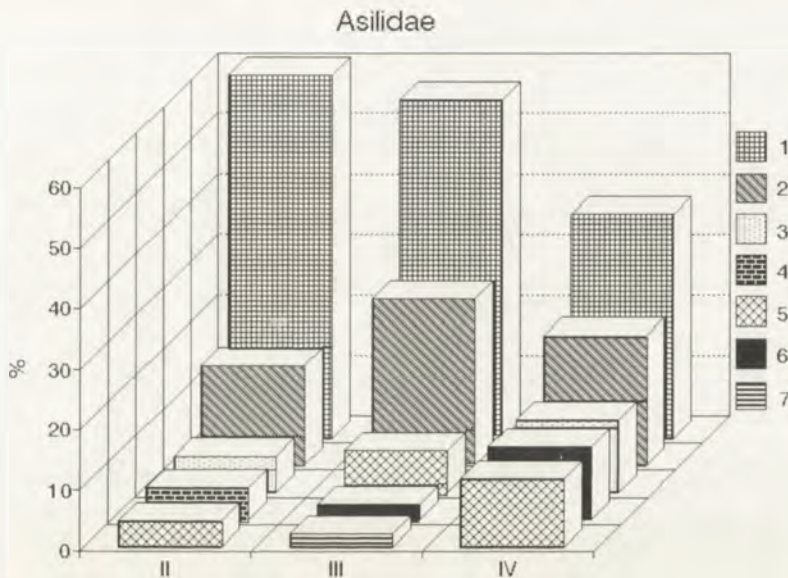


Fig. 26. Dominance structure of communities of *Asilidae* in forest stands of various ages in Puszcza Białowieska: 1 - *Neoitamus cyanurus*, 2 - *Neoitamus socius*, 3 - *Neoitamus cothurnatus*, 4 - *Dioctria hyalipennis*, 5 - *Tolmerus atricapillus*, 6 - *Lasiopogon immaculatus*, 7 - *Epitriptus arthiticus*

Digger wasps (*Sphecidae*)

In the pine forest sere of Puszcza Białowieska 77 species of digger wasps were found, accounting for $\frac{1}{3}$ of the total number of digger wasps ever found in Poland. This group of predators was also richest in young stands both in the number of species and in abundance. 53 species were found in young stands, 39 in the pole wood and 44 in mature stands.

The degree of species composition similarity was 57% for the young stand and pole wood digger wasp communities, 54% for the young and mature stand communities and 70% for the pole wood and mature stand communities of *Sphecidae*. Studies of *Sphecidae* in other habitats show that a value of

Sørensen's index equalling 70% is extremely high for this taxon. It may be thus contented that in older stands of pine *Sphecidae* are represented by a taxocoene of a rather uniform species composition.

Considerable differences were, however, noted in community abundance. The digger wasps of young stands were nearly five times as abundant as in pole wood and almost three times as numerous as in mature forests (Fig. 23).

The structure of dominance of pine forest digger wasp communities in Puszcza Białowieska is characterised by a strongly marked position of the all-stage dominant – *Mellinus arvensis* (Fig. 27). Two species with a lower rank – *Crabro cribrarius* and *Pemphredon balticus* – are in the group of 10 most abundant species that are present in each age class of the forest stand. In total, the three species accounted for about 87% of the total abundance of the young stand community, compared to about 60% of the communities inhabiting pole wood and mature forests.

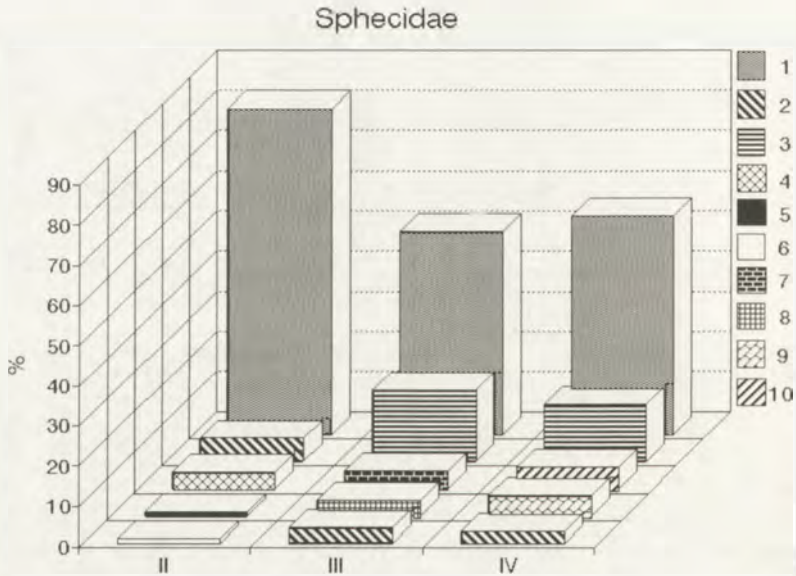


Fig. 27. Dominance structure of communities of digger wasps (*Sphecidae*) in forest stands of various ages in Puszcza Białowieska; 1 – *Mellinus arvensis*, 2 – *Crabro cribrarius*, 3 – *Passaloecus insignis*, 4 – *Crabro scutellatus*, 5 – *Nysson spinosus*, 6 – *Ammophila pubescens*, 7 – *Pemphredon balticus*, 8 – *Pemphredon lugubris*, 9 – *Trypoxylon figulus*, 10 – *Trypoxylon minus*

The character of the structure of dominance of digger wasp communities confirms the close relationship of communities occurring in older stands and the more unique character of the young stand community. Among the 10 most abundant species in the communities inhabiting the pole wood and young stands, there were 4 common species: *Mellinus arvensis*, *Crabro cribrarius*, *Pemphredon balticus* and *Passaloecus turionum*; a similar comparison for pole wood and mature stand communities yielded 7 common species – *Mellinus*

arvensis, *Crabro cribrarius*, *Pemphredon balticus*, *Passaloecus insignis*, *P. eremita*, *Rhopalum clavipes* and *Entomognathus brevis*.

One may speak of trophic specialisation among *Sphecidae*, at least some species of the taxon. The greatest number of species and the highest abundance characterizes the group of digger wasps, whose diet consists predominantly of various dipterans. In the pine forests studied in Puszcza Białowieska this trophic group was represented by a total 27 species. In young stands, the abundance of 22 of these species accounted for 94% of the total community abundance. In older stands, the group was much poorer both in the number of species and abundance, with 12 species recorded in the pole wood and 14 in mature stands and the abundance being several times lower than in young stands. The degree of similarity of the *Sphecidae* communities which feed their offspring with dipterans was 65% for young stands and the pole wood, 56% for young as compared to mature stands and 70% for the pole wood and mature forest.

Similar trends in changes in the number of species and abundance can be observed in the group of *Sphecidae* which feed their offspring with larvae of butterflies and sawflies (8 species altogether): in older stands this group is nearly 15 times less abundant than in young stands.

Reverse trends are observed in the groups of digger wasps which feed their offspring with aphids or spiders. The rank of this group rises considerably in older stands, where only a slight increase in the number of species takes place, but the abundance surges substantially. The group feeding their offspring with spider is not numerous (5 species) and 20 times more abundant in mature than in young stands.

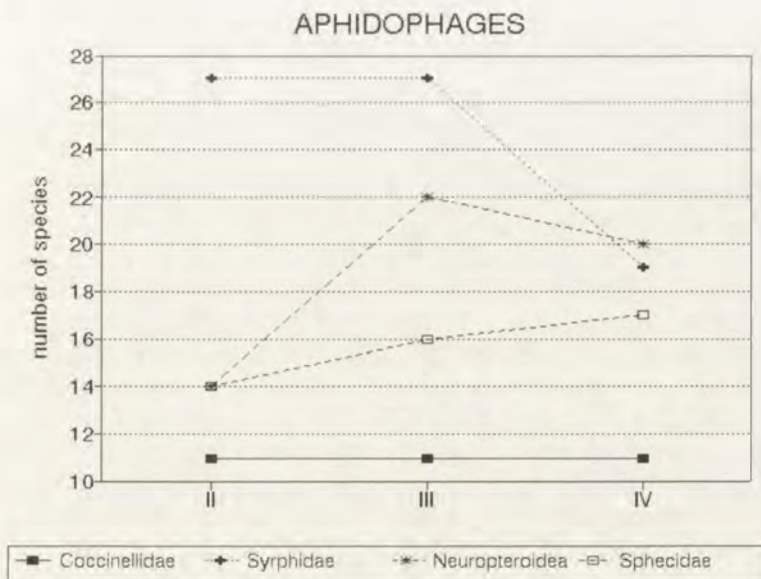


Fig. 28. Changes in the number of species of aphidophages in pine forests of three age classes of the forest stand

The aphidophagous digger wasp group is represented in the pine stands studied in Puszcza Białowieska by 22 species with 14 species in young stands, 16 in the pole wood and 17 in mature stands (Fig. 28). The degree of species composition similarity (S_o) was as high as 90% for the pole wood and mature stands, and 64–66% for young as compared to older stands. In the pole wood, the aphidophages were three times as abundant as in young stands (four times more abundant in mature stands than in young ones) (Fig. 29).

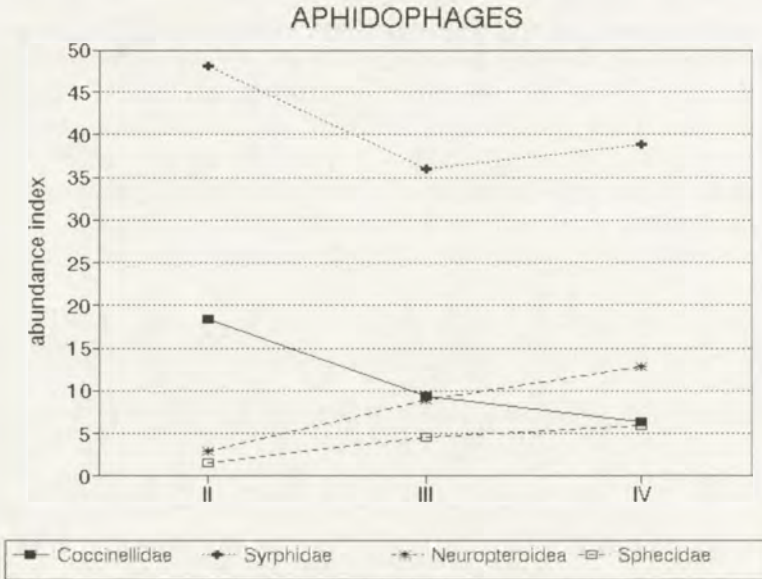


Fig. 29. Changes in the abundance of aphidophages in pine forests of three age classes of the forest stand

Neuropterans (*Neuropteroidea*)

Like aphidophagous *Sphecidae*, aphidophagous *Neuropteroidea* also increase the number of species and abundance as the stand grows older (Fig. 28–29) (CZECHOWSKA unpublished data). The total number of species recorded was 23, with 14 registered in young stands, 22 in the pole wood and 20 in mature stands. About 58% of the *Neuropteroidea* fauna (13 species) were found in every succession stage of the pine forest studied in Puszcza Białowieska. Community abundance in the pole wood and mature forest was three and four times higher than in young stands respectively (Fig. 29). The majority of the species registered were more abundant in older than younger stands. In the stands of various age under investigation the composition of the most abundant species group in neuropteran communities was similar (Fig. 30). Among the 10 most abundant species in each age class there were five common species. In young stands their shares amounted to 70% of total community abundance, while in older stands the figure was about 85%. The character of the structure of dominance testifies

to the close relationships between pole wood and mature stand *Neuropteroidea* communities.

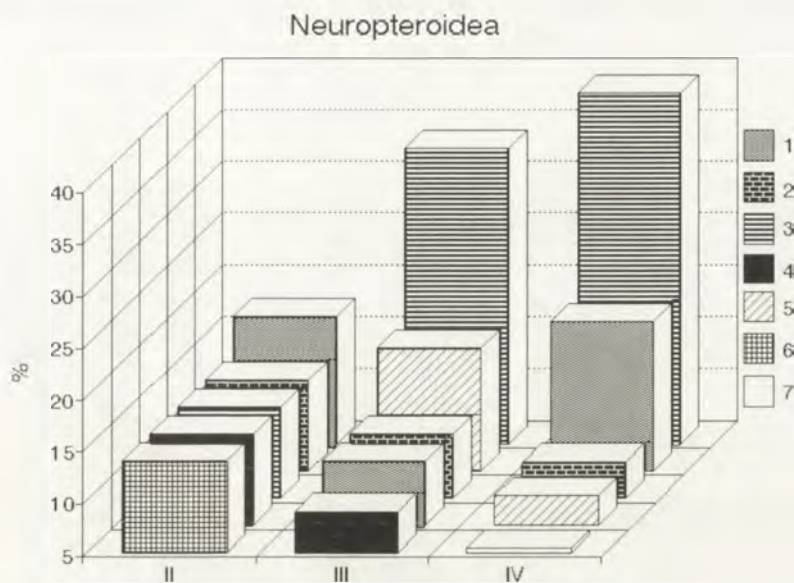


Fig. 30. Dominance structure of communities of neuropterans (*Neuropteroidea*) in forest stands of various ages in Puszcza Białowieska; 1 – *Mallada prasinus*, 2 – *Wesmaelius concinnus*, 3 – *Raphidia xanthostigma*, 4 – *Raphidia notata*, 5 – *Hemerobius stigma*, 6 – *Coniopteryx parthenia*, 7 – *Chrysopa septempunctata*

Syrphids (*Syrphidae*)

Communities of aphidophagous dipterans of the family *Syrphidae* revealed a reverse tendency: as the stand grew older, there was a decrease in both abundance and the number of species (Fig. 28–29) (BAŃKOWSKA in press). This phenomenon is due to the elimination, in older stands, of species associated with other habitats (meadows) which can occur in considerable abundance in young stands (e.g. *Pipizella varipes*). On the other hand, older stands see a rise in the abundance of species closely associated with pine forest (e.g. *Dasysyrphus venustus*, *Didea intermedia*). The total number of aphidophagous syrphid species registered in the pine forests studied in Puszcza Białowieska was 41, 13 of which were recorded in every age class of the forest stands. The species composition of aphidophagous syrphid communities inhabiting stands of various age was quite similar, but the community living in young stands was more unique when compared to communities inhabiting older stands. The values of Sørensen's index were 60% for communities from young stands and the pole wood, and 65% for communities from pole wood and mature stands. *Episyrphus balteatus*, *Metasyrphus corollae* and *Dasysyrphus venustus* were dominant in all the communities studied (Fig. 31). *Episyrphus balteatus* was a little less abundant in older stands than in young stands, but its proportion in the community

increased due to the lower abundance of the whole community of aphidophagous *Syrphidae* in older stands. Analogous trends can be detected in *Metasyrphus corollae*, which undergoes an evident decrease in abundance (nearly 2 times), while the third dominant species of *Syrphidae* – *Dasysyrphus venustus* doubles its abundance in older stands.

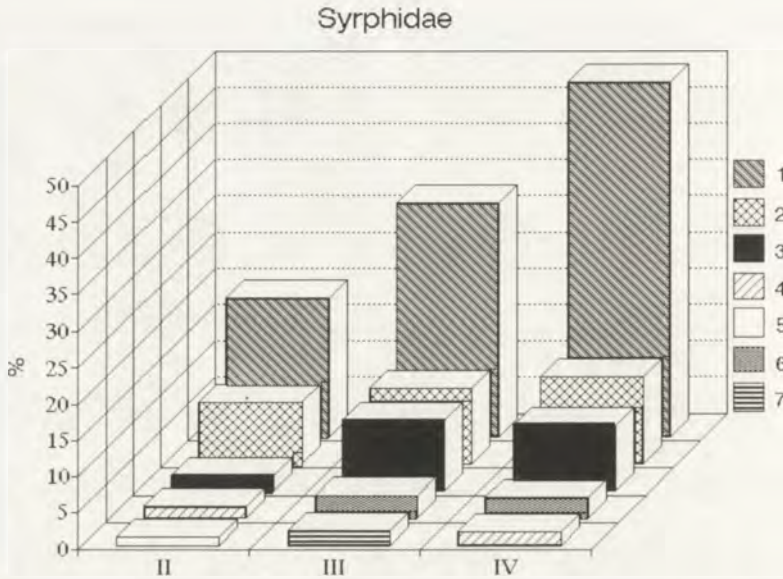


Fig. 31. Dominance structure of communities of syrphids (*Syrphidae*) in forest stands of various ages in Puszcza Białowieska; 1 – *Episyrphus balteatus*, 2 – *Metasyrphus corollae*, 3 – *Dasysyrphus venustus*, 4 – *Melanostoma mellinum*, 5 – *Sphaerohoria menthastri*, 6 – *Didea intermedia*, 7 – *Syrphus torvus*

Aphidophagous lady-birds (*Coccinellidae*) are represented by the same number of 11 species in each stand studied (Fig. 28). (CZECHOWSKA unpublished data). The species composition of this insect group in stands of various aged situated in the pine forest of Puszcza Białowieska was similar. A total of 13 species was registered including 9 common to each succession stage studied. Sørensen's index ranged from 83%–87%. While no significant differences occurred in regard to the species composition of the communities, there were differences in abundance (Fig. 29). As the stands grow older, ladybird communities decrease in abundance. In the pole wood the abundance of the community was twice lower and in mature stands three times lower, than in young stands.

The structure of dominance was similar in the communities as far as the most abundant species group was concerned (Fig. 32). In all the communities under investigation, the most numerous species included *Scymnus suturalis* and *Myrrha octodecimguttata*, which collectively accounted for about 87% of total community abundance in young stands and the pole wood, compared with 73%

in mature forests. *Coccinella septempunctata* was another rather abundant species in young stands. In older stands the species reduced its abundance just like *Scymnus suturalis*.

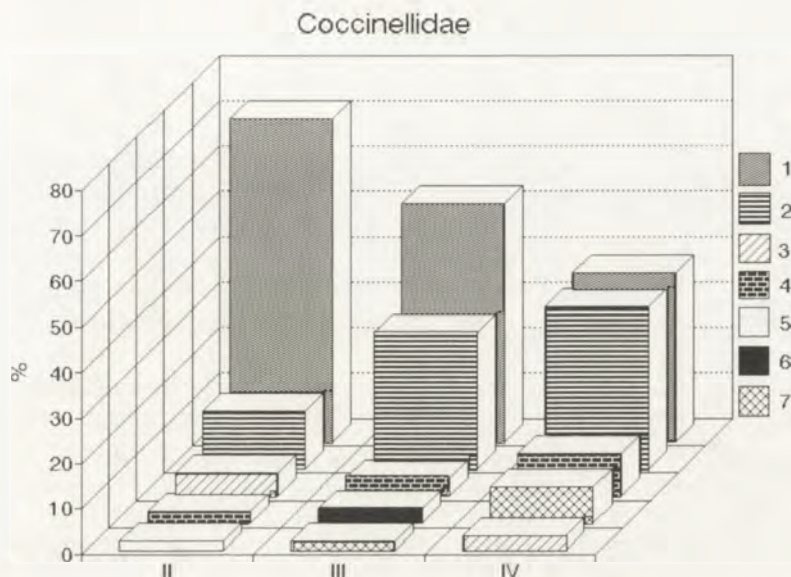


Fig. 32. Dominance structure of communities of aphidophagous coccinellids (*Coccinellidae*) in forest stands of various ages in Puszcza Białowieska; 1 - *Scymnus suturalis*, 2 - *Myrrha octodecimpunctata*, 3 - *Coccinella septempunctata*, 4 - *Harmonia quadripunctata*, 5 - *Calvia quatuordecimpunctata*, 6 - *Mysia oblongoguttata*, 7 - *Anatis ocellata*

8 species of aphidophagous *Coccinellidae* develop on coniferous trees. Their total proportion in the community was 91% in young stands and about 96% in older stands (pole wood, mature stands). As for species closely associated with pine, namely *Scymnus suturalis*, *S. nigrinus*, *Harmonia quadripunctata* and *Myrrha octodecimpunctata*, their total share in the *Coccinellidae* community was about 86% in young stands and the pole wood and 82% in older stands.

The remarkably high qualitative and structural similarity between communities of aphidophagous *Coccinellidae* in the canopy layer of pine stands of various age results from this habitat being colonized by species with definite habitat and trophic requirements. 80% of a community was composed of stenotopic species, feeding only on pine aphids. Attention should be paid to the fact that the eurytopic species (*Coccinella septempunctata* and *Calvia quatuordecimpunctata*) were more abundant in the community inhabiting young stands (7%) than in older stands (3.2%–3.9%).

Communities of predatory arthropods occurring in pine stands of various ages in Puszcza Białowieska can be classified into two groups: one comprising predators from young stands, the other composed of forms which inhabit older stands. Young stand arthropod communities are usually more unique than those

registered in pole wood and mature stands. Communities from older stands were similar to one another in species composition, dominance structure, uniformity of distribution and abundance. This regularity was observed in communities of both non-specialised predators and of aphidophages.

The degree of similarity of species composition of predators is higher for communities from older stands (pole wood and mature stands). The value of Sørensen's index for all the communities studied in older stands ranges from 65% for aphidophagous *Syrphidae* to 90% for communities of *Cantharidae*, *Neuropteroidea* and aphidophagous *Sphecidae*. The degree of species composition similarity between communities occurring in young stands and older stands is lower ranging from 54% for *Sphecidae* communities of young and mature stands to 97% for communities of *Coccinellidae* from young and mature stands. *Cantharidae* communities inhabiting young and mature stands are the only pair as similar to each other as communities from older stands.

The species composition of communities of such predators as *Asilidae*, *Aranei*, *Sphecidae* and *Syrphidae* was much richer in young stands than in older stands. On the other hand, *Neuropteroidea*, *Cantharidae* and aphidophagous *Sphecidae* were composed of a higher number of species in older stands, while aphidophagous *Coccinellidae* communities consisted of the same number of species in each age class.

In the majority of communities registered in young stands, there were higher proportions of both species from other habitats, not associated with pine forests, and of eurytopic species, than in communities studied in older stands. In older stands, species of open areas (meadows) are eliminated or their abundance decreases considerably, while forest polytopes and coniferous forest oligotopes remain, often increasing their abundance. Such a result of research conducted in Puszcza Białowieska has been confirmed by studies concerned with certain groups of predators (*Aranei*, *Syrphidae*, *Coccinellidae*, *Neuropteroidea*, *Sphecidae*) in pine forests situated in other regions of Poland (Bory Tucholskie, Puszcza Biała).

Significant changes were observed in abundance of individual groups of predatory arthropods. A decreasing pattern of abundance is characteristic of communities of *Asilidae*, *Cantharidae*, *Aranei* and *Sphecidae*. Such a direction of abundance changes was also registered for communities of polyphagous dipterans of the family *Dolichopodidae*, which are not, however, thoroughly analysed in the paper, but, nevertheless, occur numerously in canopies of pine forests in Puszcza Białowieska. Another group of non-specialized predators, namely spider wasps (*Empididae*), was also relatively abundant in the canopy layer. The dipterans occurred in approximately the same abundance in young stands and mature stands, whereas they were a little more abundant in the pole wood, but the differences were not significant (the pole wood community abundance was 25% higher than community abundance in young stands).

Among aphidophages, all the most abundant taxons are thoroughly analysed in the present paper. Although this group has the same trophic preferences, individual taxons forming the guild exhibited diverse patterns of changes in the

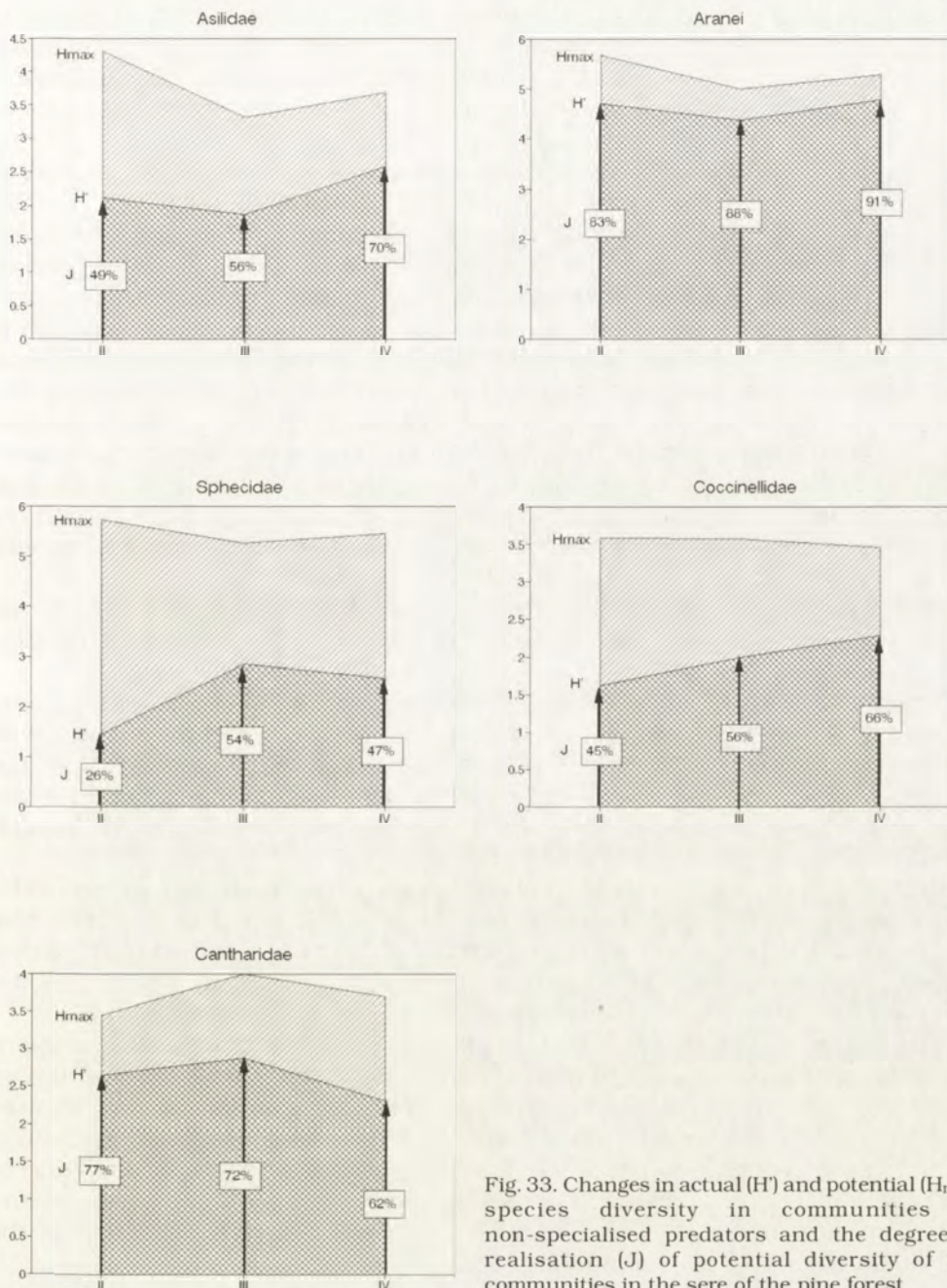


Fig. 33. Changes in actual (H') and potential (H_{max}) species diversity in communities of non-specialised predators and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

pine forest sere. The changes, both in respect to the number of species and abundance, are balanced, resulting in small total alterations.

