

FRAGMENTA FAUNISTICA

Fragm. faun.	Warszawa, 30.06.2001	44	79-128
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Secondary succession of scuttle fly communities (*Diptera: Phoridae*) in moist pine forest in Białowieża Forest

Abstract: The aim of the research was to define changes taking place in scuttle fly communities in the course of secondary succession of moist pine forest, and to determine which variant of secondary succession was being realized by this community. For this purpose the following were analysed: data on the number and abundance of species, on the species diversity of their communities and on the frequency distributions of the species which determined the structural relations within the taxon.

Key words: *Diptera, Phoridae*, colonizing species, secondary succession, Białowieża Forest, Poland

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1. INTRODUCTION

Ecological succession refers to ecological complexes in which there takes place a succession of species in time or exchange of their entire communities. Succession is a well-ordered process of changes occurring in the biocoenosis. In the course of succession the environment is modified by the biocoenosis until a stable ecosystem, called the climax, is formed (TROJAN 1977, ANDERSON 1986, KIKKAWA 1986, PAQUIN, CODERRE 1997, LICHTER 1998).

In our climate, the process of secondary succession of moist pine forest lasts from 120 to 150 years (SZUJECKI 1980). Forest regeneration is accelerated through pine plantations established in clearings. The other stages of succession are: young-growth, small pole timber, large pole timber, premature tree stand and mature tree stand (old-growth). The vegetation is being rebuilt throughout that time and, eventually, distinctly stratified forest is created. Fairly well-known transformations in the plant

structure (FALIŃSKI 1991) are accompanied by changes in the trophic structure of the forest fauna, and these changes have hardly been studied.

The most recent investigations carried out in pine forest in Białowieża Forest have provided evidence that processes of secondary succession within animal communities develop in many directions (TROJAN *et al.* 1994). Scuttle fly communities were not covered by these studies although their abundance greatly exceeds that of other families of *Diptera*. All data on Białowieża Forest are extremely valuable because this Forest is the largest faunistic refugium in Central European lowlands, and the degree of the natural character of its forest is higher while the number of exploitation cycles is lower than in other European woodlands.

The investigations into the secondary succession of phorid communities in moist pine forest in Białowieża Forest were sponsored by the Committee for Scientific Research PAS and were a continuation of studies into this group sponsored by the C. S. R. PAS to carry out a research project called "Analysis of the species composition and structure of scuttle fly communities (*Diptera: Phoridae*) in forest complexes with various degrees of environment degradation". These studies yielded a number of valuable data on phorid communities of moist pine forest. They provided evidence the response of a community to habitat degradation is very marked and that the number of scuttle fly species decreases as a result of modification of forest from its natural state. In the trophic structure of communities a very distinct reaction to habitat degradation was recorded (decreased abundance of zoophages). Moreover, thanks to the faunistic investigations conducted in moist pine forest in Puszcza Biała Forest and in Bory Tucholskie Forest in 1986 and 1987, the list of phorid species from Poland has been expanded (DURSKA 1996).

Ecological succession is an expression of dynamic processes taking place in all ecosystems (WITTAKER 1975, STUGREN 1976, ODUM 1982). Secondary succession leads to relative stabilization of the climax complex. It is also expressed by the fact that growth processes slow down or cease altogether, while the increase in energy is directed at internal regulation processes. These processes employ energy for the metabolism of the components of a given biocoenosis.

A knowledge of scuttle fly communities of moist pine forest is of great importance because more information and data will make it easier to understand the functioning and significance of this group in a type of forest most important in silviculture. Being an extremely abundant community of organisms with similar biotic properties but different scales of ecological tolerance, the *Phoridae* could form a basis on which the stabilizing mechanisms may operate in the succession series of moist pine forest in Białowieża Forest. During the course of moist pine forest development a phorid community may realize one of the five succession variants: creative, stabilizing, rise-and-fall, regressive or restorative (TROJAN *et al.* 1994).

2. STUDY AREA

Białowieża Forest lies in the north-eastern part of Poland, in the macroregion of Nizina Podlaska. This vast forest complex (its Polish part covers about 625 km²) is situated at the border between Poland and Belarus. Within its present boundaries it is

a relic of three forest complexes connected with Knyszyńska Forest in the north. In the 13th century, the entire area was depopulated and that state of affairs lasted for about 300 years (WIĘCKO 1972). If compared with woodlands situated to the west of it, the forests of Białowieża Forest have been subject to fewer exploitation cycles, even though exploitation was wasteful during both world wars. The area is dominated by deciduous forest (linden-oak-hornbeam) characteristic of the temperate zone in Europe. These forests are undergoing complete series of secondary succession (FALIŃSKI 1989). In 1977, UNESCO recognized the unique value of Białowieża National Park and granted it the status of a world biosphere reserve. In 1979, the Park was registered, as the only natural object from Poland, in the Human Heritage List.

In Białowieża Forest, besides linden-oak-hornbeam forests and alder swamps, there are pine forests represented by the forest associations *Pino-Quercetum* and *Peucedano-Pinetum* (the subboreal variety of the community) (FALIŃSKI 1988). *Peucedano-Pinetum* represents a type of moist pine forest on podsol soils. Most of these forests are in the north-western part of the complex, in the forest District Hajnówka. Within the Forest there are about 3739 ha of moist pine forest which constitute about 6.4% of the entire tree stand there. Moist-pine-forest patches consist of pine (about 76%), spruce (15%), a small proportion of birch (7%) and a very small share of other species (e.g. oak, aspen).

The studies on secondary succession of scuttle flies in moist pine forests in Białowieża Forest were carried out in the forest of Starzyna Division (District Hajnówka). Three sites were selected in the following divisions: 538 (Ba, Bc, Bd, Bf), 634 (Bc, Ef), 667Bf and 668 (Ad₂, Af₁, Cc) (Fig. 1). At each of these sites, there were chosen

several-hectare, even-aged forest plots: plantation (culture: 4–8 years), young-growth (16–22 years), large pole timber (age-class III – 50 years) and old-growth (140–145 years). The selected study areas are homogeneous in soil and phytosociological respects. They represent the association *Peucedano-Pinetum* in its subboreal variety. A phytosociological analysis has shown that there are slight differences in the floristic composition even between old-growth and a clearing with young seedlings (MATUSZKIEWICZ *et al.* 1993). Associations developing in moist-pine-forest

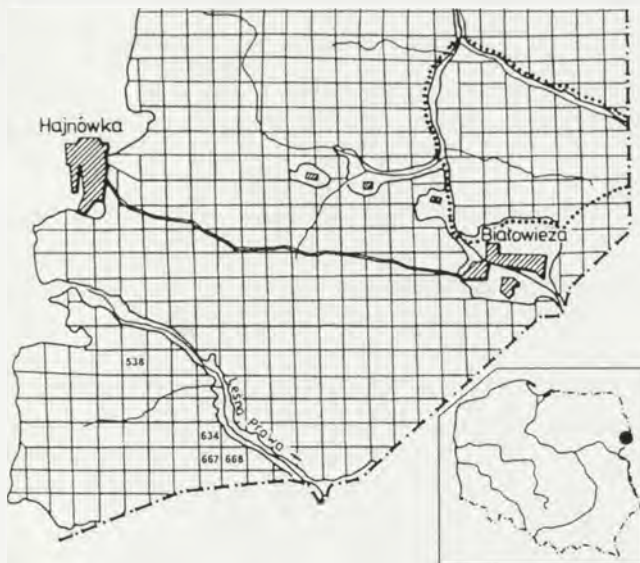


Fig. 1. Location of forest divisions; plantation: 538Bf, 538Bd, 634Bc; young-growth: 538Bc, 668Ad₂, 668Cc; large pole timber: 538Ba, 634Ef, 668Af₁, old-growth: 538Bf, 667Bf, 668Af₁.

habitats in clearings and young-growth are not distinctly individual; they are sets of forest species enriched with few species from sandy grasslands. Both in Białowieża Forest and in other woodlands of north-eastern Poland in forest habitats, pine is eliminated, under natural conditions, by spruce which strongly shades the understory forest. Total clearing is commonly employed in order to facilitate pine regeneration (SOKOŁOWSKI 1996). The area where the studies were conducted is subject to 60–80-metre-wide total clearing. Regeneration of tree cover begins with a plantation consisting of 80% of pine, 10% of spruce and 10% of birch and oak.

3. METHODS AND MATERIAL

The phorid material was collected during studies in 1986 and 1987. Insects were caught in yellow plastic traps (bowls of about 18 cm in diameter) with a water solution of ethylene glycol and with some detergent. The traps were attached to crowns of pines (*Pinus silvestris*) or placed on the ground in pine plantations; from April through October. All insects caught were collected at regular intervals, generally every fortnight. The method, first employed by MOERICKE (1950) to catch aphids and later modified by J. Sawoniewicz D. Sc., was used in zoocoenological studies conducted by the Institute of Zoology PAS to collect all insects living in tree canopies (BAŃKOWSKA, GARBARCZYK 1981). In the case of scuttle flies the "yellow-trap" method makes possible the most complete collection of material not only from tree canopies and from bushes but from understory foliage as well (DURSKA unpublished data). Unlike such catch techniques as sweep-netting, shaking or light-trapping the method under discussion allows for precise observation of the proportions in which the genus *Megaselia* occurs in the habitat; *Megaselia* is the richest in species and the most abundant genus (about 70%) (DISNEY 1994). This method guarantees continuity of catches and the efore makes it possible for researchers to collect species with different circadian activity patterns, and to determine seasonal changes. When the yellow-trap method is employed, any number of sites may be studied simultaneously.

Five traps (1 per tree) were hung or put in each plot (in pine plantations). Altogether 60 traps were placed in four age-classes of pine tree stands. The material collected contained 57181 phorid imagines; 9% of these were caught in pine plantations, 37.2% in young-growth, 27.4% in large pole timber and 26.4% in old-growth.

The aim of the research was to define changes taking place in scuttle fly communities in the course of secondary succession of moist pine forest in Białowieża Forest, and to determine which variant of secondary succession was being realized by this community. For this purpose the following were analysed: data on the number and abundance of species, on the species diversity of their communities and on the frequency distributions of the species which determined the structural relations within the taxon.

The ecological classification of the species was based on DISNEY (1994) and on the author's studies. The criteria of zoogeographic classification were adopted after CZECHOWSKI, MIKOŁAJCZYK (1981). Affiliation of particular species to definite elements was established on the basis of data on their geographic distribution published by DISNEY (1991).

The abundance of particular species and of entire scuttle fly communities was presented by means of an index defining the number of individuals collected during 100 24-hour catches (a 24-hour catch is the mean number of individuals caught into one trap in the space of 24 hours). This adopted conversion factor made it possible to employ adequately high numerical values of the index.

While examining the dominance structure of communities, the index of dominance (D) was used:

$$D = \frac{n}{N} 100\%$$

where: n - relative abundance of a given species
 N - relative abundance of the community;

Four classes of species were distinguished when index of dominance (D) was used, and their proportions were:

- eudominants - over 15.0%,
- dominants - from 5.1% to 15.0%
- subdominants - from 1.1% to 5.0%,
- accessory species - up to 1.0%;

Soerensen's formula (So) (SOERENSEN 1948) was used to calculate the similarity of species compositions (quantitative similarity) of the communities compared:

$$So = \frac{2a}{b+c}$$

where: a - number of common species,
 b - number of species of the first community,
 c - number of species of the second community;

Morisita's index (Mo) modified by HORN (1966) was used to calculate the similarity of dominance structures of the communities:

$$Mo = \frac{2 \sum_{i=1}^n x_i y_i}{\sum_{a=1}^n x_a^2 + \sum_{a=1}^n y_a^2}$$

where: x_i, y_i - percentages of common species,
 x_a, y_a - percentages of particular species in each of the communities compared,
 n - total number of species;

The fidelity formula (W) expressed quantitatively was used to distinguish species characteristic of particular habitats:

$$W = \frac{a}{b} 100$$

where: a - abundance of a given species in a given habitat,
 b - total abundance of a given species in all habitats;

Species whose value W was not lower than 51% were regarded as characteristic.

The frequency formula (F) proposed by TISCHLER (1949) was used to calculate the occurrence frequency of species in samples from a given plot.

$$F = \frac{p}{P} 100$$

where: p - number of samples containing a given species,
 P - number of all samples;

The Shannon and Weaver index of real species diversity (H') was used to estimate the biocoenotic diversity of the communities. This index assesses the structure of fauna in respect of species richness and the evenness of abundance distribution between particular species (MAGURRAN 1988, TROJAN 1992, TROJAN 1994).

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

where: n_i - abundance of i th species,
 N - total abundance of the community;

The potential diversity of communities (H_{max}), which also is a maximum value of the index H' , equals $\log S^*$. The Pielou index (J) was used to determine the degree to which potential diversity was realized by particular communities (TROJAN 1992).

$$J = \frac{H'}{\log S^*} 100$$

where: S^* - potential number of species in a given community calculated from logarithm function (Arrhenius curve) (TROJAN 1992).

A modified Arrhenius's formula was used to estimate the number of species (S^*) based on the number of species found in samples (S) (CONNOR, MCCOY 1979):

$$S = cN^z$$

where: S - number of species in a sample,
 N - number of individuals in a sample,
 c, z - equation parameters obtained as suggested by the authors of the formula (CONNOR, MCCOY 1979);

The index of homogeneity was used to determine the impact of accessory species on the similarity of dominance structures (RIEDL 1963):

a) index of homogeneity of dominance:

$$HD = \sum_{i=1}^s \left(\sum_{j=1}^k \frac{D_{ij}}{k} \right) \frac{D_{\min i}}{D_{\max i}}$$

where: D_{ij} - index of dominance for the i th species in the j th site, for the total number of s species and k sites,

b) index of homogeneity of ranks:

$$HD^* = \sum_{i=1}^s \left(\sum_{j=1}^k \frac{D_{ij}}{k} \right) \frac{D_{\min_i}}{D_{\max_i}}$$

where: D_{ij} - index of dominance for the i th species of the j th rank for the total number of s species and k ranks;

The numeric (Mn) and species (Ms) mosaic indices were used to estimate the state of the habitat (TROJAN 1997).

a) numeric index of habitat mosaic character:

$$Mn = \frac{\sum_{i=1}^{r=S^1} n_i}{N}$$

where: N_i - abundance of species consistent with the broken-stick model
 N - total abundance of the community,
 S - number of species in the community,
 S^1 - number of species consistent with the broken-stick model;

b) species index of habitat mosaic character:

$$Ms = \frac{S^1}{S}$$

where: S^1 - number of species consistent with the broken stick model,
 S - number of species in the community;

In order to estimate species richness (d) an index was used which makes the value of the result independent, to some extent, of the size of a sample (MARGALEF 1968):

$$d = \frac{S}{\log N}$$

where: S - number of species in a sample,
 N - number of individuals in a sample;

The calculations were based on a computer programme of the Museum and Institute of Zoology PAS.