Communities of predators in the pine stands of various age investigated in Puszcza Białowieska displayed similar structures. In all age classes of the stands, the group of dominants has similar species composition. The differences consist in changes of particular species' positions in the structure of dominance i.e. changes of their ranks in the communities.

Analysis of similarity of abundance distribution in the actual (empirical) communities of predators to the five theoretical statistical distributions revealed that most of the actual distributions are related to the negative binomial distribution and the logarithmic series. The similarity is significant for various groups in various pine forest succession stages: for robber-flies and aphidophagous digger wasps in the pole wood, for aphidophagous syrphids in young and mature forests. The distribution of abundance in soldier beetle communities is also closest to the negative binomial distribution (in young and mature stands) being also the only one to bear similarity to the lognormal distribution (in young stands). The distribution of spider community abundance is to some extent similar to the geometric series type of distribution (in the pole wood). The estimated number of species for all groups of predators (except the young stand community of soldier beetles) was higher than the empirical one, which suggests greater potential capacity of these habitats.

Quantitative structures of digger wasp, ladybird and neuropteran communities did not bear any similarity to any of the theoretical distribution models.

Species diversity of non-specialised predators (Fig. 33) depends on the group of animals studied. The highest actual diversity was recorded for spiders, with absence of significant differences between the various stages of succession. The maximum diversity, which is a measure of the potential habitat capacity, is also high in the case of spiders, while the degree of approximation of the habitat potential is the highest in this group ($J > 80\%$).

Similar patterns of changes, but occurring on a lower level, were observed for actual and potential species diversity in *Asilidae*. Here, actual diversity also decreases in the pole wood, whilst maximum diversity is attained in the oldest stands. The degree of approximation of the actual diversity to the habitat potential increases visibly in the consecutive stages of the sere (Fig. 33).

The lowest values of actual species diversity were noted for digger wasps (*Sphecidae*) in young stands of pine. In older stands the species diversity rises nearly two times. The actual species diversity of digger wasps is most distinct from the potential in the pine forest, particularly in young stands where $J=26\%$.

A steady increase is noted for species diversity of ladybirds (*Coccinellidae*) in the pine forest sere. The trend is observed as regards both the potential and actual species diversity as well as with respect to the approximation of the potential diversity in the habitat (Fig. 33).

Inverse tendencies are noted only in soldier beetles (*Cantharidae*), where the actual species diversity in young stands is quite high, reaching a maximum in the pole wood and visibly decreasing thereafter (i.e. in mature stands). This

group is also characterised by a decrease in Pielou's index (J) in the consecutive stages of the pine forest sere (Fig. 33).

Species diversity in aphidophages may behave according to one of three patterns in the pine forest sere. In ladybirds (*Coccinellidae*), there is an increase (Fig. 34) both in actual diversity and the degree of approximation of the habitat potential. A reverse trend is seen in neuropterans (*Neuropteroidea*) and aphidophagous digger wasps (*Sphecidae*). In aphidophagous syrphids (*Syrphidae*), however, both actual and potential species diversity reaches a maximum in the pole wood stage, but the degree of approximation of the potential diversity is the lowest here.

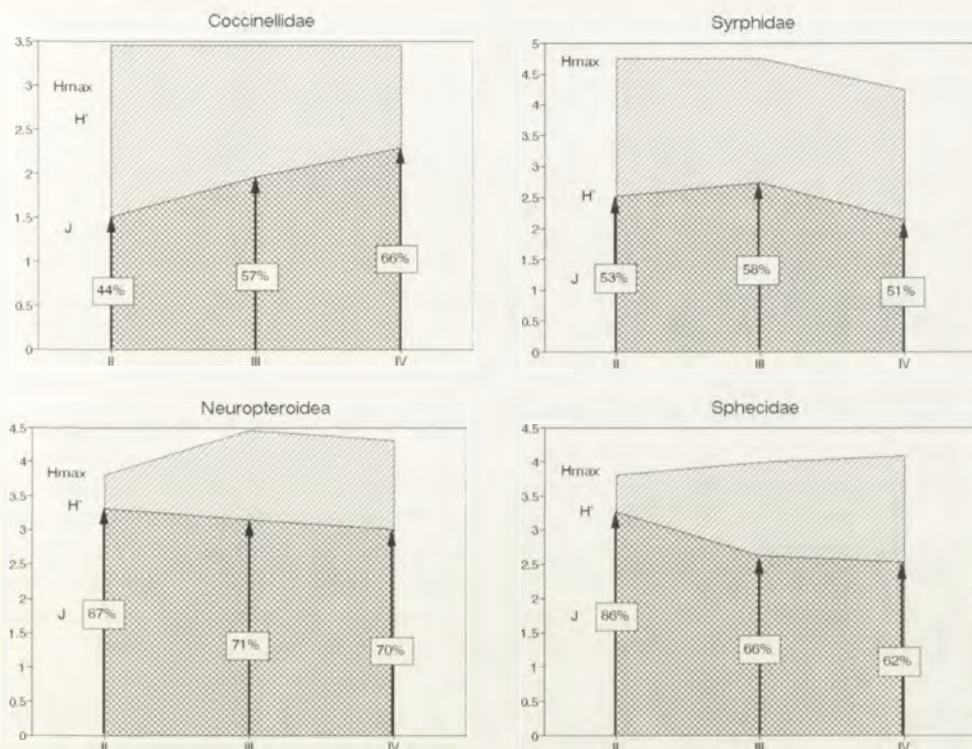


Fig. 34. Changes in actual (H') and potential (H_{max}) species diversity in communities of aphidophages and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

5.2.3. Parasitoids of phytophages

Apart from predators, parasitoids whose larvae present parasitic or semiparasitic mode of life play an important role in reducing the abundance of phytophages. Three groups of parasitoids are particularly important in ecosystems: tachinid flies (*Tachinidae*), ichneumon flies (*Ichneumonidae*) and *Pipunculidae*. They will be described successively.

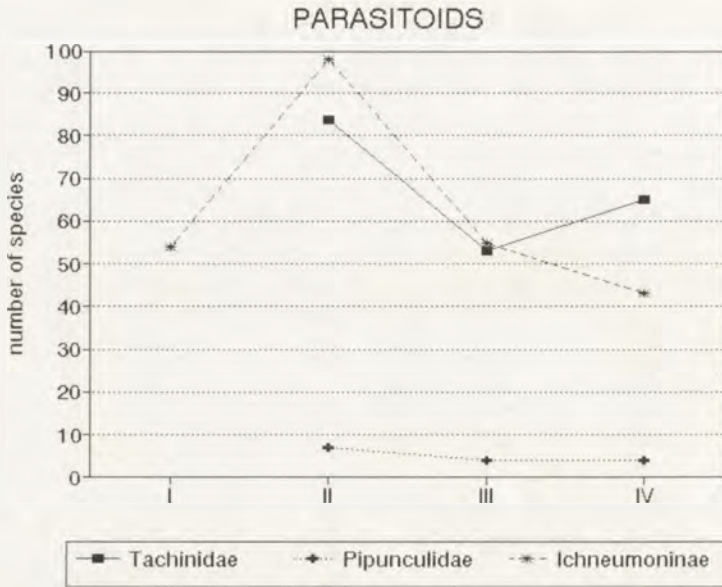


Fig. 35. Changes in the number of species of parasitoids in pine forests of three age classes of the forest stand

Tachinid flies (*Tachinidae*)

In the pine forests of Puszcza Białowieska tachinid flies are represented by 114 species (DRABER-MOŃKO unpublished data). Most of them (82 species) are parasites of lepidopterans (*Lepidoptera*). Other groups given in the order of decreasing abundance include parasites of beetles (*Coleoptera*), mostly phytophagous forms (12 species), parasites of sawflies (*Symphyla*) (7 species). Groups of tachinid flies parasitic on orthopterans (*Orthoptera*), dipterans (*Diptera*), heteropteran bugs (*Heteroptera*), centipedes (*Chilopoda*) and earwigs (*Dermaptera*) are less abundant, including no more than 5 species each.

The highest number of tachinid species is recorded in young stands (Fig. 35). This is due to the higher proportion of flowering plants than in older stands. Their nectar is essential for the development of gonads of tachinid flies. Young stands also harbour their hosts: numerous phytophagous species not associated with older stands. The lowest number of tachinid species was recorded for the pole wood, while it was a little higher in mature forests. Tachinid abundance follows a similar pattern with the lowest values in the pole wood (Fig. 36). It is interesting to note that the number of species of *Tachinidae* parasitic on butterflies, so high in young stands (65), becomes stabilised in older stands (42 species). Fluctuations of abundance in the course of the sere are observed in other host groups of tachinid flies. The number of species estimated on the basis of the lognormal distribution indicates complete convergence with empirical data in each of the three age classes of forest stands.

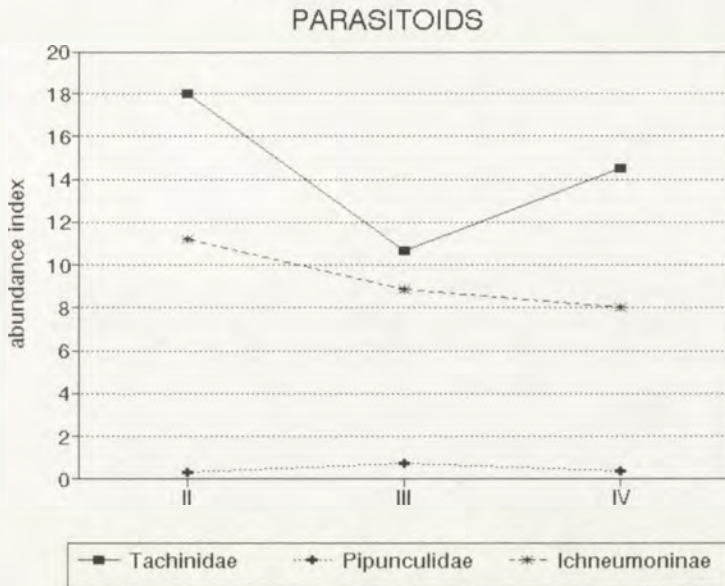


Fig. 36. Changes in the abundance of parasitoids in pine forests of three age classes of the forest stand

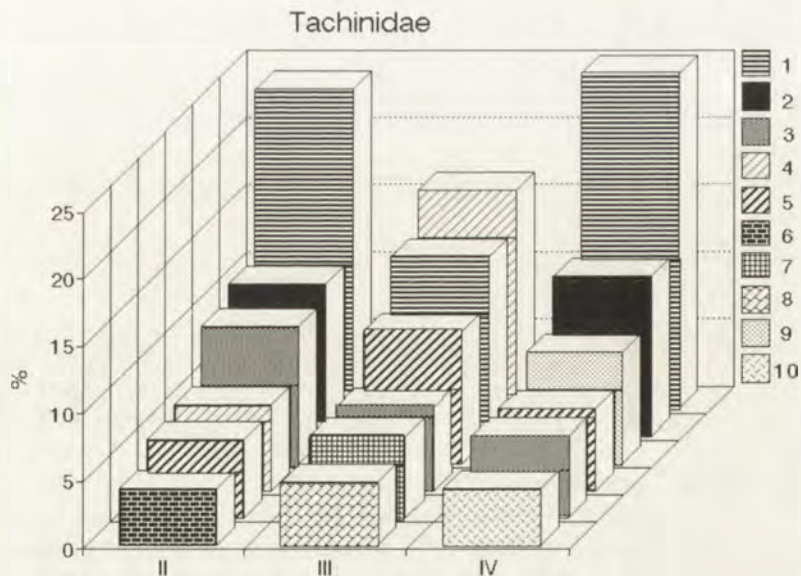


Fig. 37. Dominance structure of communities of tachinid flies (*Tachinidae*) in forest stands of various ages in Puszcza Białowiecka; 1 - *Medina separata*, 2 - *Carcelia bombylans*, 3 - *Lypha dubia*, 4 - *Ernestia rudis*, 5 - *Campylochaeta inepta*, 6 - *Eloceria delecta*, 7 - *Ceranthia abdominalis*, 8 - *Peribaea fissicornis*, 9 - *Triarthria septipennis*, 10 - *Blepharomyia angustifrons*

The structure of dominance of tachinid fly communities (Fig. 37) is of the dominant-type with a considerable overlap between the community of the young and mature stand. *Melina separata*, *Coralia bombylans*, *Lypha dubia* and *Campylochaeta inepta* are dominant in both stages. In the pole wood, the top position in the dominance structure is occupied by *Ernestia rudis*, while the other dominants occupy the second and farther positions.

The species diversity of tachinid flies in the three stages of secondary succession of the pine forest is nearly identical and quite high (Fig. 38) – a little more than 4.5. The degree of approximation of potential species diversity of tachinid flies by the actual values is also similar in all the age classes of the forest stand (the highest in pole wood, the lowest in young stands).

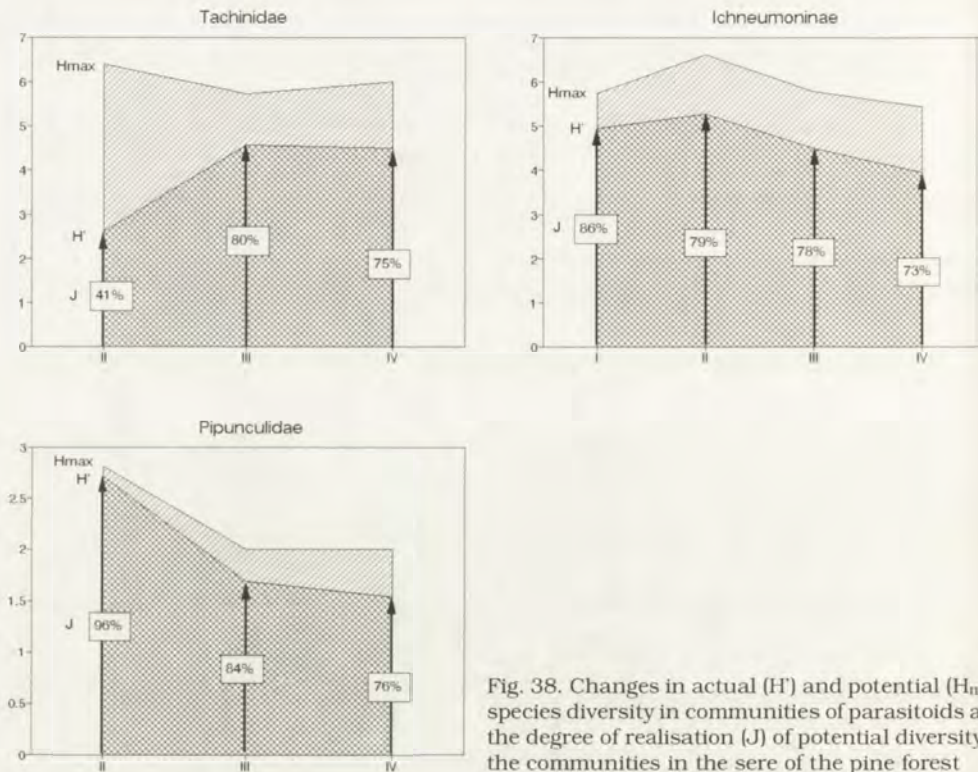


Fig. 38. Changes in actual (H') and potential (H_{max}) species diversity in communities of parasitoids and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

Ichneumon flies (*Ichneumonidae*)

In the present paper ichneumon flies are represented only by parasites of lepidopterans (*Lepidoptera*), thus including forms biologically associated with the most dangerous foliophagous pests of Polish forests.

The number of species in the pine forest sere (Fig. 35) has a maximum in young stands and a minimum in mature stands. The culture stage is inhabited mostly by open area ichneumon flies, while the community from young stands has features related to the ecotone nature of this habitat. There are numerous

species present in the culture stage and also typical forest species. In older stands, open areas species recede to be replaced by a poorer complex of parasitoids of *Microlepidoptera*, mainly *Rhyacionia buoliana*, and species parasitic on the pupae living in the litter (SAWONIEWICZ unpublished data).

The abundance of ichneumon flies presents a similar pattern (Fig. 36). It is the lowest in pine cultures, reaches a maximum in young stands to become stabilised in older stands as a community characteristic of the pine forest.

The structure of *Ichneumonidae* communities occurring in the consecutive stages of the sere in Puszcza Białowieska is similar to that registered in corresponding forest stands in other regions of Poland (Fig. 39). The core of the community is formed of 14 species with *Vulgichneumon deceptor* being the one species to assume a markedly dominant position but only in the culture stage. The community of ichneumon flies of the culture stage is quite unique. Of the six dominants, there is only one species (*Ctenichneumon funereus*) which occurs in the young stand as well. It is only in the latter stage that three typically forest species (*Aetherus nitidus*, *E. sawoniewiczi* and *Tycheurus dodecellae*) appear and occupy top positions in the structure of dominance. In older stands, the dominant species group is supplemented by three other species to form a stable core of the community.

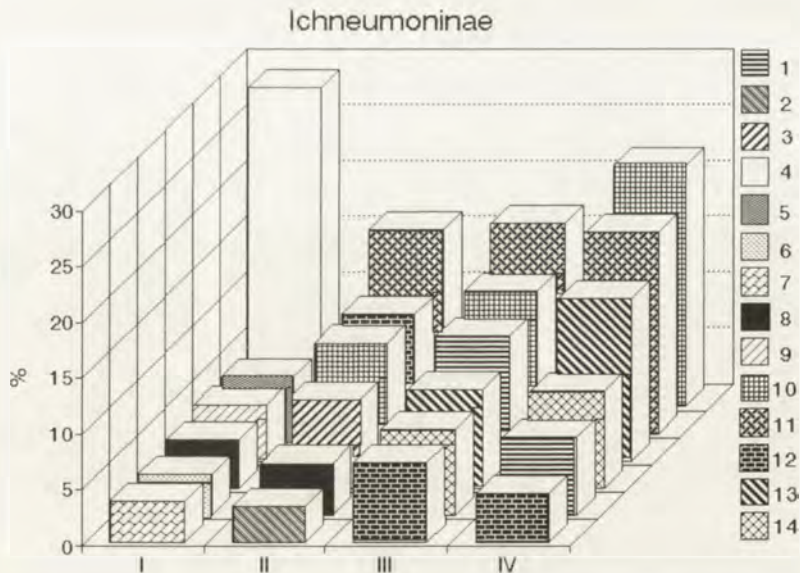


Fig. 39. Dominance structure of communities of ichneumons (*Ichneumonidae*) in forest stands of various ages in Puszcza Białowieska; 1 - *Platylabus virginalis*, 2 - *Cratichneumon sicarius*, 3 - *Cratichneumon viator*, 4 - *Vulgichneumon deceptor*, 5 - *Virgichneumon diagrammus*, 6 - *Barichneumon plagiaris*, 7 - *Ichneumon minorius*, 8 - *Ctenichneumon funereus*, 9 - *Eriplatys ardeicollis*, 10 - *Eriplatys sawoniewiczi*, 11 - *Aetherus nitidus*, 12 - *Tycheurus dodecellae*, 13 - *Tycheurus vagus*, 14 - *Tycheurus verecundus*

Ichneumonidae species diversity in pine cultures is quite high (Fig. 38), reaching a maximum in young stands which harbour the greatest number of ichneumon fly species. The diversity decreases in older stands to reach a minimum in the mature forest. A similar pattern is reported for potential diversity with a maximum in young stands and a minimum in mature stands. The degree of approximation of the potential diversity by the actual diversity decreases in the consecutive stages of the sere. The values of Pielou's index fall from 86% in cultures to 72% in mature forest. This is suggestive of the development of internal relations within the community consisting in an increase in the degree of internal organisation at the expense of decreasing species diversity, and the development of a structure of dominance characterised by a more dispersed distribution.

Pipunculidae

This is a group of small-sized dipterans functioning as specialised parasites of leafhoppers (*Homoptera*, *Auchenorrhyncha*). 9 *Pipunculidae* species occur in the pine forest of Puszcza Białowieska (BAŃKOWSKA unpublished data) with the greatest number recorded in young stands (Fig. 35) and only four species occurring in older stands. The abundance of this taxon is lowest in young stands and highest in the pole wood (Fig. 36), decreasing twice in mature forest. With the species composition growing poorer as the stand grows older, species start to appear that are restricted to older stands (*Pipunculus spinipes* and *Chalarus fimbriatus*). However, their association with older stands needs to be confirmed

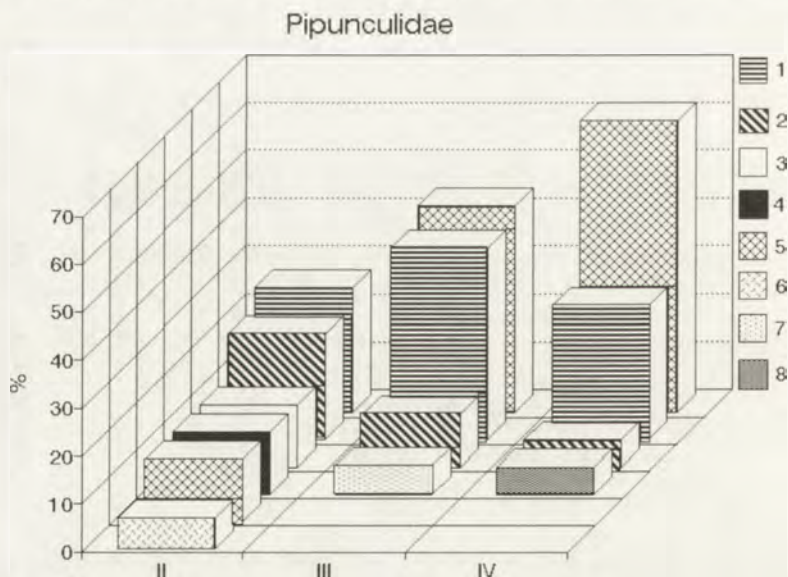


Fig. 40. Dominance structure of communities of parasitic *Pipunculidae* in forest stands of various ages in Puszcza Białowieska; 1 - *Nephrocerus scutellatus*, 2 - *Eudorylas subfascipes*, 3 - *Tomosvariella sylvatica*, 4 - *Cephalops semifumosus*, 5 - *Verrallia villosa*, 6 - *Cephalops aenus*, 7 - *Pipunculus spinipes*, 8 - *Chalarus fimbriatus*

on the basis of a more sizeable material. The dominant role in the community is played by *Nephrocerus scutellatus* and *Verralia villosa*, which occur throughout the sere and may be considered dominant species (Fig. 40).

Species diversity tends to decrease throughout the sere (Fig. 38), from a maximum in young stands to a minimum in mature forest. The values of Pielou index also exhibit that trend. This suggests an even abundance distribution of species inhabiting young stands of pine. In the subsequent succession stages, a transformation takes place in the community of *Pipunculidae* to result in a dominance-type community, the number of species decreases and differences in their proportions become sharper.

5.3. Secondary succession in the saprotrophic subsystem

The subsystem of saprotrophs is associated with dead organic matter produced within the ecosystem. Deposited as organic sediments on the surface of soil, it becomes a source of energy and minerals for the complex subsystem of saprotrophs. Owing to this subsystem, organic matter is broken down, and the organic substances it contains are recycled in the ecosystem. Another important product of saprotroph activity is soil. Its surface layers are composed largely of materials processed by the subsystem of saprotrophs. Thanks to them, the soil has a definite structure and type of humus. The subsystem is composed of saphrophages, omnivorous animals (pantophages) and predators.

Starting a pine culture on a pine clearing accelerates pine forest succession. In the first period, the soil is considerably degraded, which is accompanied by complete changes in the living conditions of animals living there. This is caused by the removal of the surface cover of the soil, strong insolation, increases in temperature amplitude and changes in moisture relations. The typical crumb-and-pore structure disappears and nutrients are leached leading to drastic impoverishment of the habitat. As the culture grows, secondary succession of plants brings about significant changes in soil conditions and in the rate of decomposition. Insolation decreases causing changes in moisture and thermal conditions, and soil receives more and more nutrients from falling needles, leaves, plants of the ground cover and dead roots. All these factors promote the development of microflora, mainly fungi so that favourable conditions are created for the formation of humus and development of soil animals. As the stand grows, it becomes thinned, the understorey develops and microclimate changes, also affecting soil conditions and the fauna inhabiting that part of the ecosystem. As a result of succession, mesotrophic pine forest develops with moder/mor type of humus possessing features of edaphic climax.

5.3.1. Soil saphrophages

Saphrophages participating in organic matter decomposition are represented by a large group of animals of diverse trophism. An important role in soil formation in pine forests is played by small soil animals such as enchytraeids (*Enchytraeidae*), mites (*Acar*), springtails (*Collembola*) and nematodes (*Nematoda*). The fauna is classified as soil saphrophages feeding on detritus together with bacteria and fungi. It stimulates the microflora.

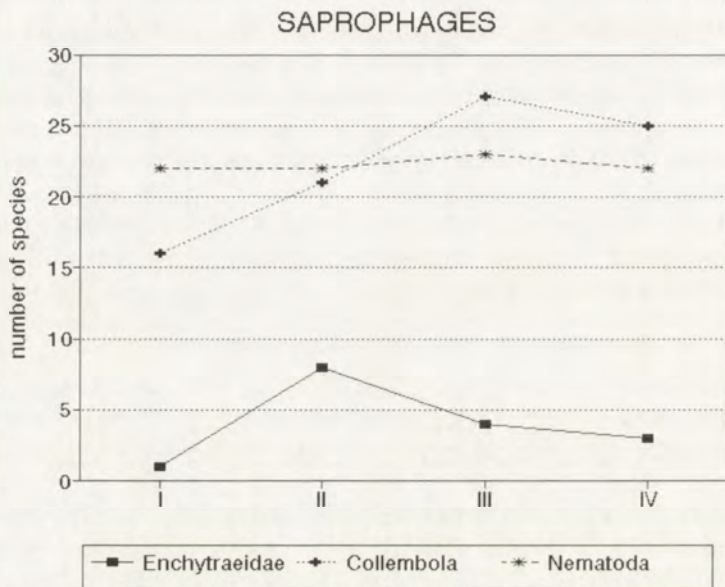


Fig. 41. Changes in the number of species of soil saprotophages in pine forests of three age classes of the forest stand

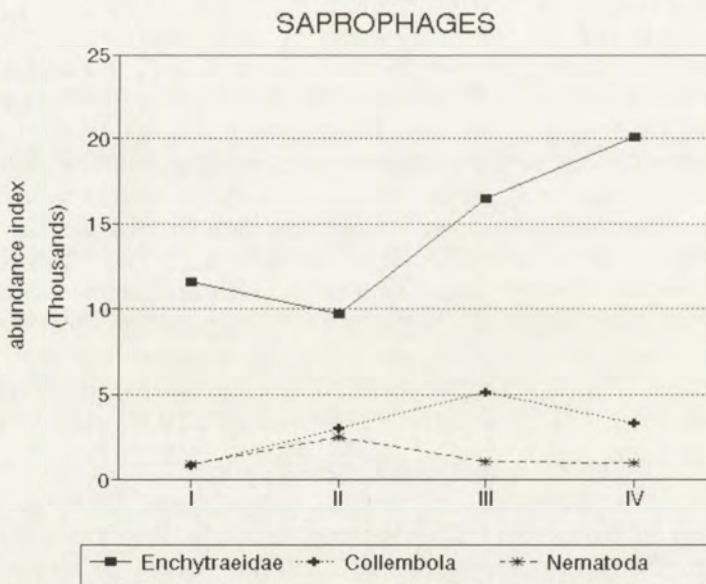


Fig. 42. Changes in the abundance of soil saprotophages in pine forests of three age classes of the forest stand

Due to changes in soil conditions observed in the course of succession and the stand growing older, changes occur also in the communities of animals inhabiting the stand (species composition, abundance and structure of dominance). The analysis of transformation of communities of selected soil saprophages (*Nematoda*, *Enchytraeidae*, *Collembola*) in pine forests of various age allows to track the progress of succession.

Studies of the effect of secondary succession on mesofaunal communities, including communities of soil saprophages, are more frequently concerned open areas (meadows, field) than with forests (KOEHLER, BORN, 1989; PETERSEN, KROGH, 1987). In pine forests, investigations of communities of soil mesofauna in forest plantations of various age have been carried out by LOHM et al. (1977).

Nematodes (*Nematoda*)

Nematodes occupy a special position among organisms participating in the secondary succession of pine forest. The number of species (Fig. 41) is not subject to changes during ecosystem transformations, with 22 species present. More considerable changes are observed in abundance of nematodes. The initial stage of succession is associated with an abundance minimum, while in young stands *Nematoda* achieve a maximum of abundance, exceeding the minimum nearly 3 times. In older stands the abundance becomes stable. However, in comparison to abundance changes in springtails and *Enchytraeidae* (Fig. 42), fluctuations in the abundance of nematodes may be considered insignificant. The pattern of changes in abundance is related to a decrease in insolation and

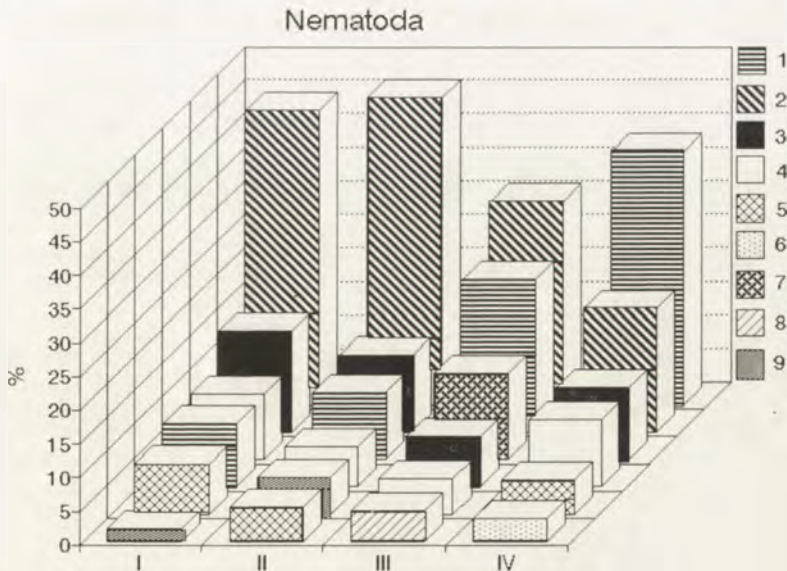


Fig. 43. Dominance structure of communities of nematodes (*Nematoda*) in forest stands of various ages in Puszcza Białowieska; 1 - *Filenchus ditissimus*, 2 - *Acroboloides nanus*, 3 - *Aphelenchoides spp.*, 4 - *Plectus pusteri*, 5 - *Wilsonema otophorum*, 6 - *Teratocephalus dadayi*, 7 - *Ypsylonellus insubricus*, 8 - *Eudorylaimus silvaticus*, 9 - *Rhabditis s. l.*

denser forest floor cover associated with succession, which results in smaller variations in soil moisture.

The structure of dominance in soil *Nematoda* communities is similar in the four succession stages (Fig. 43). The core of the community does not change, there are small changes in the dominant species group. Greater transformations are noted in the structure of less numerous species. As the stand grows older, the contribution of fungivorous nematodes increases while that of bacteriophagous *Nematoda* decreases, which is associated with an increase of the share of fungi in the forest floor microflora (BRZESKI unpublished data).

The species diversity of nematodes undergoes similar stabilisation, as the parameters discussed above (Fig. 44). The value of the diversity index (H') fluctuates around 3.0. Additionally, potential species diversity H_{max} in the consecutive stages nears 4.5 so that the degree of approximation of potential diversity does not change considerably.

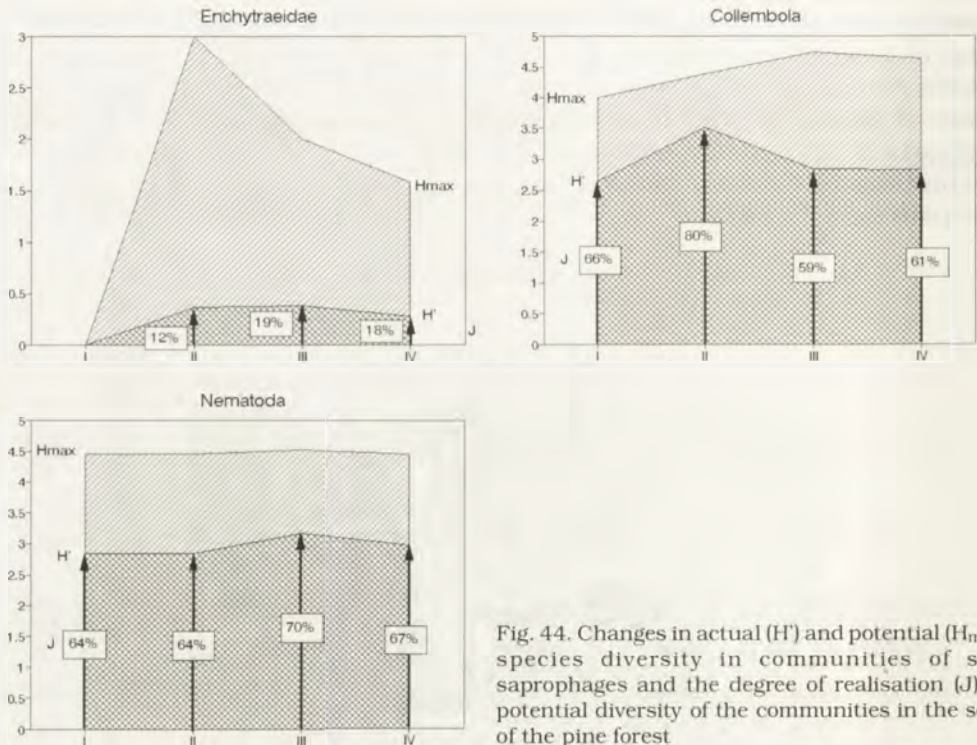


Fig. 44. Changes in actual (H') and potential (H_{max}) species diversity in communities of soil saprophages and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

Enchytraeids (*Enchytraeidae*)

Enchytraeid communities in the soil of pine forests of Puszcza Białowieska are poor in the number of species, with one dominant species, namely *Cognettia sphagnetorum*. In the initial stage of succession (culture), where the soil is most degraded, only one species was recorded. The greatest number of species was registered in the young stand. In older stands their number decreases (Fig. 41).

approaching the number characteristic of mature forests in other forest complexes in Poland (PILIPCIUK 1993). Community abundance in cultures and young stands is lower than in the pole wood stage and mature forests, where it reaches a maximum (Fig. 42).

The structure of the enchytraeid community (Fig. 45) is characterised by a marked dominance of one species in every stage of succession. *Cognettia sphagnetorum* accounts for more than 90% of the community throughout the sere, reaching a maximum in the pole wood to undergo a slight fall in the mature stand. If we ignore the restricting character of the culture stage where only one enchytraeid species is present, the young stand is capable of accommodating seven other accessory species. In the subsequent stages the structure of the community becomes poorer due to elimination of accessory species (PILIPCIUK unpublished data).

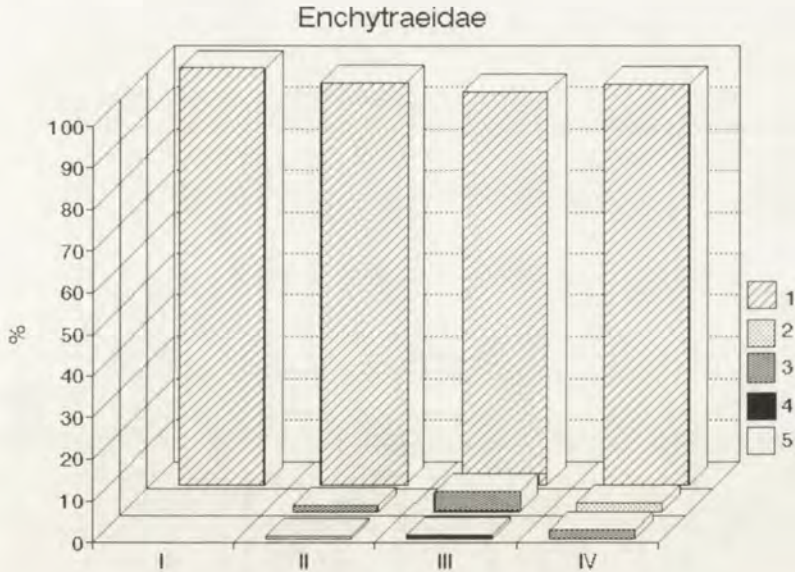


Fig. 45. Dominance structure of communities of *Enchytraeidae* in forest stands of various ages in Puszcza Bialowieska; 1 - *Cognettia sphagnetorum*, 2 - *Achaeta* sp., 3 - *Mesenchytraeus* sp., 4 - *Marionina* sp., 5 - *Buchholzia simplex*

The species diversity of enchytraeids is profoundly influenced by structural relations (Fig. 44). Actual diversity (H'), equalling 0 in the first stage of succession, never exceeds 0.5 in the subsequent stages. Greater changes occur with respect to potential diversity (H_{max}). It reaches a peak in the young stand to fall considerably in older stands. The utilisation of the potential habitat capacity to increase the diversity of the community of enchytraeids is low, never reaching 20% in the entire sere.

Springtails (*Collembola*)

The number of species of these animals in the pine forest sere tends to increase (Fig. 41). It reaches a maximum in the pole wood to fall slightly in the mature stand. A similar pattern is observed in abundance of springtails (Fig. 42), which is much lower than that of enchytraeids, while being slightly higher than the abundance of nematodes.

The species composition of *Collembola* differs considerably in the consecutive stages of the pine forest sere in Puszcza Białowiecka (Fig. 46). Convergence of species composition is only observed when comparing communities inhabiting older stands (pole wood and mature forest). There are also differences in the structure of dominance of the springtail communities. In younger stages, there is a decrease in the number of non-abundant species combined with a marked dominance of one species (80%). In older age classes (pole wood, mature forest) the core of the community is formed of a number of co-dominant species and the low-share species group is much more numerous. In the consecutive stages of the pine forest sere, species forming the dominant group are replaced by others (STERZYŃSKA unpublished data).

Species diversity of springtails (Fig. 44) is on the same level as in nematodes. However, a maximum is reached in the young stand stage, while in older stands actual species diversity (H') oscillates around 2.8. Potential diversity reaches a peak in the two age classes. The highest degree of approximation of the potential

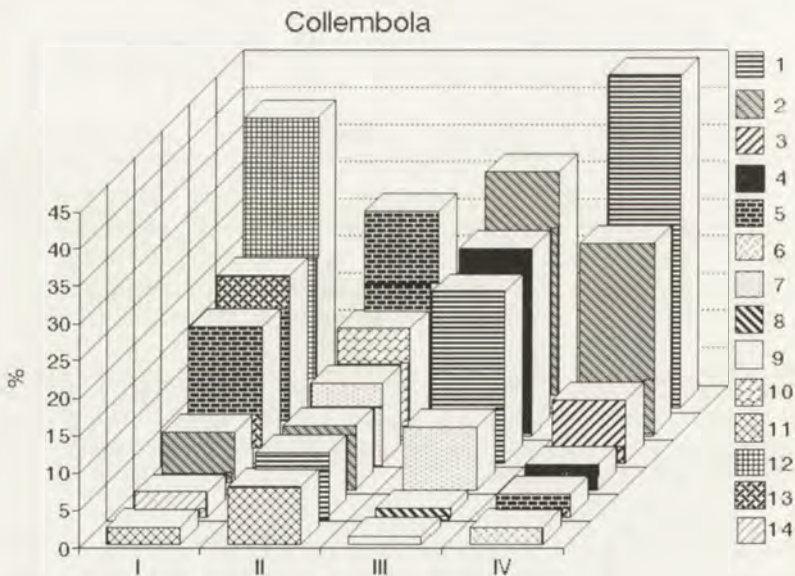


Fig. 46. Dominance structure of communities of springtails (*Collembola*) in forest stands of various ages in Puszcza Białowiecka: 1 - *Pseudosinella zygophora*, 2 - *Isotomiella minor*, 3 - *Mesaphorura macrochaeta*, 4 - *Isotoma notabilis*, 5 - *Schoetella ununguiculata*, 6 - *Onychiurus subuliginatus*, 7 - *Isotoma sp. j.*, 8 - *Folsomia quadrioculata*, 9 - *Anurophorus septentrionalis*, 10 - *Entomobryidae sp. j.*, 11 - *Willemia aspinata*, 12 - *Pogonognathellus flavescens*, 13 - *Anurida pygmaea*, 14 - *Proisotoma minima*

is seen in young stands, while the difference is the greatest in mature forests. The formation of community structure in *Collembola* is accomplished at the expense of species diversity.

Two models of dominance structure occur in the sere studied. The first of them has the same species of the dominant group forming the core of the community throughout the sere. In this model changes are seen the group of species with lower shares in the community. This model is conformed to by two groups – *Nematoda* and *Enchytraeidae* (Fig. 43 and 45). The other model of dominance structure is observed in *Collembola* (Fig. 46). In this taxon there are considerable transformations in the dominant species group with different species prevailing in young stands and older ones, although one must not speak about complete substitution of species composition. What is more, *Collembola* communities from older stands have several co-dominants, while only one marked dominant appears in younger stands. Analysis of similarity of the actual communities of soil saprophages to the five theoretical statistical distributions showed that the distribution of species in the communities under study is closest to the negative binomial distribution. The similarity is statistically significant for various groups in various succession stages. In some cases the estimated number of species is higher than the actual one (*Collembola*) indicating a higher species capacity of the habitat. In others (*Enchytraeidae*), the estimation corresponds to empirical findings.

Analysis of selected groups of soil saprophages showed that the communities of the groups under study become stabilised in older stands of pine. The communities of these animals inhabiting middle age class stands present a "preparatory stage" for the formation of communities characteristic of natural mature pine forests.

In the sere under investigation, the pole wood is a stage of greater potential for realizing species diversity in relation to communities from mature stands. In mature stands, where habitat conditions become stabilized to a certain extent, species diversity of soil saprophages is lower. GILLER (1984) claims a link between the degree of species diversity and habitat heterogeneity. In the sere studied, an increase in habitat heterogeneity is stimulated by the development of the layer structure of the stand and changes in soil conditions. Stratification, both horizontal and vertical, provides many new niches. Particularly important for saprophages are litter and humus. The relations between soil saprophage communities and the type of humus formed are described by PONGE (1993). Species diversity may also rise with increasing production of food such as fungi and microorganisms and organic matter content in the soil (PIANKA 1966). In mature climax ecosystems, productivity often decreases or remains constant. Species diversity also may fall in such ecosystems due to the rising number of interdependencies between organisms even though it is still stimulated by the growing number of niches. The mature pine forest is a mature ecosystem where habitat conditions become stabilized. The decrease in the species diversity of soil saprophages, which can be observed in the mature forest is connected above all else to the stabilization of the rate of humus fixation and of humus type.

5.3.2. Pantophages and soil predators

An important role in regulating the abundance of the saprophage subsystem is played by omnivorous and predatory animals. The former are represented in the pine forests by ants, which control the whole ecosystem feeding on a wide range of animal and plant foods. Two families of dipterans (*Rhagionidae* and *Therevidae*) serve as examples of soil predators. The limbless larvae of these dipterans penetrate into the soil habitat hunting small invertebrates.

Soil pantophages

Ants (*Formicidae*)

Ants play a particular role among the many groups of pantophagous soil invertebrates. Due to their high abundance and exceptional biological activity, they are a functional group vital to maintaining homoeostasis in forest ecosystems, particularly in coniferous forests (KARPIŃSKI 1956, KACZMAREK 1963). More or less closely associated with this habitat are about 30 species of ants of the nearly 80 species forming the Polish ant fauna (PISARSKI 1975, CZECHOWSKI unpublished data). Their role in soil formation consists in supplementing the soil with organic compounds and shaping the composition of the microflora (PETAL 1977). It is also closely linked with the changes occurring during succession.

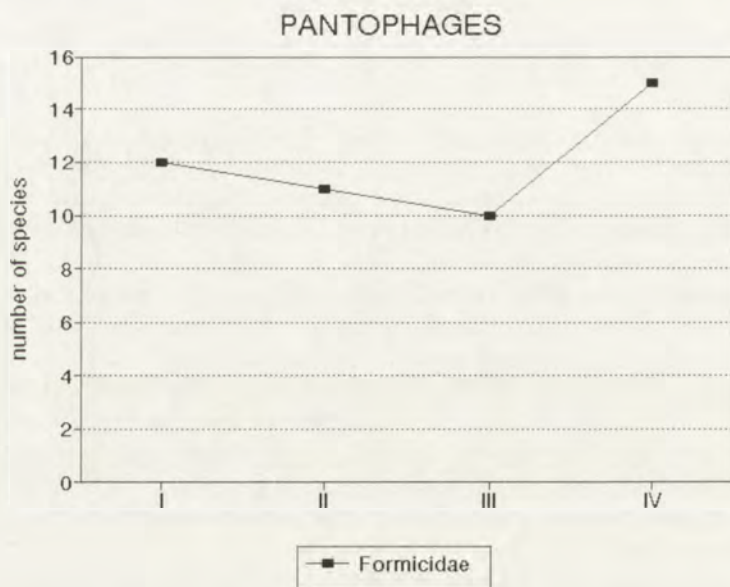


Fig. 47. Changes in the number of species of ants in the secondary sere of pine forests

Only 19 species of ants are associated with the pine forest in Puszcza Białowieska. 12 species inhabit the culture stage (Fig. 47). In the young stand

and pole wood their number decreases slightly to reach a maximum in the mature forest. During the secondary succession of the pine forests of Puszcza Białowieska substantial changes take place in the composition and structure of the ant community (CECHOWSKI unpublished data). The succession in the *Formicidae* taxocoene consists of two phases. The first of them is observed in young stands and the pole wood. The two communities bear a 70% species composition similarity (according to Sørensen's index) and identical structures of dominance (Morisita's index = 1). The most abundant species in these communities are polytopic species of dry habitats (Fig. 48), and the xerothermophilous *Tetramorium caespitum* was a dominant (64% on the average), while *Lasius niger*, a ubiquitous, typically pioneering species, was a subdominant (25%). Communities from the maturing and mature stands formed the second phase of succession with a similar degree of species composition similarity (70%) and similar structures of dominance (0.95). The most abundant species in that phase included polytopes of wet habitats with the dominant *Myrmica ruginodis* (59%). In terms of the number of ant nests, the second position was occupied by the forest oligotope *Leptothorax acervorum* (24%). *Formicidae* communities of the two distinct succession phases differed not so much in species composition (average similarity 66%) as in the structure of dominance (average similarity as low as 0.07).

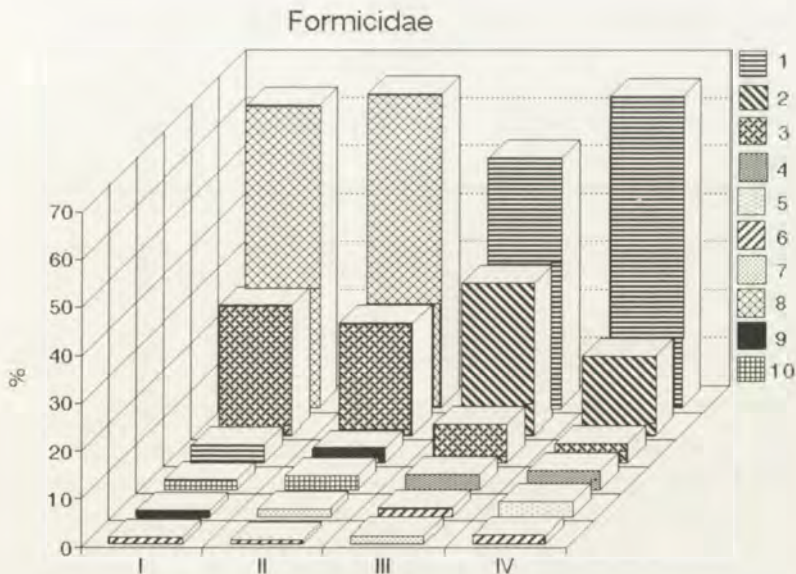


Fig. 48. Dominance structure of communities of ants (*Formicidae*) in forest stands of various ages in Puszcza Białowieska; 1 - *Myrmica ruginodis*, 2 - *Leptothorax acervorum*, 3 - *Lasius niger*, 4 - *Lasius umbratus*, 5 - *Leptothorax muscorum*, 6 - *Lasius flavus*, 7 - *Myrmica lobicornis*, 8 - *Tetramorium caespitum*, 9 - *Myrmica schencki*, 10 - *Formica fusca*

Changes in total density of ant nests were observed in the *Formicidae* communities of the pine forest sere (Fig. 49). This parameter is subject to substantial variations in consecutive stages to finally reach a value (in mature forests) similar to that recorded for the earliest stage studied (pine culture).

Actual species diversity (H') measured with Shannon-Weaver's index exhibits a gentle but steady increase with the growing age of the forest stand: from 1.52 to 1.77 (Fig. 50). Potential diversity (H_{max}) is also the highest in the mature stand stage (3.91) but the transitional stages are characterised by slightly lower values (3.32–3.58). The degree of approximation of the potential does not exhibit considerable changes either (Fig. 50), being, however, the lowest in the initial stages of succession (42% and 45% in the culture and young stand stage respectively) to grow slightly in the older stages (53% and 74% in the maturing stand and mature forest respectively).