4. RESULTS

4a. Species composition

Unlike the fauna of deciduous tree canopies in European woodlands the phorid fauna of pine canopies in moist pine forest is very rich (BUCK 1994, DISNEY 1994, DURSKA 1996, in press).

The first mention of the *Phoridae* recorded from Białowieża Forest was included in SACK'S report (1925) on the occurrence of *Megaselia pulicaria*.

During the 1986 and 1987 research in moist pine forests in Białowieża Forest there were recorded 21 genera represented by 209 species of *Phoridae*, and this made about 65% of all species recorded from Poland; the 42 species new to the Polish fauna included 9 species new to science (DURSKA 1996, DISNEY, DURSKA 1998, DURSKA in press). *Poloniphora* - a genus new to science was described (DISNEY, DURSKA 1998).

Most females of the species *Megaselia* and *Phora* are unidentifiable to species (in our present state of knowledge) and therefore they have been identified to genus only. The group of species new to science merits further study.

A detailed analysis has been carried out for material from the four age-classes of pine tree stands; the material comprises males (201 species, 11 of which probably are new to science) of all genera of *Phoridae* (Appendix).

Up till now, 87 species were known to occur in pine canopies of old-growth in moist pine forests in Białowieża Forest (DURSKA 1996). After the recent studies that number has risen to 131 (including 8 species probably new to science) (Appendix) (DURSKA in press).

The Arrhenius function was used to analyse the material, and it was found out that phorid species had gradually appeared in successive samples (Table I).

Table I. Phorid species appearing in consecutive samples collected by the yellow trap method in the four age-classes of pine tree stands of moist pine forest in Białowieża Forest (N - number of samples, S - number of species).

Habitat	Plantations		Young-growth		Large pole timber		Old-growth	
	S	%S	S	%S	S	%S	S	%S
1	15	19.73	25	18.12	19	22.10	19	14.50
10	51	67.10	109	78.98	61	70.93	81	61.83
20	71	93.42	133	96.38	80	93.02	125	95.42
25	76	100.00	138	100.00	86	100.00	131	100.00

Very similar numbers of species were obtained for scuttle fly communities in plantations and large pole timber (76 and 86 species, respectively) and also in young-growth and old-growth (138 and 131 species, respectively). The succession variant realized by the phorid community, with regard to the number of species, may be defined as a rise-fall-rise variant of change, and it is a modification of the restorative one (TROJAN *et al.* 1994). Similar rise-fall-rise tendencies were noticed when values of species richness designated for the communities in the four age-classes of forest were being compared (Table II). An increase followed by a decrease and yet another increase in the number of species indicates that the response of a phorid community to the changes in habitat is very high (TROJAN 1994, DURSKA 1996).

Table II. Changes in the number of individuals (N), in abundance (N/24-hour trap) and in the number of species (S) of the phorid communities in the four age-classes of moist pine forest in Białowieża Forest.

Habitat	Total material (females+males)			Males		
	N	N/24-hour trap	S/LogN	N	S	N/24-hour trap
plantations	5119	2.03	20.4897	2148	76	0.85
young-growth	21304	8.11	31.8820	6482	138	2.49
large pole timber	15664	6.00	20.5011	3317	86	1.29
old-growth	15094	4.83	31.3487	3466	131	1.38
sum	57181	20.97	×	15413	×	×
total	×	×	42.2513	×	201	6.01

Soerensen's formula was used to compare the species composition of the scuttle fly communities in the four age-classes of moist pine forest. The comparison was made in two ways: one for the entire composition and the other only for the group of dominants. An analysis of the entire species composition showed slight similarities between the communities occurring there (Table III).

Table III. Values of Soerensen's index for the phorid communities in the succession series of moist pine forest in Białowieża Forest.

Habitat	Plantations	Young-growth	Large pole timber	Old-growth
plantations	×	59.8	62.2	56.7
young-growth		×	60.4	65.7
large pole timber			×	60.4
old-growth				×

Different values were obtained after the group of dominants had been compared. In most cases, Soerensen's index was over 80%, and that indicated a very high similarity of the species composition of this group of the compared phorid communities from the four age-classes of moist pine forest (Table IV).

Table IV. Values of Soerensen's index for the group of dominants in the phorid communities in the succession series of moist pine forest in Białowieża Forest.

Habitat	Plantations	Young-growth	Large pole timber	Old-growth
Plantations	×	82.0	80.9	77.5
Young-growth		×	86.0	88.2
Large pole timber			×	81.6
Old-growth				×

The similarities (similarity index - I, for $0 < I < 1$), based on Soerensen's index, between the phorid communities from different age-classes of tree stand are well-illustrated by dendrograms obtained by means MOUNTFORD's method (1962) (Figs 2, 3).

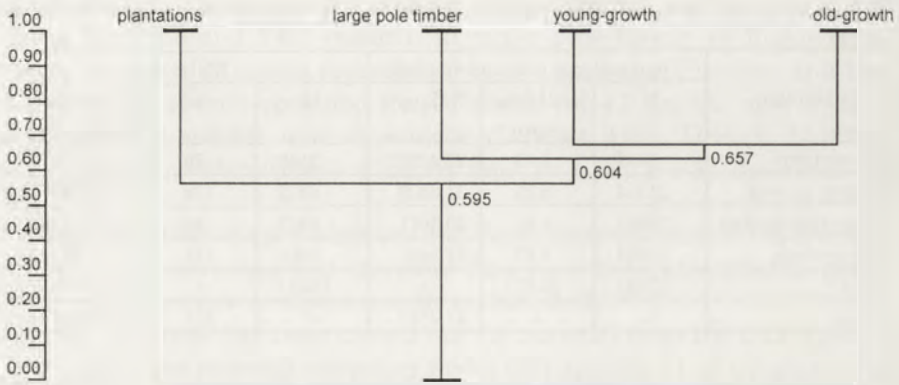


Fig. 2. Dendrogram of similarity of species composition of the phorid communities in moist pine forest in Białowieża Forest; based on Soerensen's index.

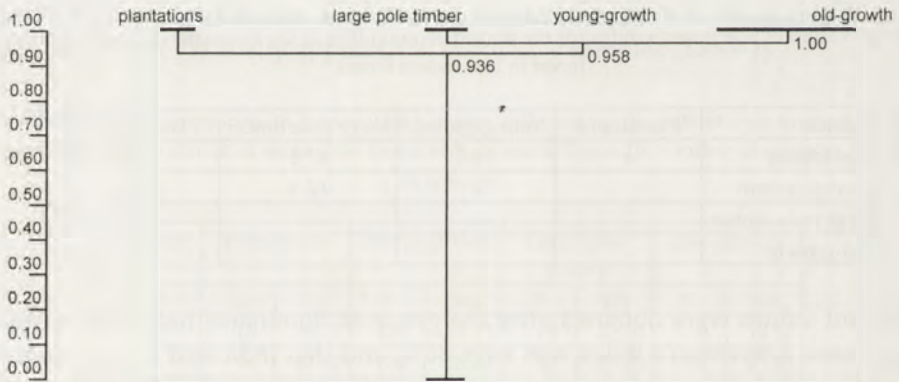


Fig. 3. Dendrogram of similarity of dominant species in the phorid communities in moist pine forest in Białowieża Forest; based on Soerensen's index.

The values of the species similarity index for the group of dominants were high (77.5–88.2%), whereas the similarity of species composition for the communities treated as a whole was lower (56.7–65.7%). This indicates that differences between communities were connected with accessory species. That group, the so-called "distribution tail", was separated using discrimination analysis based on the broken-stick model (a model of a random distribution of abundance); this issue will be discussed in more detail below.

In the scuttle fly communities of plantations and large pole timber on the one hand and in those of young-growth and old-growth on the other the number of accessory species was close and proportional to the total number of species recorded for par-

ticular communities from the four age-classes of moist pine forest. The differences between the numbers of individuals of accessory species groups were not too high (from about 300 to about 400 individuals) (Table V).

Table V. Changes in the number of accessory species and in that of individuals of these species in the phorid communities in the four age-classes of moist pine forest in Białowieża Forest.

Habitat	Total number of species	Number of accessory species	Number of individuals of accessory species
plantations	76	62	317
young-growth	138	96	332
large pole timber	86	64	399
old-growth	131	108	402

Within the group of dominants of the phorid community from plantations the fidelity (W) exceeded 51%. In the phorid communities from the older age-classes of tree stand the fidelity of species characteristic for plantations was generally over a dozen times lower. Species of open areas predominated among the most faithful ones in the communities from plantations. The fidelity of *M. verralli*, which was over 90% in plantations (Fig. 4), dropped to below 1% in the communities from old-growth.

In the dominants of young-growth, the highest fidelity was recorded for as many as 19 phorid species (Fig. 5). The species *M. sordida* was found solely in samples from young-growth (100% fidelity). Out of this considerable number of species of the highest fidelity only five have been studied thoroughly and their biology is known. Four species belonging to this group, namely *M. hyalipennis*, *M. lata*, *M. pulicaria-complex* and *M. scutellaris* are associated with fungi. This great number of high fidelity species in the scuttle fly communities from young-growth may have been connected with great masses of mushrooms, particularly of *Boletaceae*.

In the phorid communities from large pole timber, the species of the highest fidelity included *Phora pubipes*, *Ph. dubia*, *Megaselia altifrons* and *M. henrydisneyi*. Neither species of the genus *Phora* was recorded in samples from plantation plots. The common species *M. altifrons* was found in samples from all age-classes. Its fidelity in the communities in large pole timber was nearly 70%, but in old-growth it dropped to about 2.5%. *M. henrydisneyi*, a species which, as new to science, had been recorded first from Białowieża Forest, was found only in samples from young-growth and large pole

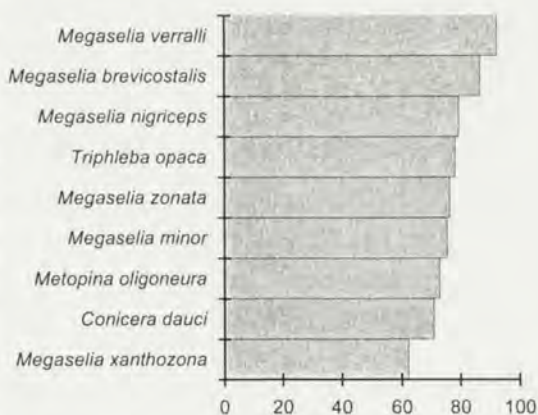


Fig. 4. Fidelity (%) of the phorid species in pine plantations.

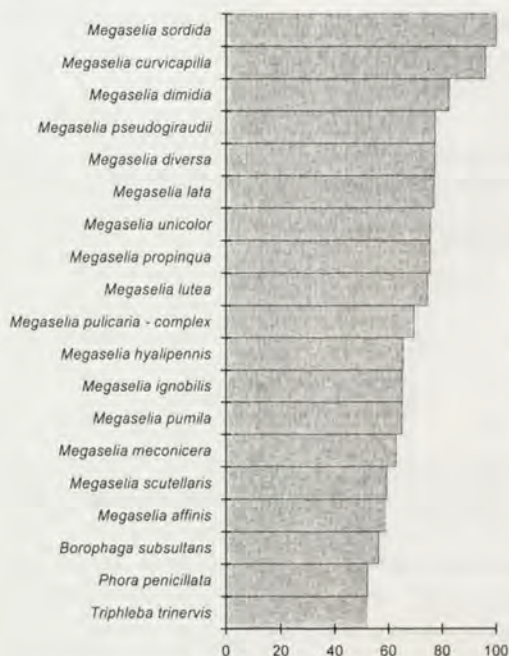


Fig. 5. Fidelity (%) of the phorid species in young-growth.

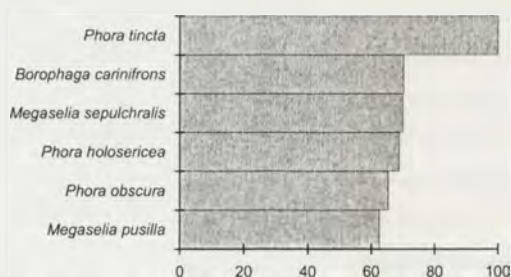


Fig. 7. Fidelity (%) of the phorid species in old-growth.

raudii was a species of the highest occurrence frequency although in the phorid communities in pine plantations its frequency was insignificant. The species *M. woodi*, whose ecological requirements are as yet unknown, was very numerous in samples from old-growth plots only towards the end of the study seasons, at a time when mushrooms sprouted in great masses (DURSKA 1996). In the communities from plantations it appeared sporadically (Table VI).

Thus it is evident that each age-class has a specific group of characteristic species (Figs 4-7). The fact that scuttle flies react to habitat pollution has been reported earlier (DURSKA 1996). This reaction, expressed by an increase in the number of species with

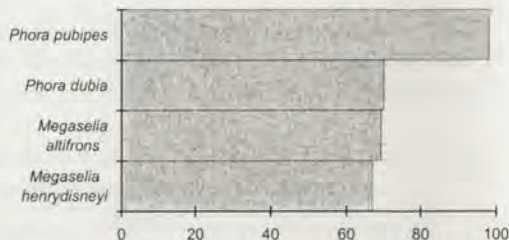


Fig. 6. Fidelity (%) of the phorid species in large pole timber.

timber plots (Fig. 6). It was an accessory species in the communities from young-growth and a subdominant in those from large pole timber (Appendix).