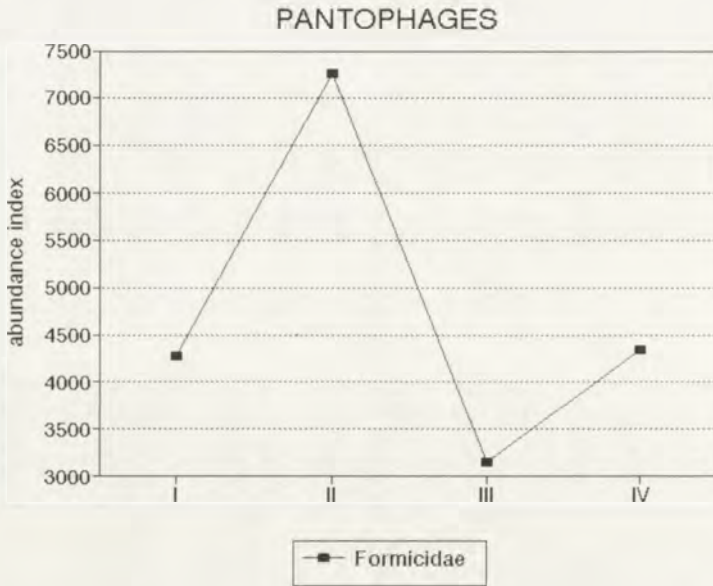


Fig. 49. Changes in the abundance of ant nests in relation to the age of pine forest stands

The specific features of the secondary succession taking place in the plots of pine forest distributed in a relatively "patchy" manner and going through various stages of maturity, include the presence of the forest ant species of the subgenus *Formica* s. str. in every succession stage, especially in the cultures, the species itself being only typical of the climax stages in forests. They represent the K-type ecological strategy i.e. conquer their environment slowly but remain there forever (PISARSKI, CZECHOWSKI 1994). Under the circumstances of the large forest complex of Puszcza Białowieska, large colonies of these ants are able to survive forest felling and silvicultural practices leading to the establishment of a

plantation, and to maintain their nests by feeding in adjacent old stands. A spectacular example was the complete absence of anthills of *Formica polyctena* in one of the mature forest areas studied, although the species had a high share in the material obtained using Barber's pitfall traps (CZECHOWSKI unpublished data).

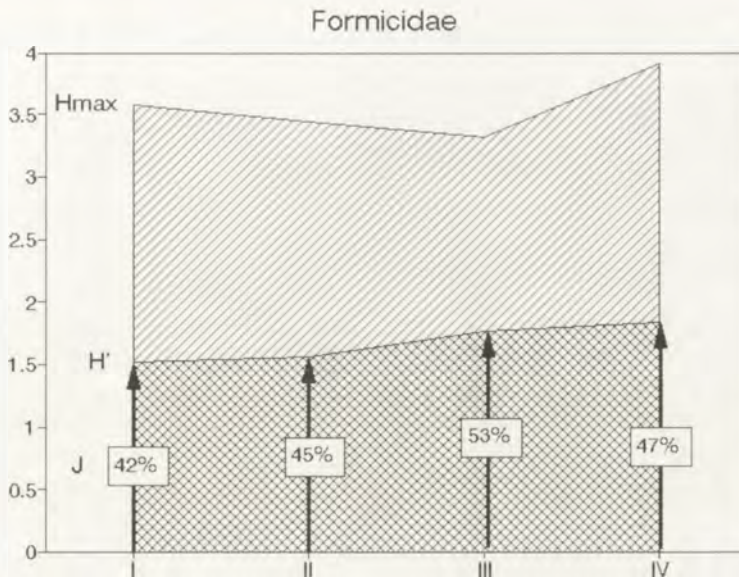


Fig. 50. Changes in actual (H') and potential (H_{max}) species diversity in communities of ants and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

Soil predators

Out of a number of groups of dipterans whose larvae develop in the soil leading a predatory mode of life, the families *Therevidae* and *Rhagionidae* are analysed in our study. The data on their occurrence in Poland in to-date literature are quite scarce (TROJAN 1970, MIKOŁAJCZYK 1991), neither has the structure of communities been studied.

Therevidae

A total of 14 *Therevidae* species were found in pine forest stands in Puszcza Białowieska based on material collected with Moericke's pitfall traps i.e. imagines (Fig. 51). The abundance of *Therevidae* and the number of species in three different age classes of the pine forest: young stand, pole wood and mature stand, do not vary significantly (Fig. 52). The communities are quite similar with regard to their species composition (the values of Sørensen's index are 78%, 82% and 76%). *Thereva handlirschi* is the dominant species at all stages (Fig. 53).

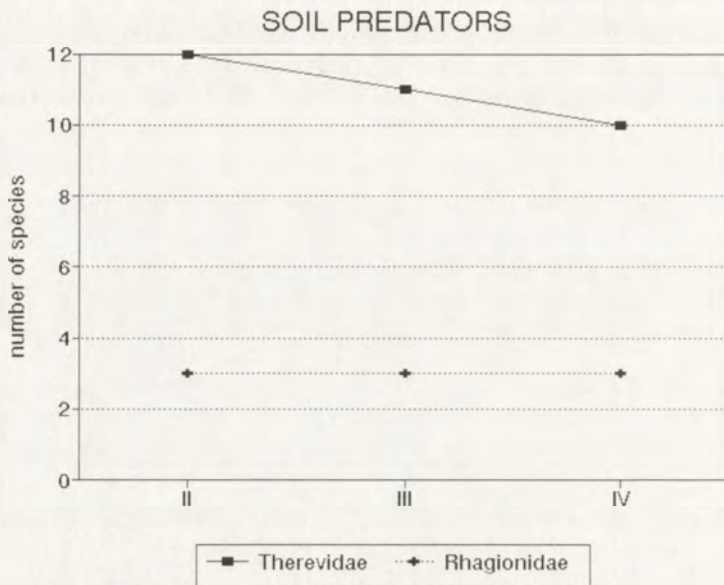


Fig. 51. Changes in the number of species of soil predators in the secondary sere of pine forests

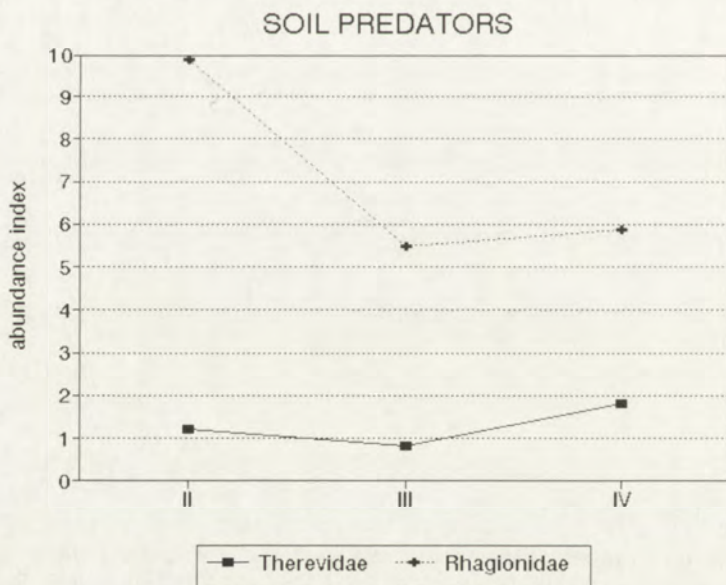


Fig. 52. Changes in the abundance of soil predators in relation to the age of pine forest stands

The species occurs commonly throughout the country. The similarity of community structures is also high in *Therevidae*, achieving values from 0.80 to 0.97 according to Morisita's coefficient. The only difference we have observed between communities of *Therevidae* in different age classes of the pine forest is that in the young stand the distribution of abundance per species parallels, in all likelihood, three distributions at the same time, namely the geometric series, the logarithmic series and the binomial negative distribution. The degree of similarity to these distributions drops considerably in communities occurring in the pole wood, while *Therevidae* abundance distribution in the mature forest does not bear any similarity to any of the theoretical distributions considered. The similarity to the geometric series, which indicates, as the theoretical principle has it, that the abundance of each species is proportional to the habitat resources it utilises, suggests that in the case of *Therevidae* such a situation may actually take place in younger age classes of pine forest. As the stand grows older, the structure of the community probably becomes less regular, which seems easy to understand considering the method of sample collection. In the consecutive stages of the pine forest sere, Moericke's pitfall traps were used to collect insects flying at increasingly high altitudes, possibly resulting in a more random selection of the *Therevidae* fauna, which might be more closely associated with the ground cover where it is often registered. The slight fall in the actual and potential diversity indices observed in the consecutive stages of the pine forest sere stems from slight variations in the number of species. The

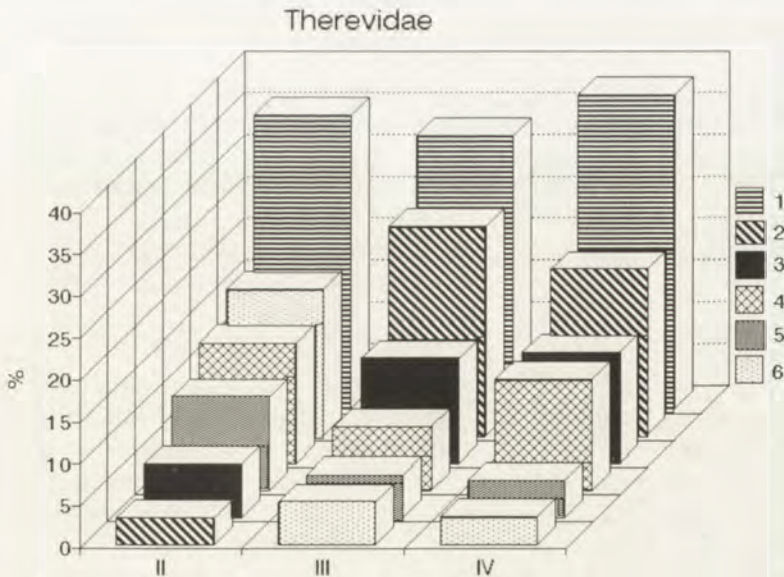


Fig. 53. Dominance structure of communities of *Therevidae* in forest stands of various ages in Puszcza Białowieska; 1 - *Thereva handlirschi*, 2 - *Thereva nobilitata*, 3 - *Thereva lanata*, 4 - *Thereva plebeja*, 5 - *Thereva circumscripta*, 6 - *Clorismia ardea*

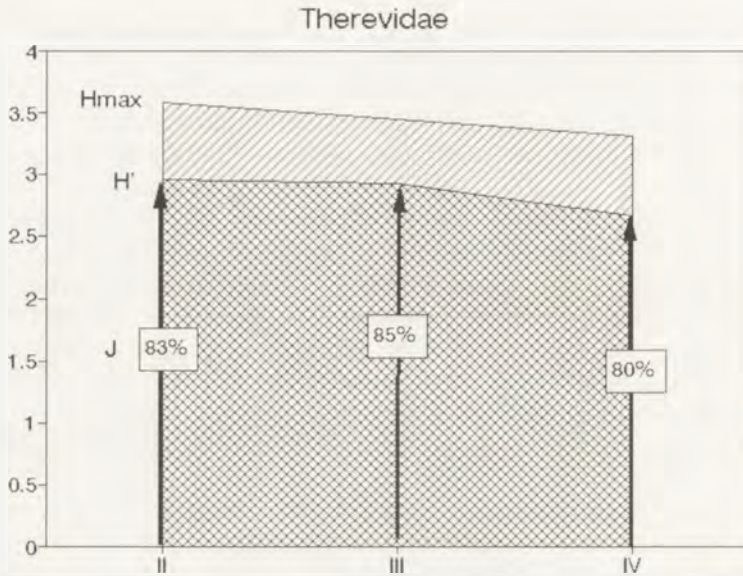


Fig. 54. Changes in actual (H') and potential (H_{max}) species diversity in communities of *Therevidae* and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

constant nature of this community parameter is confirmed by the degree of approximation of potential species diversity, which remains at a more or less the same high level ranging from 80.4 to 84.7 (Fig. 54).

Rhagionidae

Communities of *Rhagionidae*, dipterans exhibiting, in the larval and imago stages, a predatory mode of life, similar to *Therevidae*, were also studied in three stages of pine forest in Puszcza Białowieska. These communities exhibited similarly high constancy of the species composition and structure. They are composed of only three species, the common *Rhagio lineola* being the dominant with at least a 95% share in each of the communities under study.

5.4. Vertebrates

Vertebrates are considerably diversified in species composition, size and the role that individual species play in nature. In ecological terms, they are regarded as belonging to two subsystems. Phytophages, which include hoofed mammals and most rodents, are biotrophs. The other subsystem, macrotrophs, embraces predators controlling the abundance of the biotrophic and saprotrophic subsystems. Special methods are employed for assessing species composition and abundance of vertebrates, depending on the size and mode of life so that vertebrates are seldom mentioned in comprehensive faunal papers, usually dealing only with invertebrates. This analysis is based on a paper by WOLK and GUTOWSKI (1984) devoted to small mammals and birds of pine forests of Puszcza Białowieska and on studies of small mammals of pine forests (PUCEK

unpublished data). Neither of these papers includes large mammals, whether hoofed or predatory, or birds of prey. These groups, however, do not contain groups characteristic of pine forests.

Mammals (*Mammalia*)

Small mammals (*Micromammalia*) encompass two groups performing different biological roles: phytophages, which comprise rodents, and insectivores (some species may be considered polyphagous). 15 species of small mammals were found in the pine forests of Puszcza Białowieska. The number of species in individual stages of secondary succession, the number of species revolves around 10 (Fig. 55). A noticeable decrease in the number of species – down to 7 (PUCEK unpublished data) or 4 (WOLK and GUTOWSKI 1984) – is seen in the most mature stands. These differences turn out to be rather insignificant considering the period when the materials were collected and the species represented by single individuals collected during the five years of catches. These species (see inventory) are regarded as faunal rarities in the area of Puszcza Białowieska.

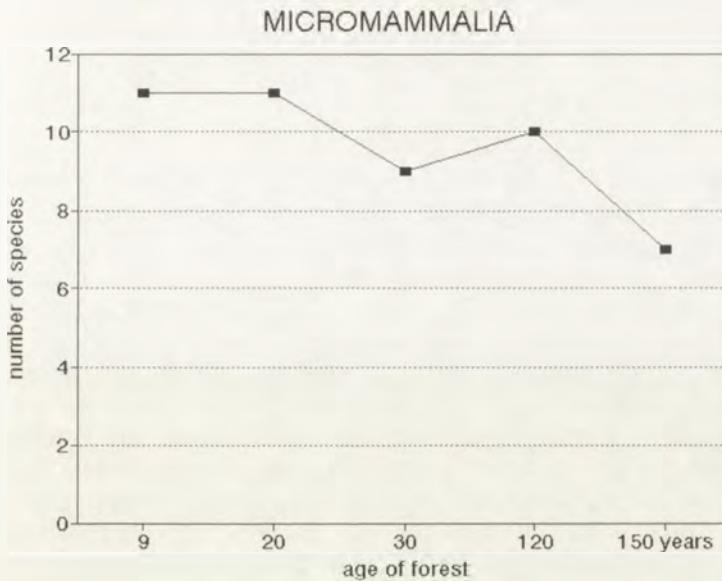


Fig. 55. Changes in the number of species of small mammals in relation to the age of pine forest stands

The pattern of changes in abundance is characterised by a high density of small mammals in pine cultures (Fig. 56). There is a 30% fall in young stands and the pole wood, and in mature forest the abundance of *Micromammalia* returns to the original values.

The structure of the small mammal community shows a stable group of dominants throughout the secondary sere (Fig. 57). It is formed of four species,

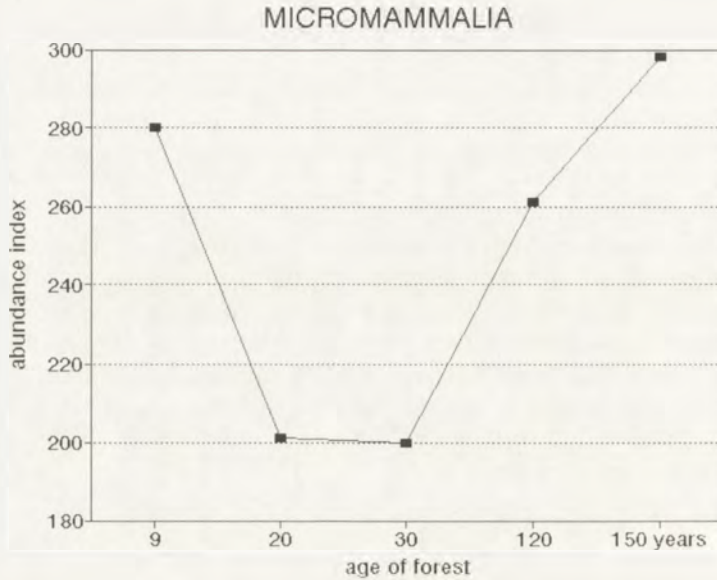


Fig. 56. Changes in the abundance of small mammals in relation to the age of pine forest stands

the rodents: bank vole (*Clethrionomys glareolus*) and field yellow-necked mouse (*Apodemus flavicollis*) and the insectivore shrews: *Sorex araneus* and *Sorex minutus*. It is interesting to note that the bank vole increases its share in the course of the sere, accounting for as many as 67% of the total number of small mammals caught, while the peak abundance of yellow-necked field mouse is registered in the pole wood. Reverse trends are observed in the zoohagous group. *S. araneus* is most abundant in pine cultures, his abundance decreasing with the growing age of the stand. *S. minutus* exhibits larger variations in abundance that are not associated with the age of the forest stand. There is a considerable age-related decrease in the share of meadow and field species. Common vole (*Microtus arvalis*), quite common in the culture stage, disappears in the pole wood not to emerge again in mature forests. Short-tailed vole (*Microtus agrestis*) has a share of several percent in communities in each age class, but it was not registered in the pole wood. Harvest mouse (*Micromys minutus*) and northern birch mouse (*Sicista betulina*) are characterised by similar shares. Other species occur in the pine forest only sporadically.

Species diversity of small mammals is highest in cultures and young stands of pine (Fig. 58) decreasing in older stands to reach a minimum in the final link of the secondary sere. In this case also, the increase of community organisation is accompanied by the elimination of accessory species and the strengthening of the dominant position of species forming the core of the community. This is obviously reflected in the value of Pielou's index (J), reflecting the degree of

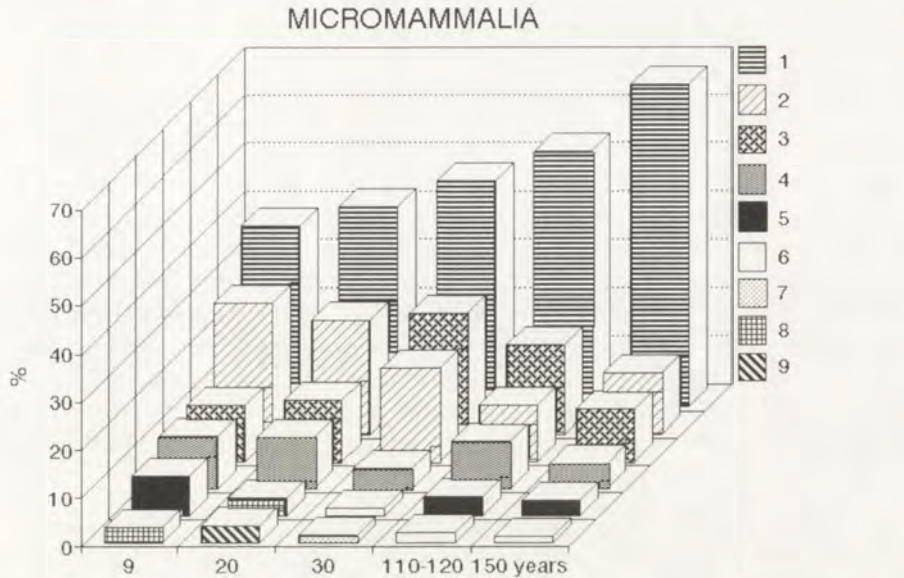


Fig. 57. Dominance structure of communities of small mammals in forest stands of various ages in Puszcza Białowiecka: 1 – *Clethrionomys glareolus*, 2 – *Sorex araneus*, 3 – *Apodemus flavicollis*, 4 – *Sorex minutus*, 5 – *Microtus agrestis*, 6 – *Sicista betulina*, 7 – *Apodemus agrarius*, 8 – *Micromys minutus*, 9 – *Microtus arvalis*

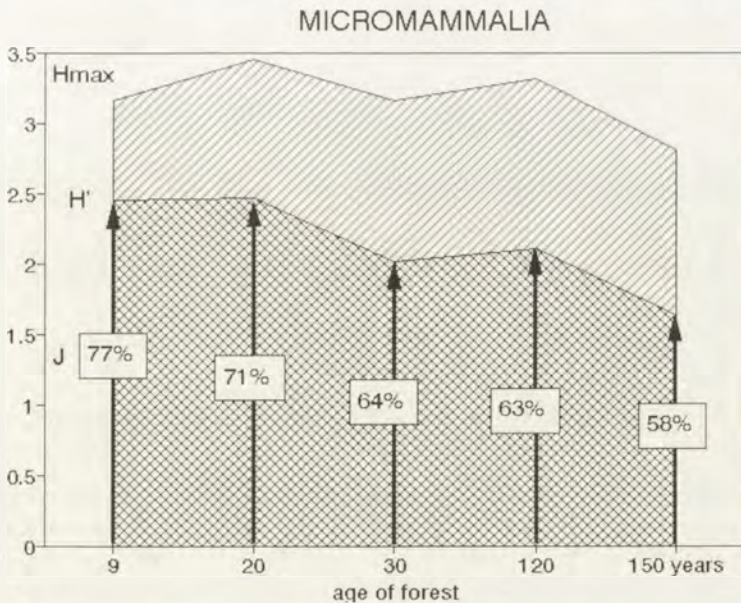


Fig. 58. Changes in actual (H') and potential (H_{max}) species diversity in communities of small mammals and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

realisation of the potential for species diversity. The value of this index falls steadily throughout the sere.

Birds (*Aves*)

Nesting birds are represented in the pine forests of Puszcza Białowieska by 23 species. None of them occurs at every stage of the secondary succession (WOLK, GUTOWSKI 1984). During the first years after a plantation of pine is started, the afforested clearings are settled by three field species. Their number increases up to eight species in a 9–17-year-old stand (Fig. 59), up to 11 after 22 years, to reach 16 in the oldest stands. In the latter stage, only typically forest species occur. This set of species, however, is only characteristic of larger and older pine forest complexes. In enclaves of mature forest surrounded by younger stands, the number of species of nesting birds falls by almost a $\frac{1}{3}$ i.e. down to 9. Distribution-based estimation of the number of species was only possible for 22–24-year-old stands. A value of $S^* = 11.07$ indicates that empirical data correspond to theoretical estimates.

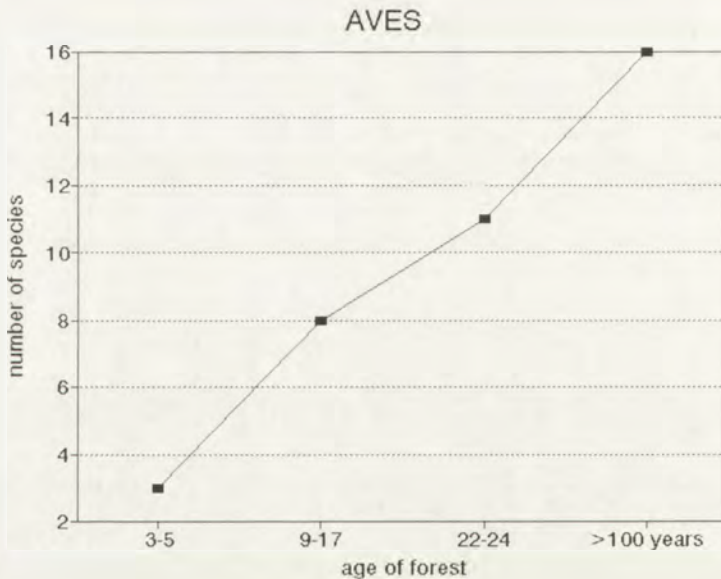


Fig. 59. Changes in the number of species of birds in relation to the age of pine forest stands

The number of couples of nesting birds per one hectare of forest is lowest in the culture stage and grows throughout the sere (Fig. 60). In cultures several years old the figure is 13, compared to 33 couples/ha in large mature complexes. In small enclaves of mature forest characterised by poorer species composition, the nest density is even higher (39 couples/ha). This effect is mostly due to the high proportion of chaffinch (*Fringilla coelebs*) and goldcrest (*Regulus regulus*) which nest in mature enclaves.

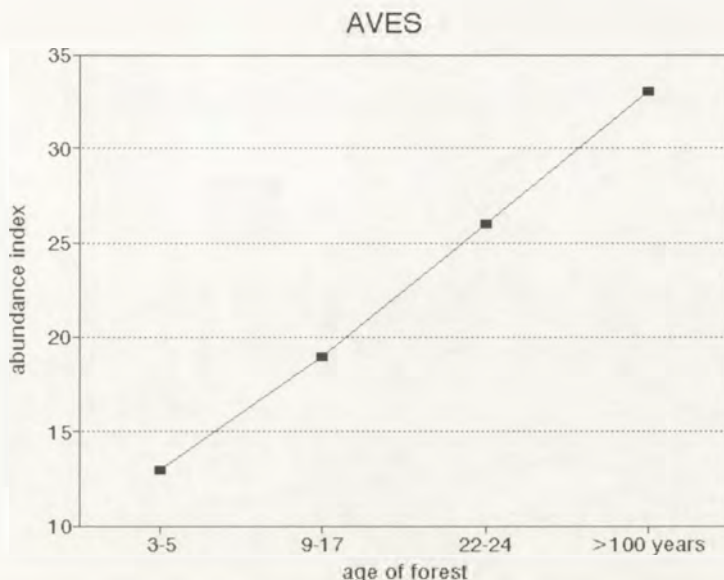


Fig. 60. Changes in the abundance of birds in relation to the age of pine forest stands

The structure of the community of birds is a dominant-type one (Fig. 61). Tree pipit (*Anthus trivialis*) is dominant in 3–5-year-old plantations, followed by wood lark (*Lullula arborea*), and yellowhammer (*Emberiza citrinella*) has the lowest share. The latter is dominant in 9–17-year-old stands, where tree pipit moves to the second position. The third position is occupied by hedge sparrow (*Prunella modularis*), a new species. In stands older than 20 years, the top position is occupied by robin (*Erithacus rubecula*), followed by two species: chiffchaf (*Phylloscopus collybita*) and wood warbler (*P. sibilatrix*). Hedge sparrow retains its high proportion. Similarly high is the share of a new species – blackbird (*Turdus merula*). In stands older than 100 years the structure of the avian community is much more uniform, with chaffinch, goldcrest and wood warbler functioning as dominants. Crested tit (*Parus cristatus*) also has a significant share. Since older stands contain trees with hollows in the stems, a group of hollow-dwelling birds also appears.