Within the group of dominants of the scuttle fly communities in old-growth *Phora tincta* was a species with the highest fidelity (100%). The occurrence fidelity of *Borophaga carinifrons*, *Megaselia sepulchralis*, *Phora holosericea*, *Ph. obscura* and *Megaselia pusilla* was between 60 and 70% (Fig. 7).

The species *M. verralli* and *M. brevicostalis*, characteristic for the youngest age-class of forest (high fidelity and frequency), in the older age-classes were in the group of species visiting pine canopies sporadically (Fig. 4; Table VI).

The observations concerning the scuttle fly communities in the older age-classes of pine forest were entirely different. Two species, typical of pine canopies, namely *M. giraudii* and *M. woodi* were easily distinguished in these communities. The polyphagous *M. gi-*

zoophagous larvae, indicates that the *Phoridae* are very sensitive to any changes in the environment.

Table VI. Frequency (%) of the phorid species dominating in the four age-classes of moist pine forest in Białowieża Forest.

Nr	species	plantations	young-growth	large pole timber	old-growth
1	<i>Megaselia altifrons</i>	0.07	0.25	0.43	0.03
2	<i>Megaselia brevicostalis</i>	0.54	0.13	0.13	0.12
3	<i>Megaselia campestris</i>	0.37	0.13	0.13	0.12
4	<i>Megaselia diversa</i>	0.06	0.41	0.32	0.14
5	<i>Megaselia giraudii</i>	0.12	0.84	0.76	0.69
6	<i>Megaselia hyalipennis</i>	0.02	0.37	0.15	0.16
7	<i>Megaselia involuta</i>	0.20	0.17	0.07	0.06
8	<i>Megaselia manicata</i>	0.34	0.19	0.18	0.20
9	<i>Megaselia meconicera</i>	0.14	0.50	0.00	0.47
10	<i>Megaselia nigriceps</i>	0.30	0.20	0.12	0.09
11	<i>Megaselia pleuralis-complex</i>	0.41	0.45	0.22	0.11
12	<i>Megaselia pulicaria</i>	0.12	0.67	0.26	0.46
13	<i>Megaselia pumila</i>	0.36	0.40	0.11	0.04
14	<i>Megaselia pusilla</i>	0.02	0.17	0.20	0.50
15	<i>Megaselia unicolor</i>	0.04	0.43	0.34	0.17
16	<i>Megaselia verralli</i>	0.69	0.06	0.05	0.04
17	<i>Megaselia woodi</i>	0.16	0.31	0.33	0.32
18	<i>Megaselia zonata</i>	0.38	0.11	0.02	0.02
19	<i>Conicera dauci</i>	0.24	0.11	0.02	0.04
20	<i>Metopina oligoneura</i>	0.36	0.07	0.06	0.07
21	<i>Phalacrotophora fasciata</i>	0.03	0.23	0.30	0.12
22	<i>Phora artifrons</i>	0.03	0.33	0.26	0.19
23	<i>Phora holosericea</i>	0.02	0.04	0.00	0.33
24	<i>Phora obscura</i>	0.03	0.21	0.03	0.48
25	<i>Phora pubipes</i>	0.00	0.02	0.36	0.02

The gradually developing vertical structure of forest, and the accompanying habitat diversification, change habitat conditions to such an extent that species richness of scuttle flies increases. Species of open areas are accompanied by typically forest ones whose habitats are in pine canopies, and also by species whose larval development is associated with fungi (DISNEY 1994). In comparison with the communities from plantations, the number of phorid species increased nearly twice and that of accessory species increased by half. In the communities from age-class III of pine tree stands the number of phorid species associated with open areas decreased. The number of species forming the distribution tail decreased, whereas there was an increase in the number of those whose optimum development was associated with formation litter and with greater thinning of tree stands. The considerable increase in the number of species (Table V), particularly of accessory ones, in the scuttle fly communities from

old-growth was connected with the fact that new niches developed in the course of secondary succession of moist pine forest.

4 b. Abundance, dominance structure and species richness

During the two study seasons, scuttle flies were the most abundant family (about 30%) within the communities of *Diptera* in the succession series of moist pine forest in Białowieża Forest.

The lowest abundance of phorid communities was recorded in pine plantations. It increased fourfold in young-growth but decreased in large pole timber. In old-growth, the abundance of the phorid community decreased once more (data for the community as a whole). With regard to males, the abundance of communities remained at almost identical levels in pole timber and old-growth. The succession variant realized by the phorid community in pine canopies of moist pine forest in Białowieża Forest is, in respect of abundance, the closest to the stabilizing variant (TROJAN 1994, DURSKA 1998). The abundance of scuttle flies in the communities from young-growth increased rapidly but then the stabilizing process began in the communities from large pole timber. In the communities from old-growth, abundance changed but little, in spite of an increase in the number of species (Table II).

The growth process of pine tree stands in the course of secondary succession was accompanied by changes in the species composition of the phorid communities that consisted in changes in the number and abundance of species (Table II) and also their fidelity and frequency (Fig. 4-7; Table VI).

In the youngest age-class of tree stand, i.e. in plantations where the abundance of phorids was the lowest, their dominance structure greatly differed from that de-

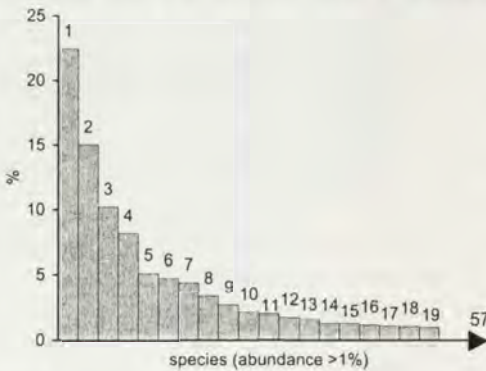


Fig. 8. Dominance structure of the phorid communities in pine plantations. 1 - *Megaselia verralli*, 2 - *M. brevicostalis*, 3 - *M. nigriceps*, 4 - *M. manicata*, 5 - *M. zonata*, 6 - *Triphleba opaca*, 7 - *M. pleuralis*, 8 - *M. pumila*, 9 - *M. latifrons*, 10 - *Metopina oligoneura*, 11 - *M. involuta*, 12 - *M. campestris*, 13 - *Conicera dauci*, 14 - *M. minor*, 15 - *M. giraudii*, 16 - *M. xanthozona*, 17 - *M. meconicera*, 18 - *M. woodi*, 19 - *M. pulicaria-complex*; 57 - number of other species.

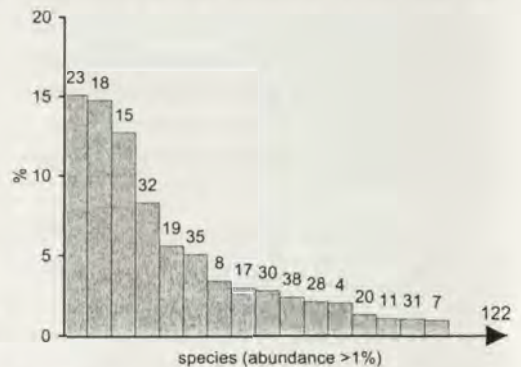


Fig. 9. Dominance structure of the phorid communities in young-growth. 23 - *Megaselia diversa*, 18 - *M. woodi*, 15 - *M. giraudii*, 32 - *M. unicolor*, 19 - *M. pulicaria-complex*, 35 - *Phora penicillata*, 8 - *M. pumila*, 17 - *M. meconicera*, 30 - *P. artifrons*, 38 - *M. hyalipennis*, 28 - *M. ignobilis*, 4 - *M. manicata*, 20 - *M. lata*, 11 - *M. involuta*, 31 - *P. obscura*, 7 - *M. pleuralis*; 122 - number of other species.

scribed for the communities occurring in the older age-classes of pine forest. *Megaselia verralli* and *M. brevicostalis* were the eudominants there and *M. nigriceps*, *M. manicata* and *M. zonata* were the dominants (Fig. 8).

In young-growth, the abundance of the phorids increased fourfold and the species of the first succession stage (the first six dominants) were entirely replaced by those whose percentage in the abundance of the communities from plantations was small. These were: five species of the genus *Megaselia*: *M. diversa*, *M. woodi*, *M. giraudii*, *M. unicolor*, *M. pulicaria* and *Phora penicillata* (Fig. 9).

In large pole timber and in old-growth, the abundance of the phorid communities decreased considerably, whereas the proportion of that of *M. woodi* and *M. giraudii* increased. These two species occupied the position of eudominants of the scuttle fly communities occurring in the two oldest age-classes of tree stand of moist pine forest (Figs 10, 11).

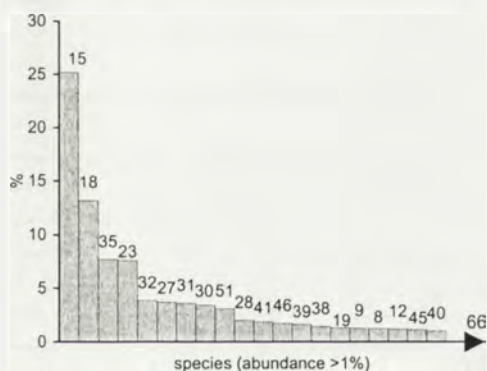


Fig. 10. Dominance structure of the phorid communities in large pole timber. 15 - *Megaselia giraudii*, 18 - *M. woodi*, 35 - *Phora penicillata*, 23 - *M. diversa*, 32 - *M. unicolor*, 27 - *M. altifrons*, 31 - *P. obscura*, 30 - *P. artifrons*, 51 - *P. pubipes*, 28 - *M. ignobilis*, 41 - *P. holosericea*, 46 - *P. dubia*, 39 - *Phalacrotophora fasciata*, 38 - *M. hyalipennis*, 19 - *M. pulicaria-complex*, 9 - *M. latifrons*, 8 - *M. pumila*, 12 - *M. campestris*, 45 - *M. henrydisneyi*, 40 - *M. ruficornis*; 66 - number of other species

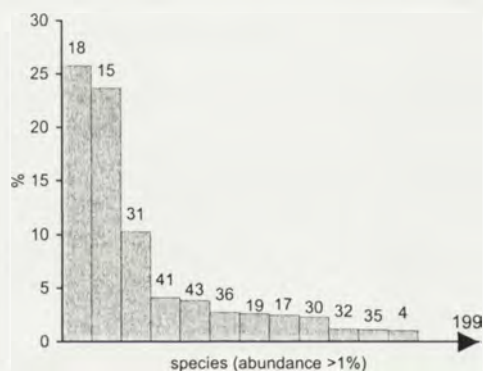


Fig. 11. Dominance structure of the phorid communities in old-growth. 18 - *Megaselia woodi*, 15 - *M. giraudii*, 31 - *Phora obscura*, 41 - *P. holosericea*, 43 - *M. sepulchralis*, 36 - *M. pusilla*, 19 - *M. pulicaria-complex*, 17 - *M. meconicera*, 30 - *P. artifrons*, 32 - *M. unicolor*, 35 - *P. penicillata*, 4 - *M. manicata*; 199 - number of other species

Megaselia verralli and *M. zonata* probably are species of open areas. They occurred in plantations, but their proportions decreased very distinctly in the communities from the older age-classes of stand. *M. pumila* occupied almost the same position in the communities in plantations and young-growth (items 8 and 7, respectively). Its tolerance to the habitats of large pole timber and old-growth decreased considerably. *Megaselia campestris*, *M. emarginata* and *Triphleba trinervis* occupied a similar position in the communities from all four age-classes of tree stand; they probably are eurytopic species of pine forest.

There was also distinguished a group of species whose status was very similar in the phorid communities in young-growth, large pole timber and old-growth but differed considerably from the positions these species occupied in the communities in plantations. Polyphagous *Megaselia giraudii*, fungivorous *M. hyalipennis*, and also *M. woodi* and *Phora artifrons* occupied very high positions in the communities from the older age-classes of tree stand. *Megaselia sordida*, recorded only from young-growth, and *Phora tincta*, occurring only in old-growth, probably are specialists. *Phora pubipes* was a species clearly preferring the habitat of pole timber (Table VII).

Table VII. Phorid species according to their status in the four age-classes of tree stand of moist pine forest in Białowieża Forest.

Nr	Species	Plantations	Young-growth	Large pole timber	Old-growth
1	2	3	4	5	6
1	<i>Megaselia verralli</i>	1	28	36	40
2	<i>Megaselia brevicostalis</i>	2	31	31	21
3	<i>Megaselia nigriceps</i>	3	26	30	29
4	<i>Megaselia manicata</i>	4	12	21	12
5	<i>Megaselia zonata</i>	5	29	41	45
6	<i>Triphleba opaca</i>	6	47	33	20
7	<i>Megaselia pleuralis</i>	7	16	23	23
8	<i>Megaselia pumila</i>	8	7	17	36
9	<i>Megaselia latifrons</i>	9	21	16	24
10	<i>Metopina oligoneura</i>	10	45	34	33
11	<i>Megaselia involuta</i>	11	14	26	31
12	<i>Megaselia campestris</i>	12	18	18	14
13	<i>Conicera dauci</i>	13	43	42	41
14	<i>Megaselia minor</i>	14	49	37	39
15	<i>Megaselia giraudii</i>	15	3	1	2
16	<i>Megaselia xanthozona</i>	16	46	38	32
17	<i>Megaselia meconicera</i>	17	8	43	8
18	<i>Megaselia woodi</i>	18	2	2	1
19	<i>Megaselia pulicaria-complex</i>	19	5	15	7
20	<i>Megaselia lata</i>	20	13	39	43
21	<i>Anevrina thoracica</i>	21	42	25	17
22	<i>Triphleba trinervis</i>	22	32	35	35
23	<i>Megaselia diversa</i>	23	1	4	16
24	<i>Megaselia scutellaris</i>	24	36	0	42
25	<i>Megaselia emarginata</i>	25	33	29	25
26	<i>Megaselia affinis</i>	26	34	32	0
27	<i>Megaselia altifrons</i>	27	23	6	37
28	<i>Megaselia ignobilis</i>	28	11	10	0
29	<i>Megaselia dimidia</i>	29	25	0	44
30	<i>Phora artifrons</i>	30	9	8	9
31	<i>Phora obscura</i>	31	15	7	3
32	<i>Megaselia unicolor</i>	32	4	5	10

Table VII. cont.