Actual species diversity (H') of the avian community of pine forest increases throughout the secondary sere from 1.42 to 3.43 in the oldest stands (Fig. 62). A similar trend is noted in potential species diversity (H_{max}), which equals 1.58 in the culture stage and 4.00 in older stands. The trend is present throughout the sere. The degree of approximation of the potential diversity, measured with Pielou's index, is very high in younger (< 25 years) stands ($J=90.0\%$). It falls in older stands to 85.8%, suggesting that in the case of birds, too, the process of formation of communities in mature ecosystems is accompanied by the increase of the degree of dominancy.

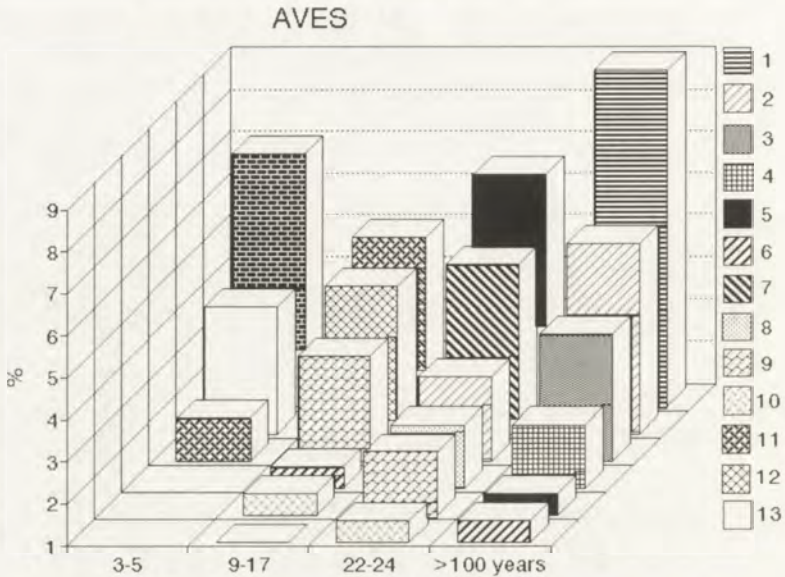


Fig. 61. Dominance structure of communities of nesting birds (*Aves*) in forest stands of various ages in Puszcza Białowieża; 1 – *Fringilla coelebs*, 2 – *Phylloscopus sibilatrix*, 3 – *Regulus regulus*, 4 – *Parus cristatus*, 5 – *Erithacus rubecula*, 6 – *Turdus philomelos*, 7 – *Phylloscopus collybita*, 8 – *Turdus merula*, 9 – *Prunella modularis*, 10 – *Phylloscopus trochilus*, 11 – *Emberiza citrinella*, 12 – *Anthus trivialis*, 13 – *Lullula arborea*

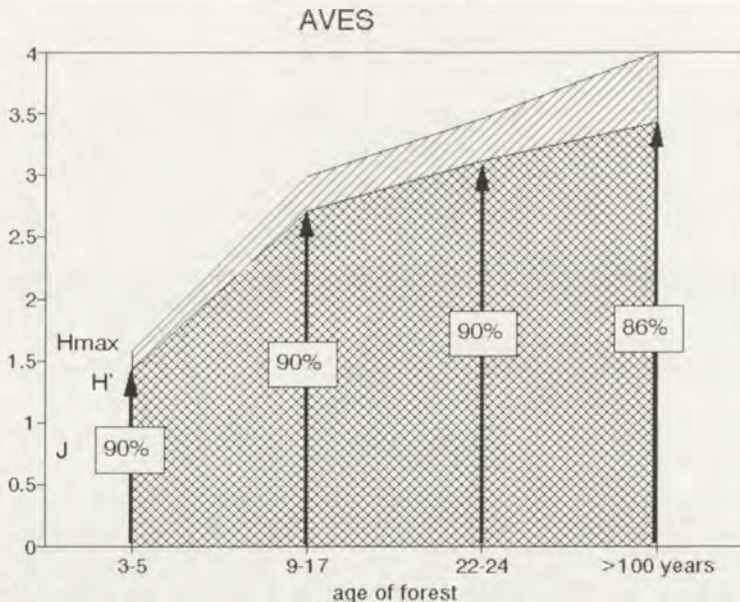


Fig. 62. Changes in actual (H') and potential (H_{max}) species diversity in communities of birds and the degree of realisation (J) of potential diversity of the communities in the sere of the pine forest

6. SUMMARY

Because of the economic value of pine timber, Polish pine forests have been exploited and cultivated for hundreds of years. Most of the forests consist of even-aged stands, which are usually formed as a result of artificial restoration of complete cut down of trees. Starting a pine plantation in a clearing, usually with an addition of companion or shelter trees, initiates the process of secondary succession. In the course of secondary succession, the forest goes through several stages: culture, young growth, thicket, pole wood and maturing stand until it reaches the mature stage. In Polish pine forests, the process takes 120–150 years (SZUJECKI 1980).

Each of these stages is characterized by slightly different forest microclimatic conditions, which depend on the composition of the stand and habitat properties (OBMIŃSKI 1978). The changes influence the reconstruction of the plant cover. Secondary succession processes in the pine forests of Puszcza Białowieska are remarkably creative in this respect as they lead to the formation of the spatial structure typical of the coniferous forest with conspicuous vertical alignment and to filling the living space of the forest interior with species adapted to the habitat conditions which have developed in the course of secondary succession. It is a repetitive process that has been observed and described in coniferous forest habitats in various parts of the country.

As regards fauna, these processes have been only partially understood and data on the secondary succession of fauna pertain only to individual groups of animals so that it is impossible to fully portray the changes in composition and organisation of faunal complexes. On the background of the bibliography concerned with ecological succession, which is quite abundant, but often poorly related to "the real thing", the authors of this paper have addressed several questions that take into account the character of faunistical data, ensuring that a well-documented answer can be obtained.

The problem which appears central to our understanding of the topic is the character of the secondary succession of fauna – what and in what way does this process lead to. It is by no means obvious, unlike the case of forest plant cover, that in the process of secondary succession of fauna the biomass increases considerably and spatial structures are formed. Even if these phenomena actually take place, they still need to be evidenced for. The most important question is whether the secondary succession of fauna is uni- or multidirectional. The question concerns the very model of the process – whether it is entirely creative, and whether its stages consist in populating the ecological vacuum, forming ecosystems and adapting them to the ecological structure of the maturing forest. This clear picture raises a number of doubts. Is there an actual ecological vacuum during some time after clear-cutting, or is the open area immediately occupied? Do the various subsystems of the zoocenosis have to come into being or do they already exist in nature? And, finally, what does the adaptation consist in? More exactly, what do the various faunal groups actually adapt to?

In order to obtain an unequivocal answer to the above questions, two working hypotheses were put forward, which were then verified with the materials collected and analysed.

The first hypothesis states that the secondary succession of fauna can develop in various ways and sometimes lead to dissimilar final systems. Five types of succession have been described: creative, stabilising, rise-and-fall, regressive and restorative (Fig. 3).

The second hypothesis interprets the interdependencies within the fauna as a hierarchical system of trophic relations. The core of the structure of the fauna is accordingly formed of systems related to one another by means of feeding relations, such as subsystem, food chain, competitive guild and population of a given animal species. These interrelations have been presented on the basis of 30 faunal groups included in the study of the final stage of secondary succession – the fauna of a mature pine forest.

So formulated, the working hypotheses have made it possible to compare faunal data with the ideas about the course of secondary succession. The following documentation materials for each of the age classes provided a basis for verifying the hypotheses:

- 1) the number of species forming the taxocenes or competitive guilds;
- 2) the abundance of these units, usually expressed in the form of indices in order to illustrate trends in abundance changes;
- 3) the structure of the taxocenes for illustrating changes in the organisation of zoocenotic systems;
- 4) actual and potential species diversity and their ratio measured with Pielou's index.

The number of species (Tab. II) exhibits six types of changes in the course of the secondary succession of pine forests in Puszcza Białowieska. The dominant trend is restorative succession where a high number of species occurs in the pine stand in the culture stage, decreasing in the pole wood stage to rise again in the mature forest. This trend was observed in half of the competitive guilds and 8 taxocenes studied. The second position is occupied by two other modes of secondary succession. Regressive succession, in the course of which the number of species constantly decreases, is found in 4 competitive groups and 5 taxocenes. Similarly, the rise-and-fall succession, where an initial increase in the number of species is followed by a fall, was observed in 5 competitive groups. Creative succession, characterized by a constant growth in the succession series, was only found in 4 competitive groups. Stabilisation of the number of species following an initial increase occurred only in 2 groups of animals. Apart from these 5 types of changes in the number of species, absence of such changes in the course of forest development was observed in the following 5 instances: the leaf beetles (*Chrysomelidae*), lady-birds (*Coccinellidae*), parasitic *Pipunculidae*, nematodes (*Nematoda*) and *Rhagionidae* (*Diptera*).

A similar diversification of responses of individual animal groups to the regeneration of a pine forest can be seen when analysing the competitive guilds separately (Tab. II). Where a group is composed of a number of taxons, the usual finding is that each of the taxons follows a different pattern of changes in the

number of species. Zoophages as well as xylo- and cambiophages are exceptional in this respect, representing mostly the restorative type of changes in the number of species, while the decreasing trends prevail in the case of chewing phytophages.

Table II. Changes in the number of species of animal communities in the course of the secondary succession of the pine forests in Puszcza Białowieńska

| Subsystem | Competitive guild | Succession type | | | | | |
|--------------|--------------------------------|-----------------|-------------|---------------|------------|-------------|------------|
| | | creativ | stabilising | rise-and-fall | regressive | restorative | no changes |
| Biotrophes | sucking phytophages | 1 | - | 1 | - | 1 | - |
| | chewing phytophages | 1 | - | - | 2 | - | 1 |
| | xylo- and cambiophages | - | 1 | - | - | 2 | - |
| | zoophages | - | - | 1 | - | 3 | - |
| | aphidophages | 1 | - | 1 | 1 | - | 1 |
| | parasitoids | - | - | 1 | - | 1 | 1 |
| Saprotrophes | saprophages | - | 1 | 1 | - | - | 1 |
| | soil pantophages and predators | - | - | - | 1 | 1 | 1 |
| Macrotophres | birds | 1 | - | - | - | - | - |
| | mammals | - | - | - | 1 | - | - |
| Total | | 4 | 2 | 5 | 5 | 8 | 5 |

The results of the analysis of changes in the basic components of forest ecosystem organisation, as one can call animal species, indicate that the constructive processes of expansion or regeneration of systems, represented by creative, stabilising and restorative succession, are as marked as the destructive processes reflected in the final outcome as a fall in the number of species. At the same time it is symptomatic that one out of every six groups of animals does not respond to the processes operating in the developing forest by changing the number of species.

The changes in the abundance of animal communities (Tab. III) are as diverse as the trends in the number of species. However, two patterns prevail: regression and restoration. About $\frac{1}{3}$ of the animal communities are more abundant at the beginning of succession than in mature stands, so that the decreasing trend predominates. The second most frequent type of succession is seen in those communities wherein in the course of succession the decrease is arrested and abundance increases in older stands. A steady increase in abundance

throughout the succession series is reported only in one out of every 7 taxocenes. Also in every seventh group no abundance changes are recorded resulting in a constant density throughout the series. A decrease following an initial rise is observed in every fifteenth taxocene, while in one case only, namely in springtails (*Collembola*), the changes in abundance indicate stabilisation in older stands.

Table III. Types of changes in species abundance in animal communities in the course of the secondary succession of the pine forests in Puszcza Białowieska

| Subsystem | Competitive guild | Succession type | | | | | |
|--------------|--------------------------------|-----------------|-------------|---------------|------------|-------------|------------|
| | | creativ | stabilising | rise-and-fall | regressive | restorative | no changes |
| Biotrophes | sucking phytophages | 1 | - | - | 2 | - | - |
| | chewing phytophages | - | - | 1 | - | - | 2 |
| | xylo- and cambiophages | - | - | - | 1 | 2 | - |
| | zoophages | - | - | - | 3 | 1 | - |
| | aphidophages | 2 | - | - | 1 | 1 | - |
| | parasitoids | - | - | - | 1 | 1 | - |
| Saprotrophes | saprophages | - | 1 | - | - | 1 | 1 |
| | soil pantophages and predators | - | - | 1 | 1 | 1 | - |
| Macrotrophes | birds | 1 | - | - | - | - | - |
| | mammals | - | - | - | - | 1 | 1 |
| Total | | 4 | 1 | 2 | 9 | 8 | 4 |

When the phenomena are analysed from the viewpoint of individual competitive groups, it can be seen that the responses to succession within each group are visibly diversified. In each group of invertebrates one can find taxocenes whose abundance increases steadily, and others, whose abundance falls. Non-specialised zoophages are an exception in this respect since the prevailing tendency in that group is a decrease in abundance.

Analysis of changes in abundance of the fauna provides an answer to two important questions related to secondary succession of pine forests. The notion of a "faunal vacuum" is not compatible with the facts. The forest clearing is immediately occupied by animal populations of high abundance; almost $\frac{2}{3}$ of animal communities decrease their abundance in the course of succession.

Increasing abundance can be observed only in $\frac{1}{4}$ of the animal groups (Tab. III): sucking phytophages, aphidophages and birds.

Abundance is a measure of the ecological success of both the species and the animal community. In the course of secondary succession of a pine forest, changes are seen in the manner of utilisation of the mass produced by the green plants. As the forest develops, phytophages with a biting mouth apparatus which eat conifers of pine are replaced by the less dangerous sucking phytophages which suck out the products of assimilation. The phenomenon can be seen at least in Puszcza Białowieska, where the pine forests are not subject to disastrous invasions of the chewing phytophages. An increase in the abundance of the sucking phytophages is accompanied by the development of groups of aphidophages which regulate the abundance of the former. Very important is the increase in abundance of the competitive group of birds, mostly insectivores, which act as an element controlling other elements, particularly the subsystem of biotrophes.

Changes in actual species diversity (Tab. IV), measured with Shannon-Weaver's index (H'), are most uniformly distributed among the various models of succession. The most frequent processes are reduction of diversity in comparison with the initial situation, but, all in all, the increasing trend in the diversity of animal communities is encountered as frequently as the reverse process. Another frequently observed phenomenon is a fall in diversity after a period of rise. The picture changes a little when one considers it from the viewpoint of realising the potential for species diversity in the ecosystem. Here, the prevailing process is reduction of diversity, especially in mature stands. Reduction was observed in 17 communities out of 28 investigated in this respect. Increase, restoration or stabilisation of diversity after an increase were registered in only $\frac{1}{3}$ of the cases. Absence of changes of diversity throughout the succession series is very rare.

The results of the above analysis indicate clearly that MacArthur's (1958) thesis "diversity makes stability" is not confirmed by empirical data. On the contrary, the decrease in species diversity observed in the mature stands of the pine forest implies that the increase in the degree of organisation of a system takes place at the expense of decreasing its internal diversification. This is related to community structure. In mature stands, there is usually one or a few dominant species in a community and the "tail" of accessory species becomes notably shorter. The organisation of a community is usually built on a few well-adapted species forming competitive groups.

In conclusion it should be stressed that the most outstanding feature of secondary succession of the fauna in the pine forests in Puszcza Białowieska is the multidirectional character of processes taking place in a growing pine forest which is developing its spatial structure. If one considers the parameters studied: the number of species, abundance, species diversity and structure, it is easy to notice that the decreasing trends in the parameters studied predominate – either throughout the succession series or in its final stage (44% of cases). Stabilisation of these parameters throughout the series or after a period of growth can only be seen in 22% of cases. An increase, either steady or following a period of reduction, is only observed in 34% of the cases.

Table IV. Types of changes in actual species diversity (H') in animal communities in the course of the secondary succession of the pine forests in Puszcza Białowieża

| Subsystem | Competitive guild | Succession type | | | | | |
|---------------|--------------------------------|-----------------|-------------|---------------|------------|-------------|------------|
| | | creativ | stabilising | rise-and-fall | regressive | restorative | no changes |
| Biotrophes | sucking phytophages | 1 | - | - | 2 | - | - |
| | chewing phytophages | - | - | 1 | - | - | 2 |
| | xylo- and cambiophages | 1 | 1 | - | - | 1 | - |
| | zoophages | 1 | 1 | 1 | - | 2 | - |
| | aphidophages | 1 | - | 1 | 2 | - | - |
| | parasitoids | - | 1 | 1 | 1 | - | - |
| Saprotrophes | saprophages | - | 1 | 1 | - | - | 1 |
| | soil pantophages and predators | - | 1 | - | 1 | - | - |
| Macrotophages | birds | 1 | - | - | - | - | - |
| | mammals | - | - | - | 1 | - | - |
| Total | | 5 | 5 | 5 | 7 | 3 | 3 |

These data confirm the hypothesis of multidirectional character of the processes of secondary succession in animal communities. Particularly important is the decrease in the value of many indices characterizing the fauna in the final stage of succession, which can be termed the stage of community organisation. It takes place at the cost of reducing the number of species and diversity for the sake of stabilisation of dominance structures. Ecosystem stability is thus ensured by the better adapted forms while the diversity potential is not fully utilised.

All elements of the zoocenotic system are formed simultaneously in the early stage of planting the stand after clear-cutting. At this stage the system is the richest. In the subsequent stages its organisation is only restructured in accordance with the development of the forest as an ecosystem.

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8. AN INVENTORY OF SPECIES OCCURRING IN THE PINE FORESTS
OF PUSZCZA BIAŁOWIESKA

LACHNIDAE (APHIDOIDEA, HOMOPTERA)

- 1 *Cinara pinea* (MORDR.)
- 2 *Cinara pilosa* (ZETT.)
- 3 *Cinara pini* (L.)
- 4 *Cinara pinihalbitans* (MORDR.)
- 5 *Schizolachnus pineti* (F.)
- 6 *Eulachnus agilis* (KALT.)

AUCHENORRHYNCHA (HOMOPTERA)

Delphacidae

- 1 *Criomorpha albomarginatus* CURT.
- 2 *Javesella pellucida* (F.)
- 3 *Paradelphacodes paludosus* (FT.)

Cicadidae

- 4 *Cicadetta montana* (SCOP.)

Cercopidae

- 5 *Aphrophora corticea* (GERM.)

Membracidae

- 6 *Centrotus cornutus* (L.)

Cicadellidae

- 7 *Oncopsis flavicollis* (L.)
- 8 *Empoasca vitis* (GOETHE)
- 9 *Eupteryx atropunctata* (GOEZE)
- 10 *Eurhadina pulchella* (FALL.)
- 11 *Wagneripteryx germari* (ZETT.)
- 12 *Arboridia parvula* (BOH.)
- 13 *Zygina flammigera* (FOURCR.)
- 14 *Allygus mixtus* (F.)
- 15 *Colobotettix morbillosus* (MEL.)
- 16 *Grypotes puncticollis* (H.-S.)
- 17 *Hesium domino* (REUT.)
- 18 *Jassargus flori* (FIEB.)
- 19 *Macrosteles laevis* (RIB.)
- 20 *Psammotettix alienus* (DHLB.)
- 21 *Speudotettix subfuscus* (FALL.)

HETEROPTERA

- 1 *Sehinus luctuosus* MULS. et R.
- 2 *Adomerus biguttatus* (L.)
- 3 *Tritomegas bicolor* (L.)
- 4 *Aelia acuminata* (L.)
- 5 *Aelia klugi* HAHN
- 6 *Eysarcoris aeneus* (SCOP.)

- 7 *Stagonomus pusillus* (H.-S.)
- 8 *Holcostethus vernalis* (WOLFF.)
- 9 *Palomena prasina* (L.)
- 10 *Palomena viridissima* (PODA)
- 11 *Pitedia juniperina* (L.)
- 12 *Pitedia pinicola* (MULS. et R.)
- 13 *Carpocoris purpureipennis* (DE GEER)
- 14 *Carpocoris fuscispinus* (BOH.)
- 15 *Carpocoris pudicus* (PODA)
- 16 *Dolycoris baccarum* (L.)
- 17 *Eurydema oleraceum* (L.)
- 18 *Piezodorus lituratus* (F.)
- 19 *Picromerus bidens* (L.)
- 20 *Troilus luridus* (F.)
- 21 *Rhacognathus punctatus* (L.)
- 22 *Acanthosoma haemorrhoidale* (L.)
- 23 *Elastotethus interstinctus* (L.)
- 24 *Elasmucha ferrugata* (F.)
- 25 *Elasmucha fieberi* (JAK.)
- 26 *Elasmucha grisea* (L.)
- 27 *Coreus marginatus* (L.)
- 28 *Corizus hyoscyami* (L.)
- 29 *Rhopalus parvopunctatus* (SCHILL.)
- 30 *Rhopalus maculatus* (FIEB.)
- 31 *Myrmus miriformis* (FALL.)
- 32 *Stictopleurus pictus* (FIEB.)
- 33 *Dicranocephalus agalis* (SCOP.)
- 34 *Nithecus jacobaeae* (SCHILL.)
- 35 *Nysius thymi* (WOLFF)
- 36 *Nysius ericae* (SCHILL.)
- 37 *Nysius helveticus* (H.-S.)
- 38 *Kleidocerys resedae* (PANZ.)
- 39 *Cymus obliquus* (HORV.)
- 40 *Cymus clavicularis* (FALL.)
- 41 *Cymus melanocephalus* (FIEB.)
- 42 *Geocoris grylloides* (L.)
- 43 *Geocoris ater* (F.)
- 44 *Stygnocoris pygmaeus* (F. SAHLB.)
- 45 *Stygnocoris pedestris* (FALL.)
- 46 *Megalonotus chiragra* (F.)
- 47 *Megalonotus sabulicola* (THOMS.)
- 48 *Pterotmetus staphylyiformis* (SCHILL.)
- 49 *Rhyparochromus pini* (L.)

- 50 *Ischnocoris angustulus* (BOH.)
 51 *Drymus ryei* DOUGL. et SC.
 52 *Drymus brunneus* (F. SAHLB.)
 53 *Eremocoris plebejus* (FALL.)
 54 *Eremocoris abietis* (L.)
 55 *Scolopostethus decoratus* (HAHN)
 56 *Pachybrachius fracticollis* (SCHILL.)
 57 *Neides tipularius* L.
 58 *Saldula vestita* (DOUGL.)
 59 *Acalypta carinata* (PANZ.)
 60 *Acalypta nigrina* (FALL.)
 61 *Acalypta marginata* (WOLFF)
 62 *Acalypta gracilis* (FIEB.)
 63 *Himacerus apterus* (F.)
 64 *Nabicula limbata* (DAHLB.)
 65 *Nabis ferus* (L.)
 66 *Nabis pseudoferus* REM.
 67 *Nabis punctatus* A. COSTA
 68 *Nabis ericetorum* SCHOLTZ
 69 *Nabis rugosus* (L.)
 70 *Myrmedobia exilis* (FALL.)
 71 *Myrmedobia distinguenda* REUT.
 72 *Anthocoris nemorum* (L.)
 73 *Anthocoris confusus* REUT.
 74 *Acomporis pygmaeus* (FALL.)
 75 *Orius niger* WOLFF
 76 *Orius minutus* (L.)
 77 *Orius agilis* (FLOR)
 78 *Monalocoris filicis* (L.)
 79 *Bothynotus pilosus* (BOH.)
 80 *Deraeocoris ruber* (L.)
 81 *Alloeotomus gothicus* (FALL.)
 82 *Myrmecoris gracilis* (J. SAHLB.)
 83 *Leptopterna ferrugata* (FALL.)
 84 *Leptopterna dolabrata* (L.)
 85 *Stenoderma calcaratum* (FALL.)
 86 *Stenoderma virens* (L.)
 87 *Stenoderma laevigatum* (L.)
 88 *Stenoderma holsatum* (F.)
 89 *Notosistra erratica* (L.)
 90 *Trigonotylus coelestialium* (KIRK.)
 91 *Trigonotylus ruficornis* (GEOFFR.)
 92 *Phytocoris longipennis* FLOR
 93 *Phytocoris pini* KIRSCHB.
 94 *Adelphocoris reicheli* (FIEB.)
 95 *Caloris biclavatus* (H.-S.)
 96 *Caloris affinis* (H.-S.)
 97 *Caloris norvegicus* (GMEL.)
 98 *Stenotus binotatus* (F.)
 99 *Lygocoris pabulinus* (L.)
 100 *Lygus rugulipennis* (POPP.)
 101 *Lygus pratensis* (L.)
 102 *Lygus punctatus* (ZETT.)
 103 *Camptozygum aequale* (VILL.)
 104 *Charagochilus gyllenhali* (FALL.)
 105 *Capsus pilifer* REM.
 106 *Capsodes gothicus* (L.)
 107 *Halticus pusillus* (H.-S.)
 108 *Heterotoma meriopterum* (SCOP.)
 109 *Heterocordylus genistae* (SCOP.)
 110 *Orthotylus ericetorum* (FALL.)
 111 *Globiceps flavomaculatus* (F.)
 112 *Globiceps cruciatus* REUT.
 113 *Blepharidopterus brevicornis* (WAGN.)
 114 *Phoenicocoris modestus* (MEY.-D.)
 115 *Phoenicocoris obscurellus* (FALL.)
 116 *Atractotomus mali* (MEY.-D.)
 117 *Psallus varians* (H.-S.)
 118 *Plesiodema pinetellum* (ZETT.)
 119 *Lopus decolor* (FALL.)