1	2	3	4	5	6
33	<i>Borophaga subsultans</i>	33	20	22	30
34	<i>Megaselia curvicapilla</i>	34	17	0	0
35	<i>Phora penicillata</i>	35	6	3	11
36	<i>Megaselia pusilla</i>	36	30	24	6
37	<i>Megaselia propinqua</i>	37	27	0	28
38	<i>Megaselia hyalipennis</i>	38	10	14	13
39	<i>Phalacrotophora fasciata</i>	39	24	13	26
40	<i>Megaselia ruficornis</i>	40	38	20	22
41	<i>Phora holosericea</i>	41	48	11	4
42	<i>Megaselia sordida</i>	0	19	0	0
43	<i>Megaselia sepulchralis</i>	0	22	26	5
44	<i>Megaselia lutea</i>	0	35	0	34
45	<i>Megaselia henrydisneyi</i>	0	37	19	0
46	<i>Phora dubia</i>	0	39	12	27
47	<i>Phalacrotophora berlinensis</i>	0	40	27	18
48	<i>Megaselia pseudogiraudii</i>	0	41	0	30
49	<i>Borophaga carimifrons</i>	0	44	40	15
50	<i>Phora tincta</i>	0	0	0	19
51	<i>Phora pubipes</i>	0	50	9	46

The graphically presented similarity of dominance structure based on Morisita's index and calculated according the Mountford's method, illustrates the increasing similarity between the communities in older and older age-classes of tree stand and the distinct separatedness of the "colonizing" phorid community in pine plantations (Fig. 12).

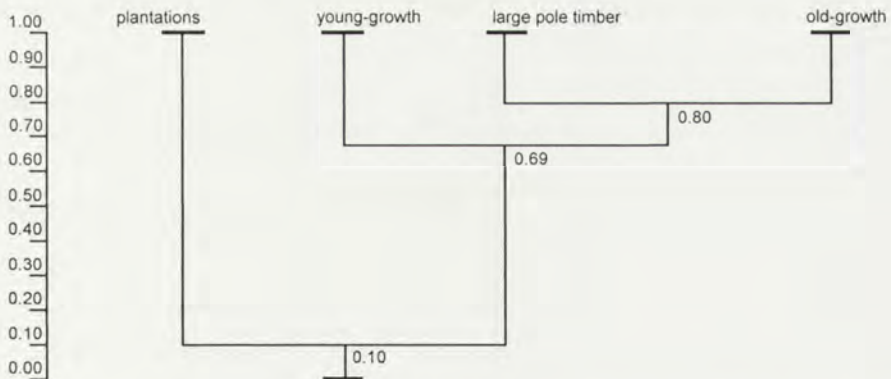


Fig. 12. Dendrogram of dominance structure similarity of the phorid communities in moist pine forest in Białowieża Forest; based on Morisita's index.

Morisita's index presents the similarity of dominance structures of high-abundance species very well while a very large group of low-abundance species is disregarded.

Small differences in the number of species with high (over 1%) and small abundances were recorded from plantations and large pole timber as well as from young-growth and old-growth. The proportion of the abundance of the most numerous species was very high in the communities in all four age-classes, ranging from about 80% in old-growth to about 90% in plantations. In the phorid communities from plantations, young-growth and large pole timber groups of species with abundance over 10% constituted about 40% of the community from a given age-class. That proportion reached nearly 60% in old-growth (Figs 8-11).

Homogeneity index (HD) was used to define the essential impact of accessory species on dominance structure similarities. This index, as a measure of overlapping of dominance structures, is more appropriate for low-abundance species (Fig. 13) (RIEDL 1963).

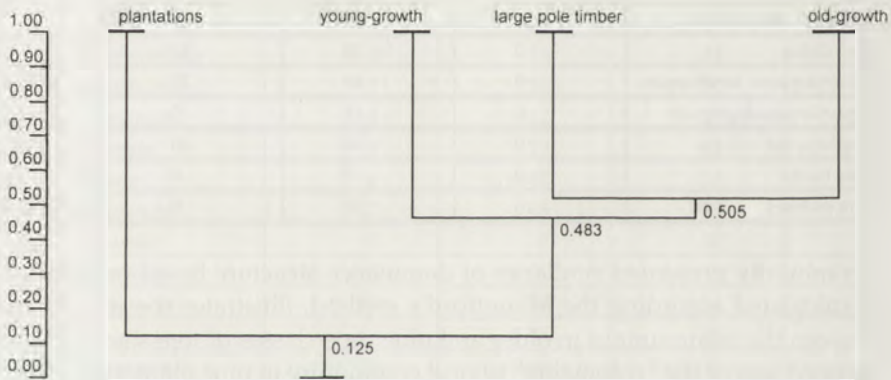


Fig. 13. Dendrogram of the similarity of dominance structures of the phorid communities in moist pine forest in Białowieża Forest; based on homogeneity index.

When links between dominance structures are presented basing on homogeneity index, or on Morisita's index, it is evident that the phorid communities in plantations differed considerably from those in the older age-classes of tree stands. However, for the scuttle fly communities in young-growth, large pole timber and old-growth, Morisita's index shows similarity much higher than does homogeneity index (Figs 12, 13).

Modified homogeneity index (HD^*) was used to define, without reference to species composition, the dominating interdependences within communities. The so-called ranks of species were created. A given rank comprised species of the same abundance proportion in a community.

The result obtained by this method reflects a relatively high (70-85%) similarity between the dominance structures of the phorid communities studied in the four age-classes of moist pine forest (Fig. 14). The highest similarity was recorded for the communities in plantations and large pole timber. An almost identical, "model" distribution of the proportion of mean abundance of the dominants was observed there. There was one distinct dominant in these communities. The proportion of particular species decreased uniformly, and low-abundance species formed the distribution tail (Figs 8, 10).

The scuttle fly communities from young-growth and old-growth lacked one single dominant, but there were two co-dominating species whose proportions in abundance percentages were very similar (Figs 9, 11). The other features of the distribution of dominance structure were similar to the distribution estimated for the communities in plantations and large pole timber (Figs 8–11).

The abundance proportion of species dominating in the older age-classes of forest, namely that of *M. woodi* and *M. giraudii*, increased with the aging of tree stand (Figs 8, 9, 10, 11). Modified homogeneity index suggests that a very high abundance (about 60%) of eudominants of the communities in the oldest age-class largely influenced a decrease in the similarity of the phorid communities in old-growth as compared with those in the younger age-classes of tree stand (Fig. 14).

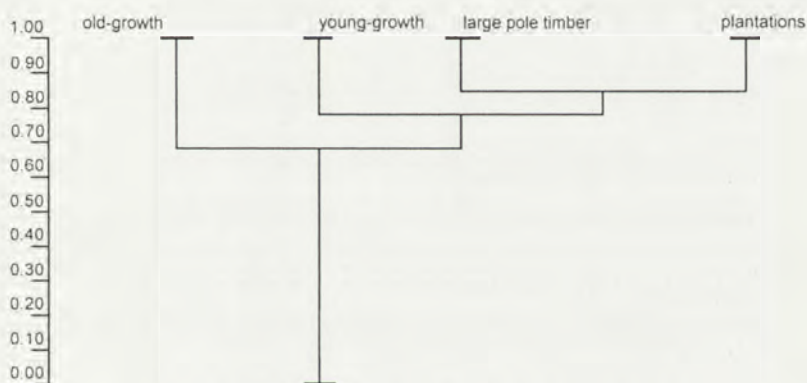


Fig. 14. Dendrogram of dominance structure similarity of the phorid communities in moist pine forest in Białowieża Forest; based on homogeneity index in accordance with species rank.

The obtained models of changes in ratios between species in the phorid communities from the four age-classes of the succession series of moist pine forest in Białowieża Forest were most frequently recorded for natural and semi-natural ecosystems. In such ecosystems, human interference is low and the habitat is highly diverse (TROJAN 1997).

M. verralli and *M. brevicostalis* played the role of colonists in the process of secondary succession of phorid communities from the moist pine forest. Tolerance of species to a new habitat decreased very distinctly even in young-growth. The fidelity (W) of *M. verralli* was below 1% in the older tree stands, whereas that of *M. brevicostalis* exceeded 4% in the communities from mature tree stands. In young-growth these species were ousted by highly expansive *M. giraudii* and *M. woodi* (Table VIII). Co-dominance of both species intensified in the course of succession of the phorid communities in moist pine forest.

On the basis of the results of the similarity of species composition and dominance structure it may be assumed that the phorid communities studied in the four age-classes of tree stand were not homogeneous in ecological respect. The species with a wide amplitude of ecological tolerance – with regard to age-classes of forest – included the dominants of the communities from young-growth, large pole timber and old-

growth. The second group comprised accessory species, associated with ecological microniches of the four age-classes of pine tree stand (Table V). The flexibility of forest species of the phorid communities in the older age-classes of tree stands was considerably higher than that of species of open areas which dominated in pine plantations. The proportion of the latter in the scuttle fly communities from the older age-classes decreased in the course of secondary succession of moist pine forest (Table VIII).

Table VIII. Fidelity (W%) of the dominant phorid species in the four age-classes of moist pine forest in Białowieża Forest.

Nr	Species	Plantations	Young-growth	Large pole timber	Old-growth
1	2	3	4	5	6
species of opened area					
1	<i>Megaselia verralli</i>	92.29	6.03	0.89	0.79
2	<i>Megaselia brevicostalis</i>	86.65	6.47	2.41	4.47
3	<i>Megaselia nigriceps</i>	79.53	13.29	3.91	3.27
4	<i>Megaselia zonata</i>	76.42	21.62	1.29	0.66
5	<i>Megaselia minor</i>	75.58	7.41	8.37	8.64
6	<i>Metopina oligoneura</i>	72.99	12.46	6.43	8.12
7	<i>Conicera dauci</i>	70.99	19.31	4.06	5.64
forest's species					
8	<i>Triphleba opaca</i>	78.30	4.14	4.33	13.23
9	<i>Megaselia xanthozona</i>	62.31	14.93	7.59	15.17
10	<i>Megaselia pleuralis</i>	47.57	31.59	13.72	7.11
11	<i>Megaselia manicata</i>	47.38	34.97	7.94	9.71
12	<i>Megaselia latifrons</i>	36.70	28.93	26.03	8.34
13	<i>Megaselia scutellaris</i>	31.71	59.34	0.00	8.95
14	<i>Megaselia involuta</i>	31.36	49.98	14.11	4.55
15	<i>Triphleba trinervis</i>	29.27	51.90	8.27	10.55
16	<i>Megaselia affinis</i>	23.21	58.83	17.96	0.00
17	<i>Megaselia campestris</i>	22.94	33.48	23.93	19.65
18	<i>Megaselia pumila</i>	21.74	64.97	12.03	1.26
19	<i>Megaselia lata</i>	18.47	76.99	2.78	1.76
20	<i>Megaselia emarginata</i>	15.80	39.01	23.39	21.80
21	<i>Megaselia dimidia</i>	13.49	82.44	0.00	4.07
22	<i>Megaselia meconicera</i>	7.92	62.82	0.32	28.94
23	<i>Megaselia pulicaria-complex</i>	4.19	69.47	8.41	17.93
24	<i>Megaselia altifrons</i>	4.14	24.12	69.32	2.42
25	<i>Megaselia curvicapilla</i>	4.02	95.98	0.00	0.00
26	<i>Anevrina thoracica</i>	3.26	21.45	37.10	38.19
27	<i>Megaselia ignobilis</i>	3.09	65.09	31.81	0.00
28	<i>Borophaga subsultans</i>	2.72	56.26	32.41	8.62
29	<i>Megaselia propinqua</i>	2.65	75.43	0.00	21.91
30	<i>Megaselia ruficornis</i>	1.37	24.54	49.47	24.62
31	<i>Phora artifrons</i>	1.21	47.38	29.92	21.49
32	<i>Megaselia giraudii</i>	1.06	32.31	33.23	33.41
33	<i>Megaselia woodi</i>	0.99	40.63	18.91	39.46
34	<i>Phalacrotophora fasciata</i>	0.85	39.20	49.72	10.23

Table VIII. cont.

1	2	3	4	5	6
35	<i>Megaselia diversa</i>	0.84	77.21	20.18	1.78
36	<i>Megaselia pusilla</i>	0.76	19.32	17.37	62.54
37	<i>Phora obscura</i>	0.66	12.43	21.48	65.42
38	<i>Phora holosericea</i>	0.43	1.82	28.94	68.80
39	<i>Megaselia unicolor</i>	0.43	75.54	18.20	5.83
40	<i>Megaselia hyalipennis</i>	0.39	65.36	20.23	14.02
41	<i>Phora penicillata</i>	0.30	52.18	41.13	6.39
42	<i>Megaselia sordida</i>	0.00	100.00	0.00	0.00
43	<i>Megaselia sepulchralis</i>	0.00	22.25	7.83	69.92
44	<i>Megaselia lutea</i>	0.00	74.51	0.00	25.49
45	<i>Megaselia henrydisneyi</i>	0.00	33.00	67.00	0.00
46	<i>Phora dubia</i>	0.00	16.24	70.04	13.72
47	<i>Phalacrotophora berlinensis</i>	0.00	26.71	31.45	41.83
48	<i>Megaselia pseudogiraudii</i>	0.00	77.38	0.00	22.62
49	<i>Borophaga carinifrons</i>	0.00	22.53	7.34	70.13
50	<i>Phora tincta</i>	0.00	0.00	0.00	100.00
51	<i>Phora pubipes</i>	0.00	0.88	98.09	1.03

Despite considerable differences in abundance there were observed similar values of the species richness indices for the communities in plantations and large pole timber on the one hand and for those in young-growth and old-growth on the other. The rise-fall changes of these indices were proportional to rise-fall changes in the number of species (Table II, Fig. 15).

Discrimination analysis was applied to separate species associated with developing microniches. It was assumed that they form a tail of species frequency distribution. This part of distribution was separated from dominants by broken-stick distribution. The tail of distribution fits well this distribution model with $p \geq 0.9$. When approaching to the dominants this probability falls rapidly below $p = 0.5$. In this manner the boundary was established between dominating group and those distributed at random (Fig. 16–19). The ratio of species and individuals which fits random distribution to dominants was accepted as an index of environment differentiation in a form of patchy microniches.