SYMPHYTA

- 1 *Xyeta julii* (BREB.)
 2 *Acantholyda posticalis* (MATS.)
 3 *Cephalcia arvensis* (PANZ.)
 4 *Pamphilius hortorum* (KLUG)
 5 *Pamphilius marginatus* (LEP.)
 6 *Pamphilius sylvaticus* (L.)
 7 *Pamphilius varius* (LEP.)
 8 *Janus femoratus* (CURT.)
 9 *Janus luteipes* (LEP.)
 10 *Arge dimidiata* (FALL.)
 11 *Arge ustulata* (L.)
 12 *Microdiprion pakkipes* (FALL.)
 13 *Macrophya duodecimpunctata* (L.)
 14 *Eriocampa ovata* (L.)
 15 *Athalia bicolor* LEP.
 16 *Athalia circularis* (KLUG)
 17 *Athalia cordata* LEP.
 18 *Athalia cordatoides* PRIESN.
 19 *Athalia glabricollis* THOMSON
 20 *Athalia lugens* (KLUG)
 21 *Athalia rosae* (L.)
 22 *Monosoma pulveratum* (RETZ.)
 23 *Empria longicornis* (THOMSON)
 24 *Ametastegia equseti* (FALL.)

- 25 *Ametastegia glabrata* (FALL.)
 26 *Ametastegia tener* (SPINOLA)
 27 *Allantus cingillum* (KLUG)
 28 *Allantus togatus* (PANZ.)
 29 *Harpiphorus lepidus* (KLUG)
 30 *Monophadnus pallescens* (GMEL.)
 31 *Stethomostus fuliginosus* (SCHRK.)
 32 *Eutomostethus luteiventris* (KLUG)
 33 *Periclista albida* (KLUG)
 34 *Claremontia alternipes* (KLUG)
 35 *Claremontia confusa* (KON.)
 36 *Diprion similis* (HART.)
 37 *Gilpinia polytoma* (HART.)
 38 *Gilpinia virens* (KLUG)
 39 *Gilpinia frutetorum* (FABR.)
 40 *Strongylogaster lineata* (CHRIST)
 41 *Strongylogaster macula* (KLUG)
 42 *Strongylogaster mixta* (KLUG)
 43 *Aneugmenus padi* (L.)
 44 *Birka cinereipes* (KLUG)
 45 *Nesoselandria morio* (FABR.)
 46 *Selandria serva* (FABR.)
 47 *Dolerus gessneri* ANDRE
 48 *Aglao stigma fulvipes* (SCOP.)
 49 *Tenthredopsis excisa* (THOMSON)
 50 *Tenthredopsis fresei* (KON.)
 51 *Tenthredopsis litterata* (GEOFF.)
 52 *Tenthredopsis nassata* (L.)
 53 *Tenthredopsis scutellaris* (FABR.)
 54 *Rhogogaster picta* (KLUG)
 55 *Rhogogaster viridis* (L.)
 56 *Tenthredo atra* (L.)
 57 *Tenthredo livida* (L.)
 58 *Tenthredo maculata* (GEOFF.)
 59 *Halidamia affinis* (FALL.)
 60 *Caliroa cinxia* (KLUG)
 61 *Hetererthrus nemoratus* (FALL.)
 62 *Hetererthrus ochropodus* (KLUG)
 63 *Hetererthrus vagans* (FALL.)
 64 *Scolioneura betuleti* (KLUG)
 65 *Messa glaucopsis* (KON.)
 66 *Messa nana* (KLUG)
 67 *Profenusa pygmaea* (KLUG)
 68 *Profenusa thomsoni* (KON.)
 69 *Fenusa dohrnii* (TISCH.)
 70 *Fenusa pusilla* (LEP.)
 71 *Cladius pectinicornis* (GEOFF.)
 72 *Priophorus morio* (LEP.)
 73 *Priophorus pallipes* (LEP.)
 74 *Hoplocampa flava* (L.)
 75 *Hoplocampa testudinea* (KLUG)
 76 *Mesoneura opaca* (FABR.)
 77 *Dineura viridorsata* (RETZ.)
 78 *Hemichroa australis* (LEP.)
 79 *Hemichroa crocea* (GEOFF.)
 80 *Nematinus lutens* (PANZ.)
 81 *Pristiphora cincta* (NEWMAN)
 82 *Pristiphora conjugata* (DHLB.)
 83 *Pristiphora melanocarpa* (HART.)
 84 *Pristiphora pallidiventris* (FALL.)
 85 *Pristiphora ruficornis* (OLIV.)
 86 *Pristiphora subbifida* (THOM.)
 87 *Pristiphora testacea* (JURINE)
 88 *Pristiphora alpestris* (KON.)
 89 *Pristiphora mollis* (HART.)
 90 *Pristiphora abietina* (CHRIST)
 91 *Pristiphora compressa* (HART.)
 92 *Pristiphora decipiens* (ENSL.)
 93 *Pristiphora genula* (KON.)
 94 *Pristiphora leucopodia* (HART.)
 95 *Pristiphora pallida* (KON.)
 96 *Pristiphora pseudodecipiens* (B & K)
 97 *Pristiphora sexesenii* (HART.)
 98 *Pristiphora tenuicornis* (LINDQUIST)
 99 *Pristiphora tenuiserra* (LINDQUIST)
 100 *Sharliphora amphibola* (FOERSTER)
 101 *Sharliphora nigella* (FOERSTER)
 102 *Sharliphora parva* (HART.)
 103 *Pikonema insigne* (HART.)
 104 *Pikonema montanum* (ZADD.)
 105 *Pikonema nigriceps* (HART.)
 106 *Pikonema pallescens* (HART.)
 107 *Pikonema scutellatum* (HART.)
 108 *Croesus septentrionalis* (L.)
 109 *Nematus princeps* (ZADD.)
 110 *Nematus cadderensis* CAM.
 111 *Nematus dispar* BRISCH.
 112 *Nematus umbratus* THOM.
 113 *Nematus viridis* STEPH.
 114 *Euura mucronata* (HART.)
 115 *Potania coriacea* (BENS.)

CURCULIONIDAE

- 1 *Rhinomacer attelaboides* F.
 2 *Doydirhynchus austriacus* (OLIV.)
 3 *Pselaphorhynchites longiceps* (THOMS.)

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|----|---|----|---|
| 4 | <i>Pselaphorhynchites nanus</i> (PAYK.) | 4 | <i>Cryptocephalus punctiger</i> PAYK. |
| 5 | <i>Deporaus betulae</i> (L.) | 5 | <i>Cryptocephalus pusillus</i> FABR. |
| 6 | <i>Deporaus mannerheimi</i> (HUMM.) | 6 | <i>Cryptocephalus saliceti</i> ZEBE |
| 7 | <i>Attelabus nitens</i> (SCOP.) | 7 | <i>Plagioderia versicolora</i> (LAICH.) |
| 8 | <i>Apoderus coryli</i> (L.) | 8 | <i>Chrysomela lapponica</i> L. |
| 9 | <i>Apion curtirostre</i> GERM. | 9 | <i>Phratora atrovirens</i> (CORNEL.) |
| 10 | <i>Apion simile</i> KIRBY | 10 | <i>Phratora laticollis</i> (SUFFR.) |
| 11 | <i>Apion virens</i> HERBST | 11 | <i>Phratora vitellinae</i> (L.) |
| 12 | <i>Apion fulvipes</i> (GEOFFR.) | 12 | <i>Phratora vulgatissima</i> (L.) |
| 13 | <i>Otiorhynchus ovatus</i> (L.) | 13 | <i>Galerucella lineola</i> (FABR.) |
| 14 | <i>Phyllobius arborator</i> (HERBST) | 14 | <i>Galerucella calnariensis</i> (L.) |
| 15 | <i>Polydrusus pallidus</i> (GYLL.) | 15 | <i>Phyllotreta vittula</i> (REDT.) |
| 16 | <i>Polydrusus pilosus</i> GREDL. | 16 | <i>Phyllotreta nemorum</i> (L.) |
| 17 | <i>Brachyderes incanus</i> (L.) | 17 | <i>Phyllotreta undulata</i> KUTSCH.) |
| 18 | <i>Strophosoma capitatum</i> (DEG.) | 18 | <i>Phyllotreta flexuosa</i> (ILL.) |
| 19 | <i>Sitona lineatus</i> (L.) | 19 | <i>Phyllotreta vittata</i> (F.) |
| 20 | <i>Hypera zoilus</i> (SCOP.) | 20 | <i>Aphthona euphorbiae</i> (SCHRANK) |
| 21 | <i>Hypera nigrostris</i> (F.) | 21 | <i>Longitarsus longiseta</i> WEISE |
| 22 | <i>Anthonomus phyllocola</i> (HERBST) | 22 | <i>Longitarsus nasturtii</i> (F.) |
| 23 | <i>Brachonyx pineti</i> (PAYK.) | 23 | <i>Longitarsus parvulus</i> (PAYK.) |
| 24 | <i>Curculio rubidus</i> GYLL. | 24 | <i>Altica quercetorum</i> FOUDR. |
| 25 | <i>Curculio pyrrhoceras</i> MARSH. | 25 | <i>Asiorestia ferruginea</i> (SCOP.) |
| 26 | <i>Magdalis exarata</i> (BRIS.) | 26 | <i>Chaetocnema heikertingeri</i> LJUB. |
| 27 | <i>Magdalis phlegmatica</i> (HERBST) | 27 | <i>Chaetocnema hortensis</i> (GEOFFR.) |
| 28 | <i>Magdalis nitida</i> (GYLL.) | | |
| 29 | <i>Magdalis linearis</i> (GYLL.) | | |
| 30 | <i>Magdalis violacea</i> (L.) | | |
| 31 | <i>Magdalis duplicata</i> GERM. | | |
| 32 | <i>Hyllobius abietis</i> (L.) | | |
| 33 | <i>Pelenomus quadricorniger</i> (COLONN.) | | |
| 34 | <i>Rhinoncusbruchoides</i> (HERBST) | | |
| 35 | <i>Rhinoncus castor</i> (F.) | | |
| 36 | <i>Coeliodes rubicundus</i> (HERBST) | | |
| 37 | <i>Ceutorhynchus pleurostigma</i> (MRSH.) | | |
| 38 | <i>Ceutorhynchus assimilis</i> (PAYK.) | | |
| 39 | <i>Ceutorhynchus erysimi</i> (F.) | | |
| 40 | <i>Ceutorhynchus punctiger</i> (GYLL.) | | |
| 41 | <i>Ceutorhynchus floralis</i> (PAYK.) | | |
| 42 | <i>Anoplus plantaris</i> (NAEZ.) | | |
| 43 | <i>Rhynchaenus avellanae</i> (DONOV.) | | |
| 44 | <i>Rhynchaenus rusici</i> (HERBST) | | |
| 45 | <i>Rhynchaenus stigma</i> (GERM.) | | |
| 46 | <i>Rhamphus pulicarius</i> (HERBST) | | |

CHRYDOMELIDAE

- 1 *Cryptocephalus flavipes* FABR.
- 2 *Cryptocephalus parvulus* MUELL.
- 3 *Cryptocephalus pini* (LINN.)

LEPIDOPTERA

Tortricidae

- 1 *Acleris laterana* (F.)
- 2 *Acleris sparsana* (DEN. et SCHIFF.)
- 3 *Acleris maccana* (TREIT.)
- 4 *Eana incanana* (STEPH.)
- 5 *Cnephasia communana* (H.-S.)
- 6 *Cnephasia stephensia* (DOUBL.)
- 7 *Cnephasia asseclana* (DEN. et SCHIFF.)
- 8 *Cnephasia genitalana* (PIERCE et MECT.)
- 9 *Capua vulgana* FROL.
- 10 *Ramapesia gnomana* (CLERCK)
- 11 *Argyrotaenia ljugiana* (THNBG.)
- 12 *Archips oporanus* (L.)
- 13 *Archips xylosteanus* (L.)
- 14 *Archips rosanus* (L.)
- 15 *Choristoneura diversana* (HBN.)
- 16 *Ptycholoma lecheana* (L.)
- 17 *Pandemis cerasana* (HBN.)
- 18 *Syndemis musculana* (HBN.)
- 19 *Adoxophys orana* (F. v. R.)
- 20 *Hedya atropunctana* (ZETT.)
- 21 *Cymolomia hartigiana* (SAX.)

- 22 *Orthotaenia undulana* (DEN. et SCHIFF.)
 23 *Pseudohermenias abietana* (FABR.)
 24 *Apotomis turbidana* (HBN.)
 25 *Apotomis betuletana* (HAW.)
 26 *Olethreutes bifasciana* (HAW.)
 27 *Olethreutes lacunana* (DEN. et SCHIFF.)
 28 *Ancylis laetana* (F.)
 29 *Ancylis upupana* (TREIT.)
 30 *Ancylis badiana* (DEN. et SCHIFF.)
 31 *Ancylis unculana* (HAW.)
 32 *Ancylis apicella* (DEN. et SCHIFF.)
 33 *Epinotia solandriana* (L.)
 34 *Epinotia tenerana* (DEN. et SCHIFF.)
 35 *Epinotia tedella* (CLERCK)
 36 *Rhopobota naevana* (HBN.)
 37 *Spilonota ocellana* (DEN. et SCHIFF.)
 38 *Blastesthia turionella* (L.)
 39 *Rhyacionia buoliana* (DEN. et SCHIFF.)
 40 *Rhyacionia pinicolana* (DOUBL.)
 41 *Rhyacionia pinivorana* (LIEN. et ZELL.)
 42 *Rhyacionia duplana* (HBN.)
 43 *Retinia resinella* (L.)
 44 *Pammene obscurana* (STEPH.)
 45 *Pammene argyrana* (HBN.)
 46 *Cydia cosmophorana* (TREIT.)
 47 *Cydia coniferana* (SAX.)
 Choreutidae
 48 *Anthophila fabriciana* (L.)
 Pyalidae
 49 *Assara terebrella* (ZINCK.)
 50 *Crambus lathoniellus* (ZINCK.)
 51 *Crambus ericellus* (HBN.)
 52 *Crambus heringiellus* (H.-S.)
 53 *Agriphila inquinatella* (DEN. et SCHIFF.)
 54 *Catoptria margaritella* (DEN. et SCHIFF.)
 55 *Scoparia basistrigalis* KNAGGS
 56 *Eudonia truncicolella* (ST.)
 57 *Eurrhynchus pollinalis* (DEN. et SCHIFF.)
 58 *Udea lutealis* (HBN.)
 Zygenidae
 59 *Adscita statice* (L.)
 Pieridae
 60 *Pieris napi* (L.)
 61 *Pieris brassicae* (L.)
 62 *Gonepteryx rhamni* (L.)
 Lycaenidae
 63 *Quercusia quercus* (L.)
 64 *Callophrys rubi* (L.)
- 65 *Lycaena virgaureae* (L.)
 66 *Lycaena tityrus* (PODA)
 67 *Plebejus argus* (L.)
 Nymphalidae
 68 *Nymphalis polychloros* (L.)
 69 *Inachis io* (L.)
 70 *Aglais urticae* (L.)
 71 *Araschnia levana* (L.)
 72 *Issoria lathonia* (L.)
 73 *Boloria dia* (L.)
 74 *Boloria euphrosyne* (L.)
 75 *Melitaea athalia* (ROTT.)
 Satyridae
 76 *Aphantopus hyperantus* (L.)
 77 *Coenonympha pamphilus* (L.)
 78 *Coenonympha arcania* (L.)
 79 *Pararge aegeria* (L.)
 Thyatiridae
 80 *Thyatira batis* (L.)
 81 *Tethea or* (DEN. et SCHIFF.)
 82 *Tetheella fluctuosa* (HBN.)
 Geometridae
 83 *Jodis putata* (L.)
 84 *Cyclophora punctaria* (L.)
 85 *Scopula nigropunctata* (HUFN.)
 86 *Scopula floslactata* (HAW.)
 87 *Idaea straminata* (BORKH.)
 88 *Xanthorrhoe spadiceraria* (DEN. et SCHIFF.)
 89 *Xanthorrhoe quadrifasciata* (CLERCK)
 90 *Xanthorrhoe montanata* (DEN. et SCHIFF.)
 91 *Chloroclysta citrata* (L.)
 92 *Chloroclysta truncata* (HUFN.)
 93 *Thara obeliscata* (HBN.)
 94 *Thera variata* (DEN. et SCHIFF.)
 95 *Thera juniperata* (L.)
 96 *Electrophaes corylata* (THNBG.)
 97 *Hydriomena furcata* (THNBG.)
 98 *Rheumaptera undulata* (L.)
 99 *Euphyia unangulata* (HAW.)
 100 *Epirrita autumnata* (BORKH.)
 101 *Perizoma alchemillata* (L.)
 102 *Perizoma hydrata* (TREIT.)
 103 *Eupithecia plumbeolata* (HAW.)
 104 *Eupithecia venosata* (FABR.)
 105 *Eupithecia intricata* (ZETT.)
 106 *Eupithecia subfuscata* (HAW.)
 107 *Eupithecia indigata* (HBN.)
 108 *Eupithecia pusillata* (DEN. et SCHIFF.)

- 109 *Eupithecia tantillaria* (BSDV.)
 110 *Chloroclystis debiliata* (HBN.)
 111 *Semiothisa liturata* (CLERCK)
 112 *Alcis repandata* (L.)
 113 *Ematurga atomaria* (L.)
 114 *Bupalus piniarius* (L.)
 115 *Hylaea fasciaria* (L.)
 116 *Gnophos obscurata* (DEN. et SCHIFF.)
 Notodontidae
 117 *Drymonia obliterata* (ESP.)
 118 *Ptilodon capucina* (L.)
 Lymantriidae
 119 *Lymantria monacha* (L.)
 Arctiidae
 120 *Eilema deplana* (ESP.)
 Hermintiidae
 121 *Herminia strigillata* (L.)
 Noctuidae
 122 *Rivula sericealis* (SCOP.)
 123 *Hypena crassalis* (F.)
 124 *Hypena proboscidalis* (L.)
 125 *Catocala fraxini* (L.)
 126 *Catocala sponsa* (L.)
 127 *Laspeyria flexula* (DEN. et SCHIFF.)
 128 *Protodeltote pygarga* (HUFN.)
 129 *Autographa gamma* (L.)
 130 *Acronicta aceris* (L.)
 131 *Amphipyra pyramidea* (L.)
 132 *Dypterygia scabriuscula* (L.)
 133 *Trachea atriplicis* (L.)
 134 *Euplexia lucipara* (L.)
 135 *Enargia paleacea* (ESP.)
 136 *Apamea crenata* (HUFN.)
 137 *Apamea remissa* (HBN.)
 138 *Oligia strigilis* (L.)
 139 *Oligia latruncula* (DEN. et SCHIFF.)
 140 *Mesoligia furuncula* (DEN. et SCHIFF.)
 141 *Mesapamea secalis* (L.)
 142 *Celaena leucostigma* (HBN.)
 143 *Archanara geminipuncta* (HAW.)
 144 *Lithophane furcifera* (HUFN.)
 145 *Conistra vaccinii* (L.)
 146 *Agrochola helvola* (L.)
 147 *Polia bombycina* (HUFN.)
 148 *Polia tincta* (BRAHM)
 149 *Polia nebulosa* (HUFN.)
 150 *Mamestra brassicae* (L.)
 151 *Melanchra persicariae* (L.)
 152 *Lacanobia thalassina* (HUFN.)
 153 *Lacanobia suasa* (DEN. et SCHIFF.)
 154 *Orthosia incerta* (HUFN.)
 155 *Mythimna albipunctata* (DEN. et SCHIFF.)
 156 *Mythimna pallens* (L.)
 157 *Euxoa nigricans* (L.)
 158 *Agrostis ipsilon* (HUFN.)
 159 *Eugraphe subrosea* (STEPH.)
 160 *Diarsia brunnea* (DEN. et SCHIFF.)
 161 *Xestia c-nigrum* (L.)
 162 *Xestia baja* (DEN. et SCHIFF.)
 163 *Eurois occulta* (L.)
 164 *Anaplectoides prasina* (DEN. et SCHIFF.)
- SCOLYTIDAE**
- 1 *Hylurgops palliatus* (GYLL.)
 2 *Hylastes ater* (PAYK.)
 3 *Hylastes opacus* ER.
 4 *Hylurgus lignipetra* (FABR.)
 5 *Tomicus minor* (HART.)
 6 *Tomicus piniperda* (L.)
 7 *Pityogenes bidentatus* (HERBST)
 8 *Pityogenes chalcographus* (L.)
 9 *Pityogenes quadridens* (HART.)
 10 *Pityogenes trepanatus* (NORDL.)
 11 *Orthotomicus laricis* (F.)
 12 *Orthotomicus proximus* (EICHH.)
 13 *Orthotomicus suturalis* (GYLL.)
 14 *Ips acuminatus* (EICHH.)
 15 *Ips sexdentatus* (BORN.)
 16 *Dryocoetes autographus* (RATZ.)
 17 *Crypturgus cinereus* (HERBST)
 18 *Crypturgus hispidulus* (THOMS.)
 19 *Crypturgus pusillus* (GYLL.)
 20 *Trypodendron lineatum* (OLIV.)
 21 *Pityophthorus lichtensteini* (RATZ.)
 22 *Pityophthorus pityographus* (RATZ.)
- CERAMBYCIDAE**
- 1 *Prionus coriarius* (L.)
 2 *Tetropium castaneum* (L.)
 3 *Tetropium fuscum* (F.)
 4 *Spondylis buprestoides* (L.)
 5 *Arhopalus rusticus* (L.)
 6 *Asemum striatum* (L.)
 7 *Molorchus minor* (L.)
 8 *Callidium aeneum* (DE GEER)
 9 *Callidium violaceum* (L.)

- 10 *Callidium coriaceum* PAYK.
- 11 *Rhagium mordax* (DE GEER)
- 12 *Rhagium inquisitor* (L.)
- 13 *Pachyta quadrimaculata* (L.)
- 14 *Cortodera femorata* (FABR.)
- 15 *Pedostrangalia pubescens* (FABR.)
- 16 *Leptura quadrifasciata* (L.)
- 17 *Anastrangalia sanguinolenta* (L.)
- 18 *Corymbia rubra* (L.)
- 19 *Brachyleptura maculicornis* (DE GEER)
- 20 *Judolia sexmaculata* (L.)
- 21 *Alosterna tabacicolor* (DE GEER)
- 22 *Strangalia attenuata* (L.)
- 23 *Stenurella melanura* (L.)
- 24 *Stenurella nigra* (L.)
- 25 *Monochamus galloprovincialis* (OLIV.)
- 26 *Monochamus sutor* (L.)
- 27 *Monochamus urussovi* (FISCH.)
- 28 *Pogonocherus fasciculatus* (DE GEER)
- 29 *Pogonocherus decoratus* (FAIRM.)
- 30 *Acanthocinus griseus* (FABR.)
- 31 *Acanthocinus aedilis* (L.)
- 32 *Leiopus nebulosus* (L.)
- 33 *Saperda populnea* (L.)

BUPRESTIDAE

- 1 *Chalcophora mariana* (L.)
- 2 *Buprestis haemorrhoidalis* HERBST
- 3 *Buprestis novemmaculata* (L.)
- 4 *Buprestis octoguttata* (L.)
- 5 *Buprestis rustica* (L.)
- 6 *Phaenops cyanea* FABR.
- 7 *Anthaxia quadripunctata* (L.)
- 8 *Anthaxia similis* (SAUND)
- 9 *Anthaxia submontana* (OBENB.)
- 10 *Agrilus angustulus* (ILL.)
- 11 *Agrilus sulcicollis* (LACORD.)
- 12 *Trachys minuta* (L.)

ASILIDAE

- 1 *Choerades fimbriata* (MG.)
- 2 *Dioctria humeralis* (ZELL.)
- 3 *Dioctria hyalipennis* (F.)
- 4 *Dioctria oelandica* (L.)
- 5 *Lasiopogon cinctus* (F.)
- 6 *Lasiopogon immaculatus* STR.
- 7 *Cyrtopogon lateralis* (FLL.)
- 8 *Leptogaster pubicornis* (LW.)

- 9 *Dysmachus cochleatus* (LW.)
- 10 *Dysmachus picipes* (MG.)
- 11 *Dysmachus trigonus* (MG.)
- 12 *Epitriptus arthriticus* (ZLL.)
- 13 *Epitriptus cingulatus* (F.)
- 14 *Neoitamus cothurnatus* (MG.)
- 15 *Neoitamus cyanurus* (LW.)
- 16 *Neoitamus socius* (LW.)
- 17 *Neomochtherus pallipes* (MG.)
- 18 *Pamponerus germanicus* (L.)
- 19 *Paritamus geniculatus* (MG.)
- 20 *Tolmerus atricapillus* (FLL.)
- 21 *Tolmerus atripes* LW.
- 22 *Tolmerus pyragra* (ZLL.)

ARANEI

- 1 *Anyphaena accentuata* (WALCK.)
- 2 *Dictyna arundinacea* (L.)
- 3 *Dictyna pusilla* TH.
- 4 *Cicurina cicurea* MG.
- 5 *Arctosa cinerea* (F.)
- 6 *Xerolycosa nemoralis* (WESTR.)
- 7 *Drassodes pubescens* (TH.)
- 8 *Micaria silesiaca* L. K.
- 9 *Phrurolithus festivus* (C.L.K.)
- 10 *Micrommata roseum* (CL.)
- 11 *Clubiona lutescens* WESTR.
- 12 *Euryclubiona stagnatilis* (KUL.)
- 13 *Euryclubiona subsultans* (TH.)
- 14 *Baltus chalybeius* (W.L.K.)
- 15 *Dendryphanthes hastatus* (C.L.)
- 16 *Dendryphanthes rudis* (SUND.)
- 17 *Heliophanus aeneus* (HAHN)
- 18 *Heliophanus dubius* (C.L.K.)
- 19 *Heliophanus flavipes* (HAHN)
- 20 *Marpissa muscosa* CL.
- 21 *Neon reticulatus* (BLACK.)
- 22 *Phlegra v-incignita* (CL.)
- 23 *Pseudicium encarpatus* (WALCK.)
- 24 *Salticus oleari* (SCOP.)
- 25 *Coriarachne depressa* (C.L.K.)
- 26 *Diaea dorsata* (F.)
- 27 *Xysticus cristatus* (CL.)
- 28 *Xysticus lanio* C.L.K.
- 29 *Artanes dispar* (WALCK.)
- 30 *Horodromoides fuscomarginatus* (DE GEER)
- 31 *Philodromus aureolus* (CL.)
- 32 *Philodromus collinus* (C.L.K.)

- 33 *Araneus angulatus* (CL.)
 34 *Araneus diadematus* (CL.)
 35 *Araniella cucurbitina* (CL.)
 36 *Araniella inospicua* (SIM.)
 37 *Atea sturmi* (HAHN)
 38 *Gibbaranea bituberculata* (WALCK.)
 39 *Mangora acalypha* (WALCK.)
 40 *Nuctenea umbratica* (CL.)
 41 *Pachygnatha clercki* SUND.
 42 *Tetragnatha pinicola* K.
 43 *Agyneta rurestris* (C.L.K.)
 44 *Centromerus sylvaticus* (BL.)
 45 *Drapetisca socialis* (SUND.)
 46 *Kaestneria dorsalis* (WID.)
 47 *Leptyphanthes flavipes* (BL.)
 48 *Leptyphanthes obscurus* (BL.)
 49 *Porrhomma convexum* (WESTR.)
 50 *Porrhomma pygmaeum* (BLACK)
 51 *Ceratinella brevis* (WIDER.)
 52 *Diplocephalus hiemalis* F. DAHL.
 53 *Dismodicus cornutus* (BL.)
 54 *Dismodicus elevatus* PETR. nec C.L.K.
 55 *Entelecara congenera* (O.P.-C.)
 56 *Erigone atra* (BL.)
 57 *Erigone dentipalpis* (WIDER.)
 58 *Gongylidiellum compar* (WESTR.)
 59 *Metopobactrus prominulis* (O.P.-C.)
 60 *Moebelia penicillata* (WESTR.)
 61 *Oedothorax gibbosus* (BL.)
 62 *Peponocranium orbiculatum* (O.P.-C.)
 63 *Savignya frontata* BL.
 64 *Tapinocyba pallens* (O.P.-C.)
 65 *Trematocephalus cristatus* (WID.)
 66 *Crustulina guttata* (WID.)
 67 *Dipoenia tristis* (HAHN)
 68 *Enoplognatha ovata* (CL.)
 69 *Neottiura bimaculata* (L.)
 70 *Theridion mystaceum* (L.K.)
 71 *Theridion pictum* (WALCK.)
 72 *Theridion pinastris* (L.K.)
 73 *Theridion sisyphium* (CL.)
 74 *Theridion tinctum* (WALCK.)
 75 *Theridion varians* HAHN.
- 3 *Ammophila luffi* SAUND.
 4 *Ammophila pubescens* CURT.
 5 *Ammophila sabulosa* (L.)
 6 *Mimumesa unicolor* LIND.
 7 *Psenulus concolor* (DAHLB.)
 8 *Psenulus fuscipennis* (DAHLB.) *
 9 *Psenulus laevigatus* (SCHUCK.)
 10 *Psenulus pallipes* (PANZ.) *
 11 *Pemphredon balticus* (MERISUO) *
 12 *Pemphredon lethifer* (SCHUCK.) *
 13 *Pemphredon lugubris* (F.) *
 14 *Pemphredon morio* LIND. *
 15 *Pemphredon shuckardi* (A. MOR.) *
 16 *Passaloeus borealis* DAHLB. *
 17 *Passaloeus brevilabris* *
 18 *Passaloeus clypealis* FAEST. *
 19 *Passaloeus corniger* SHUCK. *
 20 *Passaloeus eremita* KOHL. *
 21 *Passaloeus gracilis* (CURT.) *
 22 *Passaloeus insignis* (LIND.) *
 23 *Passaloeus monilicornis* DAHLB. *
 24 *Passaloeus singularis* DAHLB. *
 25 *Passaloeus turionum* DAHLB. *
 26 *Spilomena beata* BLUTHG.
 27 *Spilomena differens* BLUTHG.
 28 *Spilomena punctatissima* BLUTHG.
 29 *Spilomena troglodytes* (LIND.)
 30 *Spilomena vagans* BLUTHG.
 31 *Tachysphex obscuripennis* (SCHENC.)
 32 *Tachysphex pompiliformis* (PANZ.)
 33 *Tachysphex psammobius* (KOHL.)
 34 *Nitela spinolae* LATR. *
 35 *Trypoxylon attenuatum* SMITH
 36 *Trypoxylon clavicerum* LEP. et SERV.
 37 *Trypoxylon figulus* (L.)
 38 *Trypoxylon medium* BEAUMONT
 39 *Trypoxylon minus* BEAUMONT
 40 *Entomognathus brevis* (LIND.)
 41 *Lindentius albilabris* (F.)
 42 *Lindentius panzeri* (LIND.) *
 43 *Rhopalum clavipes* (L.) *
 44 *Rhopalum coarctatum* (SCOP.)
 45 *Crossocerus annulipes* (LEP. et BRUL.)
 46 *Crossocerus barbipes* (DAHLB.)
 47 *Crossocerus cetratus* SHUCK. *
 48 *Crossocerus dimidiatus* (F.)
 49 *Crossocerus inermis* THOMS.
 50 *Crossocerus megacephalus* (ROS.)

SPHECIDAE

(* gatunki afidofagiczne)

- 1 *Podalonia affinis* KIRBY
 2 *Ammophila campestris* LATR.

- 51 *Crossocerus nigrilus* (LEP. et BRUL.)
 52 *Crossocerus ovalis* (LEP. et BRUL.)
 53 *Crossocerus palmipes* (L.)
 54 *Crossocerus pusillus* LEP. et BRUL.
 55 *Crossocerus quadrimaculatus* (F.)
 56 *Crossocerus styrius* (KOH.)
 57 *Crossocerus walkeri* (SHUCK.)
 58 *Crossocerus wesmaeli* (LIND.) *
 59 *Crabro cribrarius* (L.)
 60 *Crabro peltarius* (SCHREB.)
 61 *Crabro scutellatus* (SCHEV.)
 62 *Ectemnius cavifrons* (THOMS.)
 63 *Ectemnius cephalotes* (OLIV.)
 64 *Ectemnius continuus* (F.)
 65 *Ectemnius lapidarius* (PANZ.)
 66 *Ectemnius ruficornis* (ZETT.)
 67 *Ectemnius sexcinctus* (F.)
 68 *Lestica clypeata* (SCHREB.)
 69 *Lestica subterranea* (F.)
 70 *Mellinus arvensis* (L.)
 71 *Nysson niger* CHEVR.
 72 *Nysson spinosus* (J. FORST.)
 73 *Nysson trimaculatus* (ROSSI)
 74 *Alysson fuscatus* (PANZ.)
 75 *Argogorytes mystaceus* (L.)
 76 *Cerceris arenaria* (L.)
 77 *Cerceris quadrijasciata* (PANZ.)

COCCINELLIDAE

- 1 *Scymnus haemorrhoidalis* HERBST
 2 *Scymnus suturalis* THUNB.
 3 *Scymnus nigrinus* KUGEL.
 4 *Exochomus quadripustulatus* (L.)
 5 *Aphidecta obliterated* (L.)
 6 *Adalia conglomerata* (L.)
 7 *Adalia decempunctata* (L.)
 8 *Coccinella septempunctat* (L.)
 9 *Harmonia quadripunctata* (PONT.)
 10 *Myrrha octodecimpunctata* (L.)
 11 *Calvia decempunctata* (L.)
 12 *Calvia quatuordecimpunctata* (L.)
 13 *Mysia oblogoguttata* (L.)
 14 *Anatis ocellata* (L.)

CANTHARIDAE

- 1 *Cantharis decipiens* BAUDI
 2 *Cantharis flavilabris* FALL.
 3 *Cantharis livida rufipes* HERBST

- 4 *Cantharis nigricans* (O. F. MULL.)
 5 *Cantharis obscura* L.
 6 *Cantharis pellucida* F.
 7 *Cantharis rufa* L.
 8 *Cantharis rustica* FALL.
 9 *Rhagonycha atra* (L.)
 10 *Rhagonycha elongata* (FALL.)
 11 *Rhagonycha fulva* (SCOP.)
 12 *Rhagonycha lignosa* (O.F. MULL.)
 13 *Rhagonycha limbata* THOMS.
 14 *Silis nitidula* (F.)
 15 *Malthinus biguttatus* (L.)
 16 *Malthinus facialis* THOMS.
 17 *Malthinus frontalis* (MARSH.)
 18 *Malthinus punctatus* (FOURCR.)
 19 *Malthodes brevicollis* (PAYK.)
 20 *Malthodes crassicornis* (MAEKL.)
 21 *Malthodes guttifer* KIESENW.
 22 *Malthodes mysticus* KIESENW.
 23 *Malthodes pumilus* (BREB.)

SYRPHIDAE

(* gatunki zoofagiczne)

- 1 *Eristalis arbustorum* (L.)
 2 *Eristalis tenax* (L.)
 3 *Eristalis rupium* F.
 4 *Eristalis nemorum* (L.)
 5 *Eristalis horticola* (DEG.)
 6 *Eristalinus sepulchralis* (L.)
 7 *Myathropa florea* (L.)
 8 *Helophilus pendulus* (L.)
 9 *Helophilus hybridus* LOEW
 10 *Helophilus parallelus* HARR.
 11 *Helophilus affinis* WHALB.
 12 *Helophilus lineatus* (F.)
 13 *Parhelophilus versicolor* (F.)
 14 *Helophilus lunulatus* MEIG.
 15 *Parhelophilus frutetorum* (F.)
 16 *Lathyrrophthalmus aeneus* (SCOP.)
 17 *Eumerus strigatus* (FALL.)
 18 *Temnostoma bombylans* (F.)
 19 *Temnostoma vespiforme* (L.)
 20 *Temnostoma apiforme* (F.)
 21 *Xylota segnis* (L.)
 22 *Xylota tarda* MEIG.
 23 *Chalcosyrphus piger* (F.)
 24 *Xylota femorata* (L.)
 25 *Xylota sylvarum* (L.)

- 26 *Xylota abiens* MEIG.
 27 *Xylota florum* (F.)
 28 *Chalcosyrphus nemorum* (F.)
 29 *Xylota ignava* (PANZ.)
 30 *Syritta pipiens* (L.)
 31 *Lejota ruficornis* (ZETT.)
 32 *Triglyphus primus* LOEW *
 33 *Pipizella varipes* (MEIG.) *
 34 *Neocnemodon fulvimanus* (ZETT.) *
 35 *Neocnemodon vitripennis* (MEIG.) *
 36 *Pipiza quadrimaculata* (PANZ.) *
 37 *Cheilosia pagana* (MEIG.)
 38 *Cheilosia ruralis* (MEIG.)
 39 *Cheilosia vernalis* (FALL.)
 40 *Cheilosia chloris* (MEIG.)
 41 *Orthoneura nobilis* (FALL.)
 42 *Orthoneura geniculata* MEIG.
 43 *Orthoneura intermedia* LUNDB.
 44 *Orthoneura frontalis* LOEW
 45 *Chrysogaster viduata* (L.)
 46 *Didea intermedia* LOEW *
 47 *Didea fasciata* MACQ. *
 48 *Didea alneti* (FALL.) *
 49 *Scaeva pyrastris* (L.) *
 50 *Scaeva selenitica* (MEIG.) *
 51 *Dasysyrphus albostrigatus* (FALL.) *
 52 *Dasysyrphus venustus* (MEIG.) *
 53 *Syrphus torvus* O.-S. *
 54 *Episyrphus balteatus* (DEG.) *
 55 *Metasyrphus corollae* (F.) *
 56 *Syrphus vitripennis* MEIG. *
 57 *Syrphus ribesii* (L.) *
 58 *Parasyrphus lineolus* (ZETT.) *
 59 *Meligramma cincta* (FALL.) *
 60 *Meliscaeva cinctella* (ZETT.) *
 61 *Metasyrphus latifasciatus* (MACQ.) *
 62 *Meligramma guttata* (FALL.) *
 63 *Dasysyrphus tricinctus* (FALL.) *
 64 *Epistrophe eligans* HARR. *
 65 *Melanostoma mellinum* (L.) *
 66 *Melanostoma scalare* (F.) *
 67 *Sphaerophoria scripta* (L.) *
 68 *Sphaerophoria menthastris* (L.) *
 69 *Sphaerophoria philanthri* MEIG. *
 70 *Xanthogramma citrofasciatum* (DEG.) *
 71 *Platycheirus albimanus* (F.) *
 72 *Platycheirus peltatus* (MEIG.) *
 73 *Platycheirus clypeatus* (MEIG.) *
 74 *Xanthandrus comtus* (HARR.) *
 75 *Melangyna quadrimaculata* (VERR.) *
 76 *Baccha elongata* (F.) *
 77 *Baccha obscuripennis* MEIG. *
 78 *Neoascia dispar* (MEIG.)
 79 *Neoascia aenea* (MEIG.)
 80 *Neoascia floralis* (MEIG.)
 81 *Neoascia geniculata* (MEIG.)
 82 *Chrysotoxum vernale* LOEW *
 83 *Chrysotoxum festivum* (L.) *
 84 *Chrysotoxum elegans* LOEW *
 85 *Chrysotoxum octomaculatum* CURT. *
 86 *Brachyopa panzeri* GOFFE
 87 *Brachyopa scutellaris* ROB.-DESV.
 88 *Microdon devius* (L.)
 89 *Blera fallax* (L.)
 90 *Sericomyia lappona* (L.)
 91 *Sericomyia silentis* HARR.
- NEUROPTEROIDEA
- 1 *Raphidia ophiopsis ophiopsis* L.
 2 *Raphidia notata* F.
 3 *Raphidia xanthostigma* SCHUMM.
 4 *Inocellia crassicornis* (SCHUMM.)
 5 *Coniopteryx parthenia* (NAV. et MARC.)
 6 *Conventzia pineticola* END.
 7 *Wesmaelius concinnus* (STEPH.)
 8 *Wesmaelius nervosus* (F.)
 9 *Wesmaelius mortoni* (MC LACHL.)
 10 *Hemerobius humulinus* L.
 11 *Hemerobius stigma* STEPH.
 12 *Hemerobius pini* STEPH.
 13 *Hemerobius fenestratus* TJED.
 14 *Hemerobius nitidulus* F.
 15 *Hemerobius micans* OLIV.
 16 *Symphorobius fuscescens* (WALL.)
 17 *Nineta vittata* (WESM.)
 18 *Chrysopa perla* (L.)
 19 *Chrysopa septempunctata* WESM.
 20 *Mallada prasinus* (BURM.)
 21 *Mallada ventralis* (CURT.)
 22 *Chrysoperla carnea* (STEPH.)
 23 *Cunctochrysa albolineata* (KILL.)
- TACHINIDAE
- 1 *Acemyia rufitibia* (VON ROSER)
 2 *Actia crassicornis* (MEIG.)
 3 *Actia nudibasis* (STEIN)

- 4 *Actia pilipennis* (FALL.)
 5 *Admontia blanda* (FALL.)
 6 *Admontia podomyia* (B. & B.)
 7 *Aplomyia confinis* (FALL.)
 8 *Appendicia truncata* (ZETT.)
 9 *Athrycia curvinervis* (ZETT.)
 10 *Athrycia trepida* (MEIG.)
 11 *Bactromyia aurulenta* (MEIG.)
 12 *Bessa parallela* (MEIG.)
 13 *Bessa selecta* (MEIG.)
 14 *Blepharomyia angustifrons* HERT.
 15 *Blepharomyia pagana* (MEIG.)
 16 *Blepharomyia piliceps* (ZETT.)
 17 *Blondelia nigripes* (FALL.)
 18 *Bothria subalpina* VILL.
 19 *Brachychaeta stigata* (HEIG.)
 20 *Campylochaeta inepta* (MEIG.)
 21 *Carcelia* (C.) *bombylans* R.-D.
 22 *Carcelia* (C.) *gnava* (MEIG.)
 23 *Carcelia* (C.) *rasa* (MACQ.)
 24 *Carcelia* (Euryclea) *tibialis* (R.-D.)
 25 *Caracelina stackelbergi* (MESN.)
 26 *Ceranthia abdominalis* (R.-D.)
 27 *Ceranthia lichtwardtiana* (VILL.)
 28 *Ceranthia pallida* HERT.
 29 *Ceromyia monstrosicornis* (STEIN)
 30 *Ceromyia silacea* (MEIG.)
 31 *Cylindromyia brassicaria* (FABR.)
 32 *Cylindromyia pilipes* (LOEW)
 33 *Cyzenis albicans* (FALL.)
 34 *Cyzenis jucunda* (MEIG.)
 35 *Chaetoptilia puella* (ROND.)
 36 *Compsilura concinnata* (MEIG.)
 37 *Dexiosoma canina* (FABR.)
 38 *Dinera ferina* (FALL.)
 39 *Drino bohémica* MESN.
 40 *Drino inconspicua* (MEIG.)
 41 *Elfta cingulata* (R.-D.)
 42 *Elfta nigroaenea* HERT.
 43 *Eloceria delecta* (MEIG.)
 44 *Entomophaga nigrohalterata* (VILL.)
 45 *Eriothrix accolus* KOL.
 46 *Eriothrix monochaeta* WAINWR.
 47 *Eriothrix rufomaculata* (DE GEER)
 48 *Ernestia rudis* (FALL.)
 49 *Ernestia vagans* (MEIG.)
 50 *Erycilla ferruginea* (MEIG.)
 51 *Eurithia connivens* (ZETT.)
 52 *Eurithia consobrina* (MEIG.)
 53 *Eurithia juncta* (ZIM.)
 54 *Eumea linnearicornis* (ZETT.)
 55 *Eurysthaea scutellaris* (R.-D.)
 56 *Hebia flavicornis* R.-D.
 57 *Hemydia vittata* (MEIG.)
 58 *Huebneria affinis* (FALL.)
 59 *Linnaemyia tessellans* (R.-D.)
 60 *Loewia foeda* (MEIG.)
 61 *Loewia phaeoptera* (MEIG.)
 62 *Lydina aenea* (MEIG.)
 63 *Lydella stabularis* (MEIG.)
 64 *Lypha dubia* (FALL.)
 65 *Macquartia grisea* (FALL.)
 66 *Macquartia tenebricosa* (MEIG.)
 67 *Masicera silvatica* (FALL.)
 68 *Medina collaris* (FALL.)
 69 *Medina luctuosa* (MEIG.)
 70 *Medina melania* (MEIG.)
 71 *Medina multispina* HERT.
 72 *Medina separata* (MEIG.)
 73 *Meigenia incana* (FALL.)
 74 *Myxeristops blondelli* (R.-D.)
 75 *Ocytata pallipes* (FALL.)
 76 *Oswaldia eggeri* (B. & B.)
 77 *Oswaldia muscaria* (FALL.)
 78 *Parasetigena silvestris* (R.-D.)
 79 *Parathryphera barbatula* (ROND.)
 80 *Peletachina tibialis* (FALL.)
 81 *Peribaea fissicornis* (STROBL)
 82 *Peribaea apicalis* R.-D.
 83 *Phorinia aurifrons* R.-D.
 84 *Phryxe erythrostoma* (HART.)
 85 *Phryxe magnicornis* (ZETT.)
 86 *Phryxe nemea* (MEIG.)
 87 *Platymyia fimbriata* (MEIG.)
 88 *Platymyia mitis* (MEIG.)
 89 *Prosopea nigricans* (EGG.)
 90 *Pseudopachystylum gonioides* (ZETT.)
 91 *Pseudoperichaeta nigrolineata* (WALK.)
 92 *Pales pumicata* (MEIG.)
 93 *Phebellia glauca* (MEIG.)
 94 *Phorocera obscura* (FALL.)
 95 *Rondania fasciata* (MACQ.)
 96 *Senometopia excisa* (FALL.)
 97 *Siphona flavifrons* STAEG.
 98 *Siphona confusa* MESN.
 99 *Siphona cristata* (FABR.)

- 100 *Siphona maculata* STAEG.
 101 *Siphona rossica* MESN.
 102 *Siphona setosa* MESN.
 103 *Smidtia conspersa* (MEIG.)
 104 *Tachina magnicornis* (ZETT.)
 105 *Thelaira nigripes* (FABR.)
 106 *Timavia amoena* (MEIG.)
 107 *Triarthria setipennis* (FALL.)
 108 *Vibrissina turrata* (MEIG.)
 109 *Voria ruralis* (FALL.)
 110 *Winthemia cruentata* (ROND.)
 111 *Winthemia variegata* (MEIG.)
- PIPUNCULIDAE
- 1 *Nephrocerus scutellatus* (MACG.)
 2 *Chalarus fimbriatus* COE
 3 *Verrallia villosa* (V. ROSER)
 4 *Eudorylas subfascipes* COLL.
 5 *Tomosvariella sylvatica* (MG.)
 6 *Pipunculus zugmeyerie* KOW.
 7 *Pipunculus spinipes* MG.
 8 *Cephalops semifumosus* (KOW.)
 9 *Cephalops aeneus* FALL.
- ICHNEUMONIDAE
- Protichneumonini
- 1 *Coelichneumon deliratorius* (L.)
 2 *Coelichneumon desinatorius* (THUMB.)
 3 *Coelichneumon falsificus* (WESM.)
 4 *Coelichneumon fasciatus* (GMEL.)
 5 *Coelichneumon sugillatorius* (L.)
- Heresiarchini
- 6 *Heresiarches eudoxius* (WESM.)
- Listrodonini
- 7 *Anisobas platystylus* (THOMS.)
- Acanthojoppini
- 8 *Pseudoplatybalus uniguttatus* (GRAV.)
 9 *Pseudoplatybalus violentus* (GRAV.)
- Ichneumonini
- 10 *Stenichneumon culpator* (SCHRANK)
 11 *Sypsasis alboguttatus* (GRAV.)
 12 *Sypsasis eburnifrons* (WESM.)
 13 *Sypsasis scutellartor* (GRAV.)
 14 *Stenoaopius pictus* (GRAV.)
 15 *Aoplus defraudator* (WESM.)
 16 *Aoplus ochropis* (GMEL.)
 17 *Platylobops virginialis* (WESM.)
 18 *Stenobarichneumon basalis* (PERK.)
- 19 *Lymantrichneumon dispar* (PODA)
 20 *Cratichneumon culex* (MULL.)
 21 *Cratichneumon fabricator* (F.)
 22 *Cratichneumon palliditarsus* (THOMS.)
 23 *Cratichneumon punctifrons* (GRAV.)
 24 *Cratichneumon rufifrons* (GRAV.)
 25 *Cratichneumon sicarius* (GRAV.)
 26 *Cratichneumon versator* (THUMB.)
 27 *Cratichneumon viator* (SCOP.)
 28 *Eupalamus lacteator* (GRAV.)
 29 *Eupalamus oscillator* (WESM.)
 30 *Eupalamus wesmaeli* (THOMS.)
 31 *Crypteffigies lanius* (GRAV.)
 32 *Homotherus locutor* (THUMB.)
 33 *Homotherus varipes* (GRAV.)
 34 *Eristicus clarigator* (WESM.)
 35 *Vulgichneumon bimaculatus* (SCHRANK.)
 36 *Vulgichneumon deceptor* (SCOP.)
 37 *Vulgichneumon saturatorius* (L.)
 38 *Virgichneumon ? albosignatus* (GRAV.)
 39 *Virgichneumon diagrammus* (GRAV.)
 40 *Virgichneumon dumeticola* (GRAV.)
 41 *Virgichneumon extremator* (THUMB.)
 42 *Virgichneumon faunus* (GRAV.)
 43 *Virgichneumon maculicauda* (PERK.)
 44 *Virgichneumon monostagon* (GRAV.)
 45 *Barichneumon praeceptor* (THUMB.)
 46 *Barichneumon ? "perversus* KRIECHB."
 47 *Barichneumon ? plagiaris* (WESM.)
 48 *Chasmias motatorius* (F.)
 49 *Ichneumon albicollis* WESM.
 50 *Ichneumon cessator* MULL.
 51 *Ichneumon extensorius* L.
 52 *Ichneumon grasilentus* WESM.
 53 *Ichneumon insidiosus* WESM.
 54 *Ichneumon latrator* F.
 55 *Ichneumon lugens* GRAV.
 56 *Ichneumon melanotis* HOMGR.
 57 *Ichneumon memorator* WESM.
 58 *Ichneumon minorius* DESV.
 59 *Ichneumon nereni* THOMS.
 60 *Ichneumon sarcitorius* L.
 61 *Ichneumon subquadratus* THOMS.
 62 *Limerodops elongatus* (BRISCHKE)
 63 *Ctenichneumon funereus* (GEOFFR.)
 64 *Ctenichneumon divisorius* (GRAV.)
 65 *Diphyus amatorius* (MULL.)
 66 *Diphyus luctatorius* (L.)