Indices of the mosaic-like character of the four age-classes of moist pine forest were calculated on the basis of data on the number of species and individuals within the communities studied (TROJAN 1997).

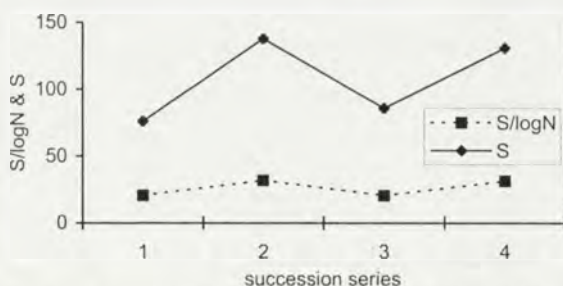


Fig. 15. Changes in the species composition ($S/\log N$; N – liczba osobników) and in the number of species (S) of the phorid communities in the four age-classes of moist pine forest in Białowieża Forest.

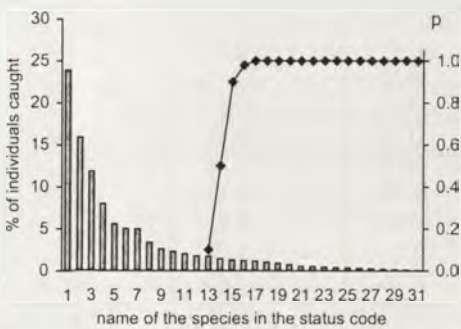


Fig. 16. Abundance distribution of phorid species in accordance with their status in the community in pine plantations.

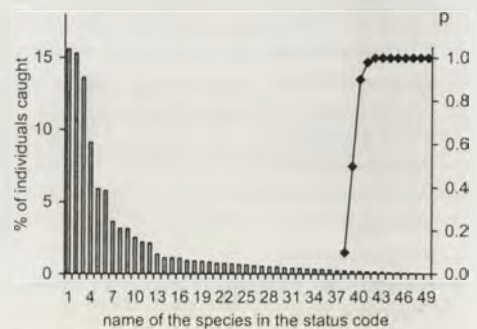


Fig. 17. Abundance distribution of phorid species in accordance with their status in the community in young-growth.

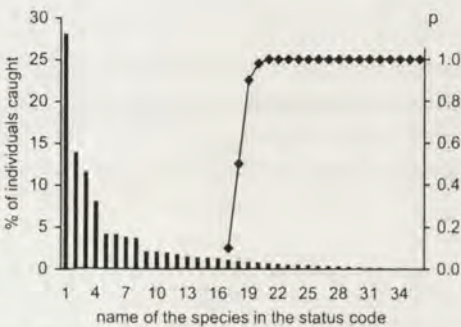


Fig. 18. Abundance distribution of phorid species in accordance with their status in the community in large pole timber.

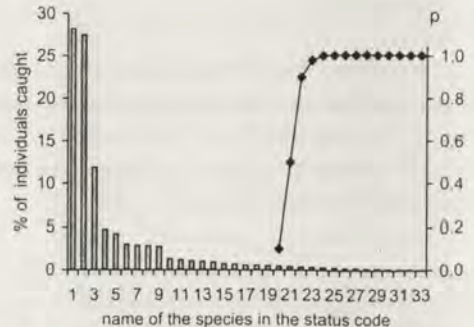


Fig. 19. Abundance distribution of phorid species in accordance with their status in the community in old-growth.

The numerical and species indices of the mosaic-like character had the lowest values in young-growth, where the greatest number of scuttle fly individuals had been recorded; the highest values were in old-growth (Table IX). The results show that also in old-growth, where most of the habitat had been subject to secondary differentiation, the highest was the proportion of species associated with developing ecological microniches in the oldest age-class of the succession series of moist pine forest.

4 c. Species diversity

Moist pine forest, which represents the association *Peucedano-Pinetum*, is phytosociologically homogeneous, and in respect of habitat too, and therefore the habitat conditions are influenced by the age of the pine tree stand of a given succession series. The species composition and abundance of phorid communities change with the growth of a given tree stand. The actual species diversity (H') of *Phoridae* also changes,

and there is empirical evidence for this. In order to estimate actual diversity (H') and the degree of realization of potential diversity (f) it is necessary to establish the potential number of species (S^*).

The differences between the potential number of species (S^*) and that obtained empirically (S) for the phorid communities in large pole timber and old-growth were small (about 5-6%). These differences reached 20% for the phorid communities in plantations and young-growth. The number of species recorded in plantations and young-growth has been lowered, whereas the empirical number of species for the communities in old-growth is slightly higher than the estimated one (Table X).

Such evident discrepancies may be due to the fact that in the course of identifying the material the number of species is lowered (in this study, some females of the genera *Megaselia* and *Phora* were unidentifiable, and about 50% of the species were determined based on one sex only) (DISNEY 1994). The number of empirically recorded species does not fully reflect the capacity of the habitats studied, but it confirms the change tendencies in the number of species (rise-fall-rise) in the course of succession of moist pine forest (Table X).

Table IX. Values of the mosaic indices for the phorid communities in the four age-classes of tree stand in moist pine forest in Białowieża Forest. Mn* - numerical index of the mosaic-like character of the habitat, Ms* - species index of the mosaic-like character of the habitat.

Habitat	Mn*	Ms*
plantations	0.0288	0.8157
young-growth	0.0148	0.6956
large pole timber	0.0198	0.7674
old-growth	0.0311	0.8244

Table X. Analysis of the estimate of the number of species using Arrhenius's function for the phorid communities in the four age-classes of moist pine forest in Białowieża Forest. S - number of species obtained empirically, S^* - estimated number of species, N - number of individuals caught into yellow traps.

Empirical data				Theoretical data						
Plantations S=76	N	N	5119	1	10	100	1000	10000	100000	1000000
	S^*	S^*	102.0948	1	21.4638	38.1686	67.8746	120.7000	214.6383	381.6869
		dS^*/dN	0.0083	1	2.2737	0.1856	0.0330	0.0058	0.0010	0.0002
Young-growth S=138	N	N	21304	1	10	100	1000	10000	100000	1000000
	S^*	S^*	189.9187	1	27.9546	49.7110	88.4001	157.2000	279.5455	497.1100
		dS^*/dN	0.0029	1	2.9950	0.2417	0.0672	0.0076	0.0014	0.0002
Large pole timber S=86	N	N	15664	1	10	100	1000	10000	100000	1000000
	S^*	S^*	91.8478	1	14.5996	25.9623	46.1682	82.1000	145.9967	259.6230
		dS^*/dN	0.0017	1	1.5110	0.1262	0.0224	0.0039	0.0007	0.0001
Old-growth S=131	N	N	15094	1	10	100	1000	10000	100000	1000000
	S^*	S^*	125.5830	1	20.1479	35.8286	63.7132	113.3000	201.4791	358.2861
		dS^*/dN	0.0024	1	2.1275	0.1742	0.0310	0.0055	0.0009	0.0002

The succession variant realized by a scuttle fly community with regard to actual diversity (H') is most similar to the stabilizing variant (TROJAN 1994).

The similar values of the actual diversity and potential diversity indices in plantations and large pole timber most probably were connected not only with a similar species richness and species capacity of these habitats but with the similarity of dominance structures as well (Table XI, Fig. 14).

Table XI. Species diversity of the phorid communities in the four agr-classes of the succession series of moist pine forest in Białowieża Forest. H' - the Shannon-Weaver index, H_{max} - maximum value of the Shannon-Weaver index, J - degree of realization of potential species diversity.

Type of habitat	H'	H_{max}	J (%)
plantations	4.203	6.674	62.98
young-growth	4.623	7.569	61.08
large pole timber	4.260	6.521	65.33
old-growth	4.141	6.973	59.39

Common species occurring in high abundances had the greatest impact on the value of the Shannon-Weaver index. In plantations they were species of the genus *Megaselia*, particularly *M. verralli* and *M. brevicostalis* - the eudominant and dominant of this age-class of tree stands. However, in older age-classes of the succession series of moist pine forest - besides *Megaselia giraudii*, a polytope associated with pine canopies, and *M. woodi* - species of other genera,

those of the genus *Phora* in particular reached higher and higher abundances (Figs 8-11) (DURSKA 1996).

In the phorid communities in plantations and large pole timber, the values of the Shannon-Weaver index reflected a similar degree of species diversity. Moreover, the degree to which species diversity was realized, expressed by the Pielou index, had similar values and was the highest (about 63-65%) for these two age-classes. These similar values of the diversity indices were probably influenced by a similar abundance distribution of species and the proportion of the eudominants: *M. verralli* and *M. giraudii* (Table XI, Figs 8, 10).

A decrease in the value of the Pielou index for the scuttle fly communities in old-growth accompanied by an increase in the numerical and species index of the mosaic-like character of the habitat was due to an increase in better internal organization and to an eventual dominance structure characteristic of phorid communities in the oldest age-class of stand in the succession series of moist pine forest (Tables IX, XI; Figs 9, 11).

4 d. Seasonal dynamics of phorid abundances

Phoridae may overwinter as eggs, larvae or pupae. They may also overwinter as imagines inside their puparia (ROBINSON 1971, ROBINSON, BROWN 1993). There are scuttle fly species, particularly of the genus *Triphleba*, whose imagines tolerate winter conditions very well (LECLERCQ, WATRIN 1973, DURSKA - unpublished data). In the *Phoridae*, seasonal variability of species composition and abundance of communities is influenced by the greatly differing time of emergence, the length of the period of occurrence and the number of generations. In the phorid communities from the four

age-classes of pine tree stand, most species reached the peak of their abundance in spring (May – lower peak) and in autumn (September – higher peak) (DURSKA 1996).

In the communities from plantations the spring abundance peak was most influenced by an increase in the abundance of species of the genus *Megaselia*, namely *M. brevicostalis*, *M. manicata* and *M. zonata*, but also of those of *Triphleba* (*T. opaca* in particular) and *Metopina*. Then in May and June, they were joined by species of the genera *Phora* and *Conicera* (*C. dauci*). The abundance of species of the genera *Megaselia*, *Metopina* and *Conicera* also increased in August. The autumn increase followed by a decrease in the abundance of the phorid communities from plantations was observed in September. These variations were due to abrupt changes in the abundance of the dominant species of the genus *Megaselia* (*M. verralli*, *M. manicata*, *M. brevicostalis*, and *M. zonata*). An increase in the abundance of species of the genus *Metopina* was recorded at that time too. During that period the number of species in the community increased to its maximum, exceeding 28% (Fig. 20).

In young-growth, just as in plantations, the phorid community reached its abundance peaks in spring and in autumn (the higher peak). From April to June, spring peaks were recorded first of all for species of the genera *Triphleba*, *Metopina*, *Megaselia*, *Phora* and *Borophaga*. The autumn abundance increase was enhanced by an increase in the abundance of species of the genus *Megaselia*: *M. diversa*, *M. giraudii*, *M. ignobilis*, *M. manicata*, *M. meconicera*, *M. pulicaria*, *M. sordida* and *M. woodi*. That was the time when the highest number of scuttle fly species (over 32%) was recorded. The abundance of the dominants of the genus *Megaselia* remained high until the end of the study seasons; the same was true for species of the genus *Triphleba*. Species of the genus *Phora* occurred in considerably higher abundances in the habitat of young-growth than in the communities from plantations. The second abundance increase recorded for species of this genus occurred at the turn of July and August. *Phalacrotophora fasciata* and *Ph. berolinensis* – parasitoids of ladybird pupae, never recorded in the communities from plantations – appeared in young-growth in May, and were recorded until September. The first abundance peak of these species was at the turn of June and July, and the second in August. During the study season, the abundance increase in the community from young-growth is overlapped with an increase in the number of its species (Appendix; Fig. 21).

An abrupt abundance rise and fall was observed in the scuttle fly communities from large pole timber in May. The abundance of species of the genus *Megaselia*, especially that of the eudominant *M. giraudii*, increased at that time. The autumn species *M. woodi* also appeared (2 individuals) in May. In species of the genus *Phora*, the first

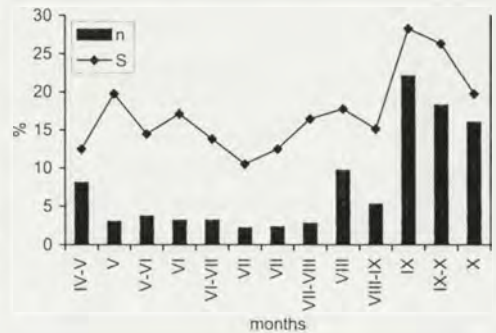


Fig. 20. Changes in the abundance (n) and number of species (S) of the phorid communities in pine plantations of moist pine forest in Białowieża Forest.

abundance peak was recorded in May, and *Ph. artifrons* reached the highest abundance then. Species of the genera *Anevrina* and *Conicera*, too, had the highest peak of abundance in May. In species of the genus *Triphleba* abundance increased earlier, i.e. at the turn of April and May, in species of the genus *Borophaga* at the turn of May and June, whereas in *Phalacrotophora* at the turn of June and July. In May, the number of species in the community increased by over 15%. At the end of May, when the abundance of scuttle flies declined abruptly, the number of species dropped gradually. In August, both the abundance of the community and the number of species increased again. The abundance increased gradually, starting in August and reaching the peak in mid-September, but at the turn of September and October it slightly decreased (by less than 5%). In October, it dropped markedly. The autumn rise and fall in abundance was accompanied by abundance increases in species of the genera *Megaselia* (mainly of the dominants), *Borophaga*, *Triphleba* and *Conicera*. The abundance of species of the genus *Phora* was high from July through September. Species of this genus occurred until October. The eudominant *M. woodi* appeared again at the turn of July and August, and an abrupt increase in its abundance was recorded at the turn of August and September. The abundance of *M. woodi* remained high until the end of the seasons. The number of species in large pole timber decreased gradually, starting already in August (Appendix; Fig. 22).

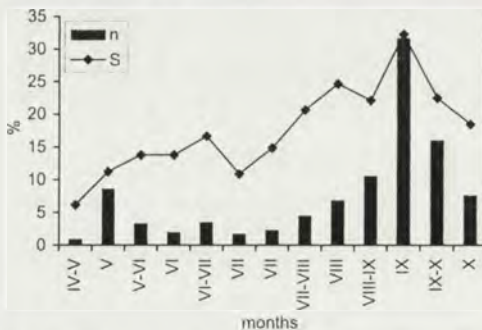


Fig. 21. Changes in the abundance (n) and number of species (S) of the phorid communities in young-growth of moist pine forest in Białowieża Forest.

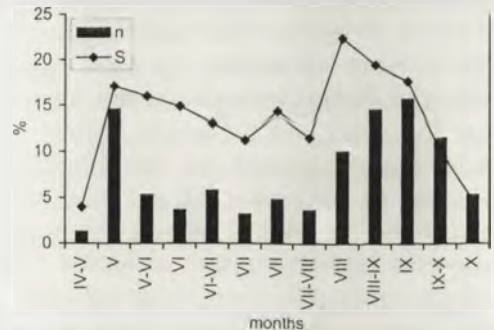


Fig. 22. Changes in the abundance (n) and number of species (S) of the phorid communities in large pole timber of moist pine forest in Białowieża Forest.

Within the phorid communities from old-growth the course of changes in abundance and number of species was similar to that of the communities in large pole timber. During the peak in May, the highest abundance was reached by species of the genus *Phora* (*Ph. obscura* in particular). The May increase in abundance is overlapped by an abundance increase of species of the genus *Megaselia*, mainly *M. giraudii*, *M. meconicera* and *M. pusilla*. The abundance of species of the genus *Anevrina* greatly increased at the same time. Just as in their communities of large pole timber, the abundance peak of species of the genus *Triphleba* occurred a little earlier, i.e. at the turn of April and May. An abundance increase in *Phalacrotophora fasciata* and *Ph. berlinensis* was recorded in May and June. The abundance of *Conicera dauci* also increased in

spring. The highest abundance rise and fall in species of the genus *Megaselia* was observed in September. The second rise and fall in abundance of species of the genus *Phora* occurred in August. That was a time when the maximum increase (by over 23%) in the number of species of the community was recorded (Fig. 23). The eudominant *M. woodi* appeared in the phorid communities from old-growth in August and its abundance was high till the end of the growing season (DURSKA 1996).

In general, it was found that species of the genera *Phora*, *Megaselia*, *Anevrina*, *Borophaga* and *Conicera* had the greatest proportion in the first, i.e. May abundance peak of the communities in the four age-classes of forest. The abundance of species of the genus *Phora* was the highest and more than twice that of the genus *Megaselia*. Species of the genera *Metopina* and *Triphleba* reached the spring peak of abundance earlier, at the turn of April and May. The second and successive peaks of abundance of species of particular genera fell at different times; *Anevrina* - in July, *Borophaga* - in July and September, *Conicera* - at the turn of June and July, and also in August, *Megaselia* - at the turn of June and July, also in September (the highest peak), *Metopina* - in July and September, *Phora* - in August, *Triphleba* - at the turn of August and September. The highest abundance peak in the genus *Phalacrotophora* recorded at the turn of June and July (Table XII) was connected with the biology of the host, i.e. of coccinellids (CERYNGIER, HODEK 1996; KATSOYANNOS, STATHAS, KONTODINAS 1997).

The September rise and fall in the abundance of species of the genus *Megaselia*, recorded in the communities in all age-classes of moist pine forest, was influenced most by an increase in the dominance of the dominants, especially of *M. woodi* and the polyphagous *M. giraudii*. The autumn species *M. woodi* whose biology is unknown, probably is associated with fungi (MALLOCH 1906; DURSKA 1996).

4 e. Changes in the diet of the Phoridae in the succession series of moist pine forest

Species whose biology is known make up only about 30% ($S = 55$) of those within the studied phorid communities from the four age-classes of tree stand. On the basis of their larval diet, they have been divided into four groups (Appendix; Table XIII).

In the communities from pine plantations the highest abundance proportion (about 90%) belonged to saprophagous species ($S = 9$), especially to *Megaselia brevicostalis* and *M. nigriceps* - the dominants of that habitat, and to *M. pleuralis* - the subdominant. The second position was occupied by *M. giraudii* and *M. pulicaria* - complex, polyphagous species. The abundance of polyphages slightly exceeded 5%. Within this group of fungivores ($S = 8$) *M. lata* reached the highest abundance. The lowest abundance pro-

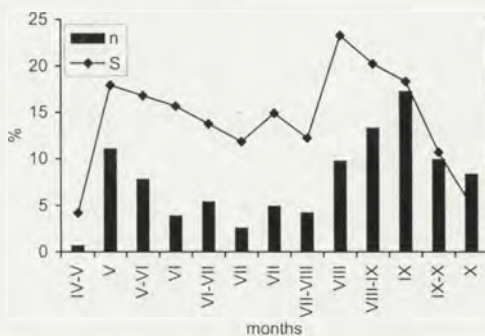


Fig. 23. Changes in the abundance (n) and number of species (S) of the phorid communities in old-growth of moist pine forest in Białowieża Forest.

Table XII. Changes, during the growing season, in the abundance (n*) of selected genera of the phorid communities in the four age-classes of moist pine forest in Białowieża Forest. n* – abundance index (females + males) converted to 100 24-hour trap.

Months	IV-V	V	V-VI	VI	VI-VII	VII	VII	VII-VIII	VIII	VIII-IX	IX	IX-X	X
1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Anevrina</i>													
	n*	n*	n*	n*	n*	n*	n*	n*	n*	n*	n*	n*	n*
Plantations	0.00	0.89	0.56	0.00	0.00	0.00	0.48	0.48	0.00	0.00	0.00	0.00	0.00
Young-growth	0.00	0.89	0.83	0.24	0.00	0.00	0.24	0.00	1.03	0.24	0.00	0.00	0.00
Large pole-timber	0.37	2.67	0.83	0.49	0.24	0.21	0.73	0.26	0.00	0.00	0.00	0.00	0.00
Old-growth	0.00	2.53	1.65	0.71	0.51	0.00	0.51	0.71	0.26	0.24	0.00	0.00	0.00
sum	0.37	6.97	3.87	1.45	0.75	0.21	1.96	1.45	1.28	0.48	0.00	0.00	0.00
<i>Borophaga</i>													
Plantations	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.55	0.00
Young-growth	0.34	1.33	0.83	0.24	0.00	0.45	0.71	2.95	2.44	2.76	1.19	0.95	0.82
Large pole-timber	0.73	1.10	1.67	0.00	0.00	0.00	3.17	0.51	1.28	0.44	1.04	0.00	0.00
Old-growth	0.00	1.16	0.28	0.48	0.26	0.48	1.28	0.00	6.92	0.49	0.77	0.48	0.00
sum	1.07	3.59	2.78	0.71	0.26	0.93	5.71	3.46	10.64	3.70	3.00	1.98	0.82
<i>Conicera</i>													
Plantations	0.00	0.67	0.56	0.48	1.91	0.00	2.45	0.46	1.69	0.22	0.00	0.00	0.00
Young-growth	0.00	0.43	0.28	0.00	0.95	0.24	0.50	0.44	0.24	0.24	0.00	0.00	0.00
Large pole-timber	0.00	0.22	0.00	0.00	0.24	0.00	0.00	0.00	0.26	0.51	0.00	0.00	0.00
Old-growth	0.00	0.48	0.56	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0.00	0.00	0.00
sum	0.00	1.80	1.39	0.48	3.10	0.24	2.95	1.38	2.18	0.97	0.00	0.00	0.00
<i>Megaselia</i>													
Plantations	27.14	7.81	9.76	16.78	14.05	7.53	10.27	11.89	52.18	29.44	121.07	108.85	95.21
Young-growth	6.63	33.03	21.90	21.43	47.86	20.18	27.75	53.67	89.36	155.38	495.95	258.10	114.07
Large pole-timber	2.38	24.31	19.59	15.61	38.33	15.42	23.43	17.59	68.24	108.59	126.73	97.45	43.13
Old-growth	1.53	19.91	15.19	17.38	44.13	16.06	30.41	25.89	58.31	120.09	160.46	95.56	76.56
sum	37.69	85.05	66.45	71.20	144.37	59.19	91.86	109.04	268.08	413.50	904.21	559.95	328.98

1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Metopina</i>													
Plantations	6.67	3.53	1.62	1.50	0.00	3.89	0.55	0.48	0.95	0.44	2.14	0.55	0.00
Young-growth	0.51	0.22	0.26	0.00	0.00	0.00	0.00	0.91	0.26	0.22	0.48	0.00	0.00
Large pole-timber	0.18	0.00	0.26	0.00	0.00	0.24	0.26	0.00	0.26	0.00	0.00	0.00	0.00
Old-growth	0.00	0.00	0.00	0.48	0.00	0.00	1.78	1.02	0.00	0.00	0.00	0.00	0.00
sum	7.36	3.75	2.14	1.98	0.00	4.13	2.58	2.40	1.46	0.67	2.62	0.55	0.00
<i>Phalacrotophora</i>													
Plantations	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Young-growth	0.00	0.21	0.26	0.95	2.86	2.98	0.97	2.38	3.33	0.22	0.00	0.00	0.00
Large pole-timber	0.00	0.00	0.51	3.88	6.67	3.33	1.21	0.26	0.26	0.22	0.28	0.00	0.00
Old-growth	0.00	0.00	1.05	2.62	1.75	0.96	0.77	0.48	0.26	0.00	0.00	0.00	0.00
sum	0.00	0.21	1.82	7.45	11.75	7.27	2.95	3.11	3.85	0.44	0.28	0.00	0.00
<i>Phora</i>													
Plantations	0.32	1.33	4.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Young-growth	1.02	17.50	1.80	0.00	0.48	0.48	0.51	2.00	1.43	0.22	0.00	0.95	5.00
Large pole-timber	6.23	93.93	19.27	4.58	2.62	6.10	10.44	11.22	9.48	5.56	4.40	0.51	0.28
Old-growth	2.72	60.15	27.91	8.81	2.77	6.96	13.03	12.00	21.00	4.78	2.30	0.00	0.00
sum	10.29	172.91	53.42	13.39	5.87	13.53	23.99	25.22	31.91	10.56	6.69	1.46	5.28
<i>Triphleba</i>													
Plantations	17.67	0.44	0.28	0.00	0.00	0.00	0.00	0.24	0.77	0.67	0.71	0.48	3.89
Young-growth	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.24	1.41	0.24	1.19	8.30
Large pole-timber	1.10	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0.77	1.75	0.53	0.00	1.17
Old-growth	2.38	0.71	0.00	0.00	0.00	0.00	0.26	0.22	2.05	1.46	0.26	0.00	3.13
sum	22.17	1.16	0.28	0.00	0.00	0.48	0.26	0.90	3.82	5.30	1.74	1.67	16.48

portion, below 2%, was recorded for the group of zoophages ($S = 7$). In this group *Triphleba lugubris* had the highest abundance (Appendix). The larvae of this species feed on dead or living pupae of wasps (MACDONALD *et al.* 1975).

Table XIII. Number of species (S) and share (%) of the trophic groups in the phorid communities the four age-classes of moist pine forest in Białowieża Forest.

Habitat	Plantations		Young-growth		Large pole timber		Old-growth	
	S	%	S	%	S	%	S	%
saprophages	9	88.17	13	18.42	11	8.19	11	15.32
fungivores	8	4.79	16	16.39	5	4.75	13	6.17
zoophages	7	1.89	12	5.13	12	13.49	13	5.22
polyphages	2	5.14	3	60.06	2	73.57	2	73.29

The highest abundance share (about 60%) in the phorid communities in young-growth was recorded for three polyphagous species: *M. giraudii* and *M. pulicaria-complex* - the dominants, and *M. scalaris*. The abundance of saprophages ($S = 13$) declined by about 60%. In the community in young-growth the number of fungivorous species ($S = 16$) increased twofold and their abundance, as compared with the community in plantations, increased fourfold. The number ($S = 12$) and abundance of zoophages (about 5%) increased too. The highest abundance in this trophic group was reached by species of the genus *Phalacrotophora*: *Ph. fasciata* and *Ph. berolinensis* whose larvae are parasitoids of ladybird pupae (Appendix) (MENOZZI 1927, WYLIE 1958).

In the phorid community in large pole timber the abundance proportion of two polyphagous species: *M. giraudii* - the dominant and *M. pulicaria* - complex was over 70%. The abundance proportion of zoophages ($S = 12$) increased, particularly that of species of the genus *Phalacrotophora* and also of *Phora holosericea*. The last species is a predator of root aphids (YARKULOV 1972). The number ($S = 5$) and abundance of fungivorous species decreased threefold. The abundance proportion of saprophages ($S = 11$) slightly exceeded 8%.

The polyphages *M. giraudii* (eudominant) and *M. pulicaria* - complex (subdominant) in the phorid communities in old-growth constituted a group with the highest abundance proportion (over 73%), just as was the case in the communities in young-growth and large pole timber. The second position was occupied by a group of saprophages ($S = 11$) whose abundance was over 15%. In the communities in old-growth, as compared with those in large pole timber, the number of fungivorous species ($S = 13$) increased twofold while the abundance of fungivores rose insignificantly. The abundance of zoophages ($S = 13$) decreased by half. In this group, as compared with the community from large pole timber, there was observed a very distinct (over fivefold) decrease in the abundance of *Phalacrotophora fasciata* and an over twofold increase in the abundance of *Phora holosericea* (Appendix).

The abundance proportions of the trophic groups within the phorid communities in the four age-classes of moist pine forest were decided by the abundance of species whose biology is known and which dominated in these communities. In the commu-

nity from pine plantations the highest abundance was reached by the group of saprophages with the eudominant *M. brevicostalis* whose fidelity in this habitat was over 80% (Fig. 4). Species belonging to the other trophic groups had low abundance shares. In the communities in the older age-classes of pine tree stand the proportion of polyphages increased more and more: about 60% in young-growth, about 73% in large pole timber and old-growth. The increase in the abundance proportion of the group of polyphagous species ($S = 3$) was radically influenced by an increase in the abundance of *M. giraudii* which was the subdominant in the communities in plantations (1.22%), the dominant in young-growth (12.73%) and the eudominant in large pole timber and old-growth (about 23–25%) (Figs 7–10). In the group of fungivores ($S = 22$) there was recorded an increase, then a decrease and yet another increase in the number of species and also an increase, followed by a decrease and a slight increase in the proportion of their abundance in the succession series of moist pine forest. The considerable increase in the number and abundance of fungivores within the communities from young-growth probably was closely connected with sprouting mushrooms, particularly those of the genus *Suillus* (GUTOWSKI pers. comm., DURSKA unpublished data) the development of which is symbiotically associated with the youngest developmental stages of pine. To date, there are known about ten species of *Phoridae* that are developmentally associated with *Suillus* (DISNEY 1994). Five of these species, namely *Megaselia bernsdensi*, *M. lata*, *M. lutea*, *M. rubella* and *M. scutellaris* were found in the communities from young-growth. Of these, *M. lata* had the greatest increase in abundance in the communities from young-growth (Appendix). Within the group of zoophages ($S = 18$) changes in the abundance of *Phalacrotophora fasciata* were the most distinct. The abundance increase of this species from age-class III and the decrease in the communities from old-growth precisely correlated with changes in the abundance of its hosts (coccinellid pupae), particularly of *Myzia oblongoguttata*, a ladybird whose development is associated with coniferous trees (Appendix) (DISNEY 1994, CZECHOWSKA 1995).

4 f. Zoogeographic components of *Phoridae* in the succession series of moist pine forest

The ranges of the *Phoridae* are poorly-known. The scuttle flies recorded from the four age-classes of moist pine forest in Białowieża Forest belong to four zoogeographic components: cosmopolitan, Holarctic, Palaearctic and European (Table XIV). The group of Palaearctic species also comprises those recorded from the Canary Islands (*Megaselia hirticrus*, *M. manicata*, *M. meigeni*, *M. minor* and *Metopina heselhausi*) (DISNEY 1991). Two species: *Megaselia dimidia* recorded from Europe and the Oriental Region and *Phora pubipes* recorded from the Palaearctic and the Orient are defined as "other" zoogeographic elements in the Table. These species probably have a cosmopolitan range.

Palaearctic species and those recorded only from Europe occurred in similar proportions (from about 32% to about 41%) within the phorid communities in each of the four age-classes of pine tree stands; the Palaearctic species were the most numerous (from about 42% to about 59%). It is quite probable that when the family *Phoridae* has

been studied more extensively, the number of European species will gradually decrease in favour of that of Palaearctic ones.

Table XIV. Proportions of particular zoogeographic components in the phorid communities in moist pine forest in Białowieża Forest. S – number of species, n – abundance index.

Habitat		Zoogeographic components				
		cosmopolitan	Holarctic	Palaearctic	European	others
Plantations	S	4	17	28	25	1
	%S	5.3	22.7	37.3	33.3	1.3
	n	6.95	8.31	23.71	3.43	0.13
	%n	16.4	19.5	52.4	8.1	3.6
Young-growth	S	5	27	44	56	2
	%S	3.7	20.1	32.8	41.8	1.5
	n	16.48	17.81	74.43	15.12	0.79
	%n	13.2	14.3	59.7	12.1	0.6
Large pole timber	S	3	17	33	28	1
	%S	3.7	20.7	40.2	34.1	1.2
	n	16.97	5.32	30.54	9.71	3.10
	%n	25.9	8.1	46.5	14.8	4.7
Old-growth	S	3	24	47	47	2
	%S	2.4	19.5	38.2	38.2	1.6
	n	16.88	10.75	29.12	12.38	0.06
	%n	24.4	15.5	42.1	17.9	1.0
Total	S	5	37	61	85	2
	%S	2.6	19.5	32.1	44.7	1.1
	n	57.28	42.21	157.66	40.64	2.98
	%n	19.0	14.0	52.4	13.5	1.0

In the communities from plantations the most abundant of the four cosmopolitan species were: *Megaselia brevicostalis* – the eudominant and *M. giraudii* – the subdominant but also the dominant and eudominant in the older age-classes of pine tree stand. Within the group of the Holarctic components ($S = 17$) in the phorid communities six species reached the highest abundance and these were: *Megaselia nigriceps*, *M. pleuralis*, *M. pumila*, *M. meconicera*, *M. pulicaria-complex* and *Conicera dauci*. *Megaselia verralli*, the eudominant of the communities in plantations was the Palaearctic species with the highest abundance. The other most abundant representatives of this component were: *Megaselia manicata*, *M. zonata*, *M. latifrons*, *M. campestris*, *M. minor*, *M. xanthozona*, *M. woodi* and *Triphleba opaca*. The group of Palaearctic species within the communities in plantations was the most numerous ($S = 28$) and the most abundant (52%). The European component occupied the second position in respect of the number of species ($S = 25$), but its abundance was sixfold lower than that of the Palaearctic species. Two European species, namely *Metopina oligoneura* (eurytope) and *Megaselia involuta*, were recorded among the dominants (Appendix).

Within the five cosmopolitan species of the phorid communities in young-growth *Megaselia giraudii*, one of the dominants in this habitat, was the most abundant.

Holarctic species ($S = 27$) with the highest abundance were: *Megaselia pulicaria-complex*, *M. pumila*, *M. meconicera* and *M. pleuralis*. The Palaearctic component ($S = 44$) occupied, in respect of abundance, the first position among the scuttle flies from young-growth, and its most abundant species were: the eudominant – *Megaselia diversa*, the dominant – *M. woodi*, *M. unicolor*, *M. pulicaria-complex* and *Phora penicillata*, and also subdominants – *Megaselia hyalipennis*, *M. manicata* and *M. lata*. In the communities in young-growth, as compared with those in plantations, the number of species of the European component ($S = 56$) increased more than twofold, but the proportion of species recorded only from Europe increased slightly (about 4%). The results obtained were decided, first of all, by a considerable increase in the number of accessory species whose ranges of occurrence have hardly been studied. Of the species of the European component the most abundant were subdominants of the communities in young-growth: *Phora artifrons*, *Ph. obscura*, *Megaselia ignobilis* and *M. involuta* (Appendix).

Within the three cosmopolitan species in the phorid communities in large pole timber *Megaselia giraudii*, an eudominant in this age-class of pine tree stands, was the most abundant, just as it was in the communities from young-growth. An increase in the abundance of this species in the communities from large pole timber, as compared with those from plantations, brought about a nearly twofold increase in the abundance proportion of the cosmopolitan component. The abundance proportion of the Holarctic component ($S = 17$) was the lowest in large pole timber as compared with the communities in the other age-classes of tree stand. The group of Holarctic species with the highest abundance included *Phora holosericea*, *Megaselia pulicaria-complex*, *M. pumila* and *M. ruficornis*. The Palaearctic component took the first position in respect of the number ($S = 33$) and abundance ($n = 46.5$) in the communities from large pole timber. The group of Palaearctic species with the highest abundance proportion comprised the dominants – *Megaselia woodi*, *M. diversa*, *Phora penicillata* and subdominants – *Megaselia unicolor*, *M. altifrons*, *M. hyalipennis*, *M. latifrons*, *M. campestris* and *Phora dubia*. The number of species of the European component ($S = 28$), as compared with the communities in young-growth, was twofold lower and the abundance only slightly higher (by about 2.5%). The most abundant of the species recorded from Europe were: *Phora obscura*, *Ph. artifrons*, *Megaselia ignobilis*, *M. henrydisneyi* and *Phalacrotophora fasciata*. *Phora pubipes*, a species recorded from the Palaearctic and the Oriental Region, belonged to the subdominants in age-class III of tree stands (Appendix; Table XIV).

In the phorid communities from old-growth, within the three cosmopolitan species, *Megaselia giraudii*, one of the eudominants, was the most abundant, just as it also was in young-growth and large pole timber. *Phora holosericea*, *Megaselia pusilla*, *M. pulicaria-complex* and *M. meconicera*, subdominants, were the most abundant species of the Holarctic component ($S = 24$). In the group of Palaearctic species ($S = 47$) the highest proportions belonged to a eudominant *Megaselia woodi* and to subdominants *M. sepulchralis*, *M. unicolor*, *M. manicata* and *Phora penicillata*. The European and Palaearctic components had the same number of species ($S = 47$), but the abundance proportion of European species was lower by half. Of these species *Phora obscura* (dominant) and *Ph. penicillata* (subdominant) had the highest abundance (Appendix).

Species recorded from Europe and Palaearctic species ($S = 44.7\%$ and $S = 32.1\%$, respectively) were the most significant components of the phorid communities in the four age-classes of moist pine forest in Białowieża Forest. The Palaearctic component occupied the top position in respect of abundance ($n = 52.4\%$) and the cosmopolitan component, although with a small number of species ($S = 5$), occupied the second position ($n = 19.0\%$) (Table XIV).

The other - Holarctic and European - components comprised over three-fourths of the phorid species (this applies to males) recorded from moist pine forest in Białowieża Forest and yet they were not significant in respect of abundance ($n = 27.5\%$) (Appendix; Table XIV).

5. DISCUSSION

Of the 326 species of *Phoridae* recorded from Poland, 209 species (about 65%) were found occurring in the four age-classes of moist pine forest in Białowieża Forest. As much as 20% ($S = 42$) of the material studied were species new to the Polish fauna, and over 21% of these in turn ($S = 9$) were species new to science (DURSKA in press).

Scuttle flies are one of the most abundant and specifically richest families within the communities of *Diptera* in the studied fauna of the succession series in moist pine forest in Białowieża Forest (TROJAN *et al.* 1994). With respect to abundance, the core of the phorid communities in pine plantations and young-growth was made by species with Palaearctic and Holarctic ranges and that in large pole timber and old-growth by species with Palaearctic and cosmopolitan ranges. This dependence was closely connected with an increase in the abundance of species dominating in the older age-classes of pine tree stand, especially that of polyphage *Megaselia giraudii*, a cosmopolitan eudominant (Table XIV).

The phorid community in plantations greatly differed, in its species composition, from the communities in the older age-classes of the succession series of pine forest. *Megaselia verralli* and *M. brevicostalis*, colonizing species, were the dominants. The fidelity and frequency of both species were the highest in this habitat (Fig. 4; Table VI). Many scuttle fly species are known to be very sensitive to changes in their habitat. During dry years, *M. brevicostalis* reaches its abundance peak much earlier than in years when humidity is normal (DISNEY *et al.* 1981). Phorid communities also react very strongly to habitat pollution. An increase in pollution brings about significant changes in the proportion of trophic groups; the number of zoophages decreases while that of saprophages increases (DURSKA 1996). Such a conspicuous reaction to changes in forest habitat in the course of succession was also recorded for the community studied. A complete exchange of dominant species was observed even in young-growth. The colonizing species were replaced by *Megaselia giraudii* and *M. woodi*, strongly expansive species whose dominance intensified in the older age-classes of tree stand. These two species, which in 1986 and 1987 had occurred in high abundances (eudominants and dominants), had been recorded in phorid communities from old-growth in Bory Tucholskie Forest and Puszcza Biała Forest. The species composition of phorid communities from old-growth of moist pine forest in three

regions of Poland (Bory Tucholskie Forest, Puszcza Biała Forest, Białowieża Forest) had been similar, about 60% (DURSKA 1996). Each of the four age-classes of the succession series of moist pine forest had an individual group of characteristic species (fidelity > 51%). These species belonged to 6 genera: *Borophaga*, *Conicera*, *Megaselia*, *Metopina*, *Phora* and *Triphleba*. The greatest number of these species, as many as 19, was recorded for the communities in young-growth, the least – only 4 species – for those in large pole timber (Figs 4-7). Phorid communities might be regarded as highly indicative because they are very sensitive to habitat changes and because there are specific groups of characteristic species in all four age-classes.

The restorative variant is one of the five types of secondary succession. It has been recorded for about 50% of the studied competitive communities and 8 taxa of moist pine forest in Białowieża Forest (TROJAN *et al.* 1994). The numbers of phorid species in plantations and large pole timber and also in young-growth and old-growth differed very little. Likewise the values of species richness which changed in the rise-fall-rise manner. Such a variant of succession realized by the phorid community was a modification of the restorative variant. This sixth type of secondary succession has been called a rise-fall-rise variant of changes (Table II; Fig. 15).

With regard to abundance, the course of succession processes in animal communities in the succession series of moist pine forest most frequently runs in the direction of regression and restoration (TROJAN *et al.* 1994). A slight decrease in the abundance of the phorid community in old-growth while (as compared with large pole timber) the number of species greatly increased was the only indication that the community was realizing the stabilizing variant of succession in the older tree stands (Table II). Stabilization of abundance began in age-class III, i.e. in large pole timber. Such a course of reactions within a phorid community probably reflect the presence of well-functioning homeostatic mechanisms developed in the course of secondary succession, mechanisms which make it possible for species to survive abrupt changes due to ecosystem destruction in the form of forest felling.

The growth of tree stands was accompanied by distinct succession changes in the phorid communities from moist pine forest. Plantations were inhabited by colonizing species, mainly those of the genus *Megaselia*. They were species of open areas – eudominants: *M. verralli* and *M. brevicostalis*, and dominants: *M. nigriceps*, *M. zonata* and also *M. minor*, *Metopina oligoneura* and *Conicera dauci* (Table VIII). In the changing vertical structure of young-growth the dominating species in plantations were replaced by forest species, mainly of the genus *Megaselia*: *M. diversa*, *M. woodi* and *M. giraudii* (Fig. 9). The last two species were eudominants and dominants of the phorid communities in the oldest age-classes in the succession series of moist pine forest (Figs 10, 11). Thus the species composition of the dominants of the phorid community in plantations differed very clearly from that of the communities in the older age-classes of tree stands (Figs 12, 13). In the course of secondary succession the changing internal structure of forest exerts a significant impact on shading. Photophilous species of open areas are ousted by forest species which are ideally adapted to the new conditions. Shade not only drastically reduces the abundance of colonizing species but it

also prevents their repeated invasion in the course of maturing of pine tree stand (HORN 1974).

Different dependences were obtained after the proportions of species in the communities had been compared according to status based on the abundance share of species. When a modified homogeneity index (HD^*) was used, a high similarity between the dominance structures of the phorid communities in the four age-classes of moist pine forest was obtained (Fig. 14). The distribution of the proportion of the mean abundance of dominants was the most similar in the communities in plantations and large pole timber. There was one conspicuous eudominant there (Figs 8, 10). Two species of similar abundance proportions co-dominated within the communities from young-growth and old-growth. The other features of the dominance structure of the communities in the four age-classes were similar: the proportion of particular species decreased evenly and species of low abundance formed the so-called "distribution tail". The fact that the abundance proportions of species in the communities from plantations and large pole timber and also from young-growth and old-growth were similar while the sequence of particular species in the dominance structure kept changing was excellent proof that the biocoenosis first and foremost built the community structure (quantitative ratios) and that species compositions (qualitative ratios) were not that important. A diverse habitat and small human interference are essential in the development of this type of dominance structure characteristic of natural and semi-natural ecosystems (TROJAN 1997).

Species of wide ecological tolerance to age-classes of forest were distinguished for comparison of similarities of species composition and dominance structure. They were dominants of the communities in young-growth, large pole timber and old-growth. Another group comprised accessory species associated with ecological microniches of each age-class. These were the species that had contributed most to the different character of the species composition of the communities studied (Appendix; Table V). That fact was confirmed by small values of Soerensen's index obtained for the phorid communities, treated as a whole, in the succession series of moist pine forest in Białowieża Forest (Table III). Discrimination analysis (TROJAN 1997) was used to distinguish accessory species, and then it was possible to evaluate the extent of secondary diversification of the habitat (Mn) and to define the proportion of species associated with its mosaic-like character (Ms). The numerical and species indices of the mosaic-like character differed considerably between young-growth and old-growth yet the number of species in the phorid communities and species richness (Fig. 15) in these age-classes of tree stands were similar. Mn and Ms indices had the lowest values for the communities in young-growth and the highest for those in old-growth, i.e. in the habitat where the greatest number of ecological niches was formed (Table IX).

The age of the tree stand of each age-class of the succession series exerted the greatest impact on the habitat conditions of moist pine forest. The organization of the zoocenotic complex changed in the course of the development of the forest ecosystem. Results of ecosystem remodelling may also be observed in the course of succession changes with respect to actual species diversity (H'). The succession variant realized by the phorid community is the closest to the stabilizing variant. Differences in

the values of actual diversity for the phorid communities in large pole timber and old-growth were small (Table XI) although there was a considerable difference in the empirically determined number of species (Table X).

Processes of decrease, however small, in species diversity were observed in the older tree stands in over 60% of animal groups. In old-growth, elimination of species reduces potential species diversity (TROJAN *et al.* 1994). Within the phorid communities in the succession series of moist pine forest potential species diversity (H_{max}), just as the number of species and species richness, changed in the rise-fall-rise manner. The values of the Pielou index (J) for these communities differed slightly (Table XI). The decrease in values of index J for the phorid communities in old-growth was connected with the forming of dominance structure characteristic of communities in mature tree stands (Table XI; Fig. 11). In these tree stands, as compared with the communities from the younger age-classes, there was recorded the smallest number of species (only 12 species with an abundance of over 1%) and a very elongated distribution tail ($S = 119$). Such proportions of dominant and accessory species corresponded to the highly mosaic-like character of the habitat (TROJAN *et al.* 1982), a degree that reached its highest value in old-growth. In this habitat there was observed an increase in fauna richness while the number of species dominating in the community was lower (Table IX; Fig. 11).

The abundance proportion of the trophic groups in the communities from the four age-classes of forest distinctly changed in the course of secondary succession of the phorid communities from moist pine forest. The number of saprophagous species decreased, whereas the abundance of polyphages increased (Table XIII). Such an abundance distribution was decided by dominating species with known life histories. In plantations it was *Megaselia brevicostalis*, a saprophagous eudominant, in the older age-classes it was *M. giraudii*, a polyphage which contributed to dominance increase (Appendix). Very abundant species perfectly adapted to the habitats of growing pine tree stand played an important role during rebuilding and building of the forest ecosystem (*M. brevicostalis* and *M. veralli* in the former, *M. giraudii* and *M. woodi* in the latter). These species and also the other dominants of the four age-classes of tree stand in the succession series of moist pine forest were essential elements in biocoenotic regulation. Stabilization of the abundance in the older age-classes could be a very useful basis to work on the function of the phorid community in the succession series of moist pine forest. Accessory species were another important element that improved the functioning of the forest ecosystem. Their number in the four age-classes of tree stand changed in the rise-fall-rise manner, just as the number of species in the community. However, the number of individuals in the groups of accessory species in particular classes was very similar (Table V). These species form the ecological stock which is activated when habitat changes take place (TROJAN, WYTWER 1996).

Secondary succession of the phorid communities in moist pine forest in Białowieża Forest was characterized by a pronounced reaction (exchange of dominants) to changing habitat conditions in the course of growth of pine forest. During each study season, a great number of species and genera was exchanged, species characteristic of particular age-classes were present, abundance and actual species diversity (H') were

stabilized, while the number of species from the older tree stands increased and abundance was high (a measure of ecological success). All this justifies the assumption that phorid communities are closely connected with developmental processes operating in the course of secondary succession of moist pine forest.

6. CONCLUSIONS

1. In the course of succession of moist pine forests in Białowieża Forest the phorid community in pine plantations [with the eudominants *Megaselia verralli* and *M. brevicostalis* (saprophage)] very clearly differed from the communities in the older pine tree stands [with the eudominants *Megaselia woodi* and *M. giraudii* (polyphage)].

2. The phorid communities in the older tree stands of moist pine forest in Białowieża Forest showed a great similarity between their dominance structures (large pole timber and old-growth - 0.85). The dominance structure of the phorid communities in young-growth, pole timber and old-growth started to differ on the level of accessory species. *Megaselia woodi* and *M. giraudii* were the eudominants in the older-age classes of pine tree stands, and their co-domination increased in the course of secondary succession of the phorid communities.

3. Change in the positions of dominant species in the course of secondary succession were a characteristic feature of the phorid communities there. The dominance structure of the phorid communities in moist pine forests in Białowieża Forest developed the final form already at the stage of young-growth.

4. With regard to the changing number of species in the four age-classes of pine tree stands the phorid community realized the variant of rise-fall-rise changes in succession.

5. The succession variant realized by the phorid community in relation to abundance and to actual species diversity (H') was the closest to the stabilizing variant.

ACKNOWLEDGEMENTS

I especially thank Prof. Przemysław Trojan and Dr R. Henry L. Disney for their help during my study. I am grateful to Prof. Eliza Dąbrowska-Prot for her comments on earlier version of the manuscript.

E. Durska's work on *Phoridae* are funded by Komitet Badań Naukowych, PAN (Committee for Scientific Research, PAS).

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STRESZCZENIE

[Tytuł: Sukcesja wtórna zgrupowań *Phoridae* w borach świeżych Puszczy Białowieskiej]

W czterech klasach wiekowych borów świeżych Puszczy Białowieskiej, z 326 gatunków *Phoridae* wykazanych z Polski, stwierdzono występowanie 209 gatunków (ok. 65%). W zbadanym materiale aż 20% (S = 42) to gatunki nowe dla fauny krajowej, a wśród nich ponad 21% (S = 9) stanowią gatunki nowe dla nauki.

Zadrowate należą do jednej z najbardziej licznych i najbogatszych w gatunki rodzin wśród zgrupowań muchówek badanej fauny szeregu sukcesyjnego borów świeżych Puszczy. Trzon zgrupowania *Phoridae*, pod względem liczebności, w uprawach

sosnowych i w młodnikach tworzą gatunki o zasięgu palearktycznym i holarktycznym, a w drągowinach i starodrzewach – palearktycznym i kosmopolitycznym. Zależność ta ma ścisły związek ze wzrostem liczebności gatunków dominujących w starszych klasach wiekowych drzewostanów sosnowych, szczególnie kosmopolitycznego eudominanta – polifaga *Megaselia giraudii* (Table XIV).

Zgrupowanie zadrowatych upraw znacznie różni się składem gatunkowym od zgrupowań starszych klas wiekowych szeregu sukcesyjnego. Dominantami są tu kolonizujące gatunki – *Megaselia verralli* i *M. brevicostalis*. W tym środowisku wierność występowania i frekwencja obu gatunków jest najwyższa (Fig. 4, Table VI).

Już w młodnikach zaobserwowano całkowitą wymianę gatunków dominujących. Gatunki kolonizujące są tu wypierane przez silnie ekspansywne – *Megaselia giraudii* i *M. woodi*, a ich dominacja nasila się w starszych klasach wiekowych drzewostanów.

Każda z czterech klas wiekowych szeregu sukcesyjnego borów świeżych ma swoistą grupę gatunków charakterystycznych (wierność > 51%). Należą one do 6 rodzajów: *Borophaga*, *Conicera*, *Megaselia*, *Metopina*, *Phora* i *Triphleba* (Figs 4-7). Ze względu na dużą wrażliwość reakcji zgrupowania na zmiany środowiskowe, a także występowanie swoistych grup gatunków charakterystycznych, każdej z czterech klas wiekowych, można sądzić, że zgrupowania *Phoridae* mogą być wybitnie wskaźnikowe.

Liczby gatunków zgrupowań zadrowatych upraw i drągowin, a także młodników i starodrzewów niewiele się różnią. Podobnie, wartości bogactwa gatunkowego zmieniają się skokowo. Taki wariant sukcesji realizowany przez zgrupowanie *Phoridae* jest modyfikacją wariantu restauracyjnego. Ten szósty typ sukcesji wtórnej został nazwany wariantem zmian skokowych (rise-fall-rise) (Table II, Fig. 15).

Niewielki spadek liczebności zgrupowania *Phoridae* w starodrzewach, przy znacznym wzroście liczby gatunków w porównaniu z drągowinami wskazuje, że zgrupowanie realizuje stabilizujący wariant sukcesji w starszych drzewostanach (Table II). Stabilizacja liczebności rozpoczyna się w III-iej klasie wieku sosny – drągowinach. Ten typ przebiegu reakcji wewnątrz zgrupowania zadrowatych może świadczyć o sprawnie działających mechanizmach homeostatycznych, które wykształciły się w trakcie sukcesji wtórnej i pozwoliły przetrwać gwałtowne zmiany powstałe po zniszczeniu ekosystemu, jakim jest wyrąb lasu.

Wraz ze wzrostem drzewostanu obserwowane są wyraźne zmiany sukcesyjne zgrupowań *Phoridae* borów świeżych. Uprawy zasiedlane są przez kolonizujące gatunki, głównie z rodzaju *Megaselia*. W zmieniającej się strukturze pionowej drzewostanów sosnowych młodników, gatunki dominujące upraw zastąpione zostają przez gatunki leśne, też przede wszystkim z rodzaju *Megaselia*: *M. diversa*, *M. woodi* i *M. giraudii* (Fig. 9). Dwa ostatnie gatunki są eudominantami i dominantami zgrupowań zadrowatych najstarszych klas wiekowych drzewostanów sosnowych szeregu sukcesyjnego borów świeżych. (Figs 10, 11). Tak więc, skład gatunkowy dominantów zgrupowania *Phoridae* upraw bardzo wyraźnie różni się od składu gatunkowego dominantów zgrupowań starszych klas wiekowych drzewostanów. (Figs 12, 13). W trakcie sukcesji wtórnej borów zmieniająca się struktura wewnętrzna lasu wpływa bardzo istotnie na zacienienie. Światłolubne gatunki terenów otwartych zostają wyparte przez gatunki leśne, doskonale przystosowane do nowych warunków. Cień nie tylko

drastycznie zmniejsza liczebność gatunków kolonizujących, ale również zapobiega ich ponownej inwazji w trakcie dojrzewania drzewostanu sosnowego.

Inne zależności otrzymano, gdy udziały gatunków w zgrupowaniach zostały porównane według rang odnoszących się do procentowego udziału liczebności gatunków. W oparciu o zmodyfikowany współczynnik homogeniczności (HD^*) uzyskano wysokie podobieństwo pomiędzy strukturami dominacyjnymi badanych zgrupowań zadrowatych czterech klas wiekowych borów świeżych (Fig. 14). Rozkład udziału średniej liczebności dominantów jest najbardziej podobny w zgrupowaniach upraw i drągowin. Występuje tu jeden wyraźny eudominant (Figs 8, 10). W zgrupowaniach młodników i starodrzewów współdominują dwa gatunki o podobnych udziałach procentowych liczebności. Pozostałe cechy struktury dominacyjnej zgrupowań czterech klas wiekowych borów świeżych są podobne: udział procentowy poszczególnych gatunków spada równomiernie, a gatunki o niskiej liczebności tworzą tzw. „ogon rozkładu”. Zróżnicowane środowisko i niewielka ingerencja człowieka mają znaczący wpływ na ukształtowanie się tego typu struktury dominacyjnej charakterystycznej dla ekosystemów naturalnych i półnaturalnych.

W celu porównania podobieństwa składu gatunkowego i struktury dominacyjnej wyodrębniono gatunki o szerokim zakresie tolerancji ekologicznej w odniesieniu do klas wiekowych borów. Są to dominanty zgrupowań młodników, drągowin i starodrzewów. Drugą grupę tworzą gatunki akcesoryczne powiązane z mikroniszami ekologicznymi każdej z czterech klas wiekowych drzewostanów sosnowych. Właśnie te gatunki mają największy wpływ na odrębność składu gatunkowego badanych zgrupowań (Appendix, Table V). Fakt ten potwierdzają uzyskane niewielkie wartości współczynnika Soerensena dla całości zgrupowań zadrowatych szeregu sukcesyjnego borów świeżych Puszczy Białowieskiej (Table III). Wyodrębnienie, za pomocą analizy dyskryminacyjnej gatunków akcesorycznych, pozwoliło na ocenę stopnia zróżnicowania wtórnego środowiska (Mn) i określenie udziału gatunków związanych z jego mozaikowością (Ms). W młodnikach