- 67 *Spilothyrates punctus* (GRAV.)
 68 *Spilichneumon ammonius* (GRAV.)
 Platylabini
 69 *Platylabus nigrocyaneus* (GRAV.)
 70 *Poecilosticus cothurnatus* (GRAV.)
 71 *Cyclolabus nigricollis* (WESM.)
 72 *Lincycus exhortator* (F.)
 Phaeogenini
 73 *Eriplatys ardeicollis* (WESM.)
 74 *Eriplatys sawoniewiczzi* (DILLER)
 75 *Hemichneumon elongatus* (RATZ.)
 76 *Trachyarus corvinus* THOMS.
 77 *Stenodontus marginellus* (GRAV.)
 78 *Dicaelotus crassifemur* THOMS.
 79 *Dicaelotus inflexus* THOMS.
 80 *Dicaelotus pumilus* (GRAV.)
 81 *Dicaelotus rufilimbatus* (GRAV.)
 82 *Deloglyptus pictus* SCHMIED.
 83 *Diadromus subtilicornis* (GRAV.)
 84 *Diadromus troglodytes* (GRAV.)
 85 *Colpognathus celerator* (GRAV.)
 86 *Aetheurus discolor* WESM.
 87 *Aetheurus nitidus* WESM.
 88 *Phaeogenes melanogonos* (GMEL.)
 89 *Phaeogenes spiniger* (GRAV.)
 90 *Dirophanes callopus* (WESM.)
 91 *Dirophanes maculicornis* (STEPH.)
 92 *Dirophanes fulvitaris* (WESM.)
 93 *Tycherus amoenus* (WESM.)
 94 *Tycherus clypearis* (BRISCHKE)
 95 *Tycherus coriaceus* (PERK.)
 96 *Tycherus dodecellae* RANIN
 97 *Tycherus cf. jucundus* (WESM.)
 98 *Tycherus ophthalmicus* (WESM.)
 99 *Tycherus osculator* (THUMB.)
 100 *Tycherus vagus* (BERTH.)
 101 *Tycherus verecundus* RANIN
 102 *Epitomus infuscatus* (GRAV.)
 103 *Misetus oculatus* (WESM.)

ENCHYTRAEIDAE

- 1 *Mesenchytraeus pelicensis* ISSEL.
 2 *Mesenchytraeus* sp. EIS.
 3 *Buchholiza simplex* NIEL. et CHRIST.
 4 *Buchholiza* sp. MICH.
 5 *Buchholiza ehlersi* UDE
 6 *Cognettia sphagnetorum* (VEJD.)
 7 *Marionina* sp. MICH.

- 8 *Fridericia ratzeli* EIS.
 9 *Fridericia* sp. MICH.
 10 *Achaeta* sp. VEJD.

COLLEMBOLA

Hypogastruridae

- 1 *Schoetella ununguiculata* (TULLB.)
 2 *Xenylla brevicauda* TULLB.
 3 *Xenylla boernerii* AXEL.
 4 *Willemia anophthalma* BORNER
 5 *Willemia aspinata* STACH
 6 *Hypogastrura* sp. j.

Neanuridae

- 7 *Pseudachorutes parvulus* BORNER
 8 *Microanurida pygmaea* BORNER
 9 *Neanura muscorum* (TEMPL.)

Onychiuridae

- 10 *Oligaphorura absoloni* (BORNER)
 11 *Propaphorura armata* (TULLB.)
 12 *Propaphorura subuliginatus* GISIN
 13 *Propaphorura furcifera* (BORNER)
 14 *Mesaphorura macrochaeta* RUSEK
 15 *Mesaphorura yossi* RUSEK

Isotomidae

- 16 *Anurophorus laricis* STACH
 17 *Anurophorus septentrionalis* PALISSA
 18 *Folsomia quadrioculata* (TULLB.)
 19 *Proisotoma minima* (ABS.)
 20 *Isotomiella minor* (SCHAFF.)
 21 *Isotoma notabilis* SCHAFF.
 22 *Isotoma hiemalis* SCHOTT
 23 *Isotoma tigrina* (NIC.)
 24 *Isotoma* sp. j.
 25 *Vertagopus cinereus* (NIC.)
 26 *Pachyotoma* sp.n.

Entomobryidae

- 27 *Orchesella flavescens* (BOURL.)
 28 *Entomobrya nivalis* (L.)
 29 *Entomobrya* sp. j.
 30 *Lepidocyrtus cyaneus* TULLB.
 31 *Lepidocyrtus lignorum* (FABR.)
 32 *Lepidocyrtus* sp. j.
 33 *Pseudosinella zygodora* (SCHILLE)
 34 *Cyphoderus albinus* NIC.
 35 *Pogonognathellus flavescens* (TULLB.)
 36 *Tomocerus* sp. j.
 Sminthuridae
 37 *Lipothrix lubbocki* (TULLB.)

- 38 *Allacma fusca* (L.)
Bourletiellidae
- 39 *Bourletiella hortensis* (FITCH)
- NEMATODA
- 1 *Rhabditis* s. L.
2 *Bunonema reticulatum* RICHT.
3 *Heterocephalobus elongatus* (DE MAN)
4 *Acrobeloides nanus* (DE MAN)
5 *Ypsylonellus insubricus* (STEIN.)
6 *Teratocephalus dadayi* ANDR.
7 *Teratocephalus tenuis* ANDR.
8 *Metateratocephalus crassidens* (DE MAN)
9 *Filenchus ditissimus* (BRZ.)
10 *Malenchus bryophilus* (STEIN.)
11 *Ditylenchus anchilispomus* TARIAN
12 *Ditylenchus equalis* HEINS
13 *Ditylenchus longimatrix* (KAZ.)
14 *Geocenamus longus* (WU)
15 *Helicotylenchus pseudorobustus* STEIN.
16 *Paratylenchus nanus* COBB.
17 *Aphelenchoides* spp.
18 *Seinura winchesi* GOODEY
19 *Paraphelenchus* sp.
20 *Eymonchystera* sp.
21 *Geomonchystera* sp.
22 *Plectus geophilus* DE MAN
23 *Plectus longicaudatus* (BUT.)
24 *Plectus pusteri* FUCHS
25 *Wilsonema otophorum* (DE MAN)
26 *Prodesmodora terricola* MICOLETZKY
27 *Alaimus mucronatus* ALTH.
28 *Prionchulus punctatus* (COBB.)
29 *Mesodorylaimus* sp.
30 *Eudorylaimus silvaticus* BRZ.
31 *Aporcelaimellus* sp.
32 *Tylencholaimus mirabilis* BUT.
33 *Tylencholaimus stecki* STEIN
- FORMICIDAE
- 1 *Myrmica ruginodis* NYL.
2 *Myrmica scabrinodis* NYL.
3 *Myrmica sabuleti* MEIN.
4 *Myrmica lobicornis* NYL.
5 *Myrmica schencki* EM.
6 *Leptothorax acervorum* (FABR.)
7 *Leptothorax muscorum* (NYL.)
8 *Tetramorium caespitum* (L.)
- 9 *Strongylognathus testaceus* (SCHENCK)
10 *Camponotus herculeanus* (L.)
11 *Lasius niger* (L.)
12 *Lasius flavus* (FABR.)
13 *Lasius umbratus umbratus* (NYL.)
14 *Lasius fuliginosus* (LATR.)
15 *Formica fusca* L.
16 *Formica truncorum* F.
17 *Formica rufa* L.
18 *Formica polyctena* FOERST.
19 *Formica sanguinea* (LATR.)
- THEREVIDAE
- 1 *Acrosathe annulata* (F.)
2 *Clorismia ardea* (F.)
3 *Dialineura anilis* (L.)
4 *Spiriverpa lunulata* (ZETT.)
5 *Thereva cinifera* (MEIG.)
6 *Thereva fulva* (MEIG.)
7 *Thereva circumscripta* LW.
8 *Thereva handlirschi* KROEBER
9 *Thereva lanata* ZETT.
10 *Thereva microcephala* LW.
11 *Thereva inornata* VERR.
12 *Thereva nobilitata* (F.)
13 *Thereva strigata* (F.)
14 *Thereva plebeja* (L.)
- RHAGIONIDAE
- 1 *Rhagio lineola* (F.)
2 *Rhagio scolopaceus* (L.)
3 *Rhagio tringarius* (L.)
- MICROMAMMALIA
- Rodentia
- Arvicolidae
- 1 *Clethrionomys glareolus* (SCHREB.)
2 *Pitymys subterraneus* (S.-L.)
3 *Microtus agrestis* (L.)
4 *Microtus arvalis* (PALLAS)
5 *Microtus oeconomus* (PALLAS)
- Muridae
- 6 *Micromys minutus* (PALLAS)
7 *Apodemus agrarius* (PALLAS)
8 *Apodemus flavicollis* (MELCH.)
9 *Apodemus sylvaticus* (L.)
- Zapodidae
- 10 *Sicista betulina* (PALLAS)

Insectivora

Soricidae

- 11 *Sorex araneus* (L.)
- 12 *Sorex caecutiens* LAXMANN
- 13 *Sorex minutus* (L.)
- 14 *Neomys anomalus* (CABR.)
- 15 *Neomys fodiens* (SCHREB.)

AVES

Passeriformes

Alaudidae

- 1 *Lullula arborea* (L.)

Motacillidae

- 2 *Anthus trivialis* (L.)

Troglodytidae

- 3 *Troglodytes troglodytes* (L.)

Prunellidae

- 4 *Prunella modularis* (L.)

Turdidae

- 5 *Erithacus rubecula* (L.)
- 6 *Phoenicurus phoenicurus* (L.)
- 7 *Turdus merula* (L.)
- 8 *Turdus philomelos* (C. L. BREHM)

Sylviidae

- 9 *Sylvia atricapilla* (L.)
- 10 *Sylvia borin* (BODD.)
- 11 *Phylloscopus collybita* (VIEILL.)
- 12 *Phylloscopus sibilatrix* (BECHST.)
- 13 *Phylloscopus trochilus* (L.)
- 14 *Regulus regulus* (L.)

Aegithalidae

- 15 *Aegithalos caudatus* (L.)

Paridae

- 16 *Parus ater* (L.)
- 17 *Parus cristatus* (L.)

Certhiidae

- 18 *Certhia familiaris* (L.)

Fringillidae

- 19 *Fringilla coelebs* (L.)
- 20 *Carduelis spinus* (L.)
- 21 *Pyrrhula pyrrhula* (L.)

Emberizidae

- 22 *Emberiza citrinella* (L.)

Picidae

- 23 *Dendrocopos major* (L.)

STRESZCZENIE

[Tytuł: Sukcesja wtórna fauny w borach świeżych Puszczy Białowieskiej]

Bory sosnowe Polski ze względu na wartości użytkowe drewna sosnowego eksploatowane są i uprawiane od setek lat. Na większość z nich składają się drzewostany jednowiekowe, powstałe najczęściej w wyniku sztucznego odnowienia zrębów zupełnych. Założenie na porębie uprawy sosny, zwykle z domieszką drzew towarzyszących bądź osłonowych, uruchamia proces sukcesji wtórnej. W jej trakcie bór przechodzi przez kilka etapów: uprawy, młodnika, tyczkowiny, drągowiny, drzewostanu dojrzewającego aż do stadium dojrzałości. Proces ten, w przypadku borów sosnowych świeżych, trwa w naszych warunkach 10–150 lat (SZUJECKI 1980).

Każdy z tych etapów charakteryzuje się nieco odmiennymi warunkami mikroklimatu leśnego, zależnie od składu drzewostanu i właściwości siedliska (OBMIŃSKI 1978). Zmiany te znajdują swe odzwierciedlenie w przebudowie szaty roślinnej. Tu procesy sukcesji wtórnej w borach świeżych Puszczy Białowieskiej mają charakter wybitnie kreatywny. Prowadzą bowiem do uformowania

struktury przestrzennej boru o wyraźnej piętrowości, a przestrzeń życiowa wnętrza lasu jest zapełniona przez gatunki dopasowane do uformowanych w toku sukcesji wtórnej warunków środowiska. Jest to proces powtarzalny, obserwowany i opisany dla siedlisk borowych z różnych regionów kraju.

Procesy te w odniesieniu do fauny rozpoznane są fragmentarycznie, a dokumentacja sukcesji wtórnej fauny obejmuje tylko poszczególne grupy zwierząt i nie pozwala na stworzenie pełnego obrazu przemian zachodzących w składzie i organizacji kompleksów faunistycznych. Na tle dość bogatego, lecz często słabo powiązanego z realiami przyrodniczymi, piśmiennictwa poświęconego tematyce sukcesji ekologicznej autorzy niniejszego opracowania postawili szereg pytań dostosowanych do charakteru materiałów faunistycznych, więc takich, które dają możliwość uzyskania udokumentowanej odpowiedzi.

Podstawową w naszym rozumieniu tematu kwestią jest charakter sukcesji wtórnej fauny, czyli jak i do czego ona prowadzi. Nie jest bowiem oczywiste, tak jak w przypadku szaty roślinnej boru, że w procesie sukcesji wtórnej ma miejsce wyraźny rozwój biomasy zwierząt i uformowanie się struktur przestrzennych. Zjawiska takie, jeśli nawet mają miejsce wymagają udokumentowania. Na czoło wysuwa się kwestia jednorodności czy wielotorowości procesu sukcesji wtórnej fauny. Chodziło tu o sam model procesu. Czy jest on w pełni kreatywny, a jego etapy polegają na zasiedlaniu pustki ekologicznej, formowaniu podsystemów i dopasowywaniu ich do ekologicznej struktury dojrzewającego lasu. Ten klarowny obraz budzi szereg wątpliwości. Czy istnieje bowiem przez jakiś okres pustka faunistyczna po wycięciu lasu, czy też otwarta przestrzeń jest natychmiast zasiedlana? Czy poszczególne podsystemy zoocoenozy dopiero się formują, czy są już gotowe w przyrodzie? I w końcu, na czym ma polegać owo dopasowywanie, lub dokładniej, do czego w rzeczywistości dopasowują się poszczególne grupy fauny?

Dla uzyskania jednoznacznej odpowiedzi na postawione pytania zbudowano dwie hipotezy robocze, które stanowiły następnie podstawę do weryfikacji w oparciu o zebrane i opracowane materiały.

Hipoteza pierwsza określa, że sukcesja wtórna fauny może mieć rozmaity przebieg i prowadzić do odmiennych niekiedy układów końcowych. Opisano pięć typów przebiegu sukcesji: kreatywny, stabilizujący, załamany, regresywny i restauracyjny (Fig. 3).

Hipoteza druga określa powiązania fauny w system zależności troficznych o charakterze hierarchicznym. Zgodnie z nią zróżnicowane struktury fauny stanowią powiązane zależnościami pokarmowymi układy takie jak podsystem, łańcuch pokarmowy, zespół konkurencyjny i populacja określonego gatunku zwierząt. Zależności te przedstawiono w odniesieniu do 30 grup fauny objętej programem badań dla stadium końcowego sukcesji wtórnej, fauny starodrzewu boru sosnowego świeżego.

Tak sformułowane hipotezy robocze pozwoliły na konfrontację danych o faunie z wyobrażeniami o przebiegu sukcesji wtórnej. Jako materiału do weryfikacji hipotez użyto materiałów dokumentacyjnych dla poszczególnych klas wieku lasu: 1) liczbę gatunków tworzących poszczególne taksony lub zespoły

konkurencyjne; 2) liczebność tych jednostek, zwykle ujmowaną wskaźnikowo dla zobrazowania tendencji zmian liczebności; 3) strukturę taksocenów dla zobrazowania zmian w organizacji układów zoocenotycznych; 4) różnorodność gatunkową aktualną i potencjalną oraz zachodzący między nimi stosunek mierzony wskaźnikiem Pielou.

Liczba gatunków (Tab. II) w toku sukcesji wtórnej borów sosnowych świeżych w Puszczy Białowieskiej wykazuje zmiany idące w sześciu kierunkach. Dominuje typ sukcesji restauracyjnej charakteryzujący się wysoką liczbą gatunków w uprawach sosny, spadkiem w fazie dragowiny i odbudową w starodrzewie. Ten typ przebiegu został stwierdzony w połowie zbadanych zespołów konkurencyjnych i 8 taksocenach. Na drugim pod względem udziału miejscu znalazły się dwa dalsze typy przebiegu sukcesji wtórnej. Sukcesja regresywna, polegająca na spadku liczby gatunków w całym szeregu sukcesji występuje w obrębie 4 zespołów i 5 taksocenów zwierząt. Podobnie sukcesja zalamana, w której po początkowym wzroście ma miejsce spadek liczby gatunków została stwierdzona w 5 zespołach konkurencyjnych. Sukcesja kreatywna charakteryzująca się stałym wzrostem liczby gatunków w szeregu sukcesyjnym wystąpiła tylko w obrębie 4 zespołów konkurencyjnych. Stabilizacja liczby gatunków po początkowym ich wzroście miała miejsce tylko w 2 zespołach zwierząt. Poza tymi 5 typami zmian liczby gatunków należy wymienić 5 przypadków braku zmian liczby gatunków w toku procesów rozwoju boru. Taki stan rzeczy stwierdzono dla stonkowatych (*Chrysomelidae*), afidofagicznych biedronek (*Coccinellidae*), pasożytniczych muchówek *Pipunculidae*, nicieni (*Nematoda*) i *Rhagionidae* (*Diptera*).

Podobny obraz zróżnicowania reakcji poszczególnych grup zwierząt na proces odbudowy boru świeżego ma miejsce przy rozpatrywaniu poszczególnych zespołów konkurencyjnych (Tab. II). Tam, gdzie mamy do czynienia z kilkoma taksonami wchodzącymi w skład zespołu, zazwyczaj każdy z nich prezentuje odmienny kierunek zmian liczby gatunków. Wyjątek pod tym względem stanowią zoofagi oraz ksylo- i kambiofagi, wśród których dominuje restauracyjny kierunek zmian liczby gatunków. Natomiast wśród fitofagów zgryzających przeważają tendencje spadkowe w odniesieniu do liczby gatunków w toku sukcesji wtórnej.

Wynik analizy zmian w tworzywce organizacji ekosystemu leśnego, jaki stanowią gatunki zwierząt, wskazuje na to, że procesy twórcze rozbudowy lub odbudowy układów, reprezentowane przez typ sukcesji kreatywnej, stabilizującej i restauracyjnej są równie silne jak procesy destrukcyjne wyrażające się w ostatecznym rachunku spadkiem liczby gatunków. Znamienne jest przy tym, że co 6 grupa zwierząt nie reaguje zmianą liczby gatunków na procesy zachodzące w rozwijającym się borze. Liczebność zgrupowań zwierząt (Tab. III) przedstawia również zróżnicowany obraz przebiegu zmian jak liczba gatunków, jednak dwa kierunki procesów są dominujące: regresja i restauracja. Około 1/3 zgrupowań zwierząt startuje do procesu sukcesji z większą liczebnością populacji niż w drzewostanach dojrzałych, dominuje więc spadek liczebności. Na drugim miejscu znajdują się te zgrupowania, których spadek zostaje w toku sukcesji zatrzymany i w drzewostanach starszych ma miejsce wzrost liczebności populacji. Tylko co 7 taksocen wykazuje wzrost liczebności

populacji w całym szeregu sukcesji i taka sama liczba grup nie wykazuje zmian liczebności utrzymując się w całym szeregu sukcesji na tym samym poziomie zagęszczenia. Co 15 taksocen po początkowym wzroście liczebności wchodzi w fazę spadku, zaś tylko 1 taksocen wśród saprofagów, mianowicie skoczogonki (*Collembola*) ma przebieg liczebności wskazujący na stabilizację zgrupowania w drzewostanach starszych.

Zjawiska te rozpatrywane od strony poszczególnych zespołów konkurencyjnych wykazują wyraźne rozstrzelenie reakcji liczebności w ich obrębie. W każdym zespole bezkręgowców spotykamy obok siebie taksoceny wykazujące, jedno wzrost, drugie spadek liczebności. Wyjątek pod tym względem stanowią niewyspecjalizowane zoofagi, wśród których dominują tendencje spadku liczebności.

Analiza zmian liczebności fauny pozwala na uzyskanie odpowiedzi odnośnie dwóch ważnych kwestii związanych z sukcesją wtórną borów sosnowych świeżych. Pojęcie "pustki faunistycznej" nie odpowiada rzeczywistości przyrodniczej. Poręba leśna zostaje natychmiast zasiedlona przez populacje zwierząt o wysokiej liczebności, niemal 2/3 zgrupowań zwierząt w toku sukcesji zaniża swą liczebność w stosunku do jej stanu w uprawach sosny.

Wzrost liczebności wykazuje tylko 1/4 zespołów zwierzęcych (Tab. III), są to fitofagi ssące, afidofagi i ptaki. Liczebność stanowi miarę sukcesu ekologicznego zarówno gatunku jak i zgrupowania zwierzęcego. W toku sukcesji wtórnej boru sosnowego świeżego ma miejsce zastępowanie systemu eksploatacji produkowanej przez rośliny zielonej masy. Zjadanie igieł sosny przez fitofagi o zgrzyżającym aparacie gębowym, typowe dla szkodników pierwotnych sosny, wraz z rozwojem lasu ustępuje na rzecz wysysania produktów asymilacji przez mniej groźne dla lasu fitofagi ssące. Zjawisko to występuje, w każdym razie w Puszczy Białowieskiej, której bory sosnowe nie są dotykane kłeszkowymi pojawami fitofagów zgrzyżających. Wzrostowi liczebności fitofagów ssących towarzyszy rozwój zespołów afidofagów regulujących ich liczebność. Duże znaczenie ma wzrost liczebności zespołów ptaków (w większości owadożernych), które stanowią ogniwo kontrolujące szczególnie podsystem biotrofów.

Różnorodność gatunkowa aktualna (Tab. IV) oceniana miarą Shannona i Weavera (H') w toku sukcesji wtórnej boru świeżego wykazuje najbardziej równomierny rozkład typów reakcji. Najczęściej mają miejsce procesy zmniejszania się różnorodności względem jej stanu wyjściowego, jednak sumarycznie, procesy wzrostu różnorodności są równie częste w zgrupowaniach zwierzęcych jak procesy jej spadku. Znaczny udział mają również procesy załamania się różnorodności po okresie wzrostu. Nieco inaczej przedstawia się ta kwestia oglądana od strony wypełniania możliwości potencjalnych rozwoju różnorodności gatunkowej w ekosystemie. Tu procesy zmniejszania się różnorodności, szczególnie w drzewostanach dojrzałych mają charakter dominujący, stwierdzono je w obrębie 17 zgrupowań zwierzęcych na 28 przeanalizowanych pod tym względem. Wzrost, odbudowa lub stabilizacja różnorodności po wzroście dotyczyły tylko 1/3 obserwowanych przypadków. Stabilizacja różnorodności na tym samym poziomie w całym szeregu sukcesji należy do wyjątków.

Wynik przedstawionej analizy wskazuje wyraźnie, że teza Mac Arthura "diversity makes stability" nie znajduje żadnego odbicia w danych empirycznych (MACARTHUR 1955). Wręcz przeciwnie, spadek różnorodności gatunkowej zgrupowań zwierząt w starodrzewach boru sosnowego wskazuje na to, że wzrost stopnia organizacji układu odbywa się kosztem zmniejszenia jego różnorodności wewnętrznej. Ma to ścisły związek ze zjawiskami strukturalnymi. W drzewostanach starych, zazwyczaj w każdym zgrupowaniu zwierzęcym jest jeden lub parę gatunków wyraźnie dominujących, "ogon" gatunków akcesorycznych ulega zwykle skróceniu. Organizacja zgrupowania oparta jest zwykle na kilku dobrze dostosowanych gatunkach budujących zespoły zwierzęce.

W zakończeniu należy podkreślić, że cechą najbardziej charakterystyczną sukcesji wtórnej fauny w borach sosnowych świeżych Puszczy Białowieskiej jest wielokierunkowość procesów zachodzących na tle rosnącego, rozwijającego się struktury przestrzennej boru świeżego. Jeśli wziąć pod uwagę przeanalizowane parametry: liczbę gatunków, liczebność, różnorodność gatunkową i strukturę, to dominujące znaczenie mają procesy spadku wartości wskaźników, w całym szeregu sukcesji lub w jej końcowej fazie (44% przypadków). Stabilizacja tych wartości w całym szeregu lub po okresie wzrostu obejmuje tylko 22% przypadków. Tylko w 34% przypadków obserwujemy rozwój od początku sukcesji do stadium dojrzałego lub po okresie spadku w środkowym stadium.

Dane te potwierdzają hipotezę o wielokierunkowości przebiegu procesów sukcesji wtórnej w obrębie zgrupowań fauny. Szczególne znaczenie ma spadek wartości wielu wskaźników charakteryzujących faunę w końcowym etapie sukcesji, który można określić jako fazę organizacji zgrupowań, która odbywa się kosztem redukcji liczby gatunków i różnorodności na rzecz ustabilizowania struktur dominacyjnych. Tak więc stabilność ekosystemów tworzą lepiej przystosowani, a różnorodność jest jej budulcem nie wykorzystanym w pełni.

Cały układ zoocenotyczny powstaje równocześnie już w fazie nasadzenia drzewostanu po wyrębie i tu jest najbogatszy. Dalej toczy się jedynie przebudowa jego organizacji wraz z rozwojem boru jako ekosystemu.

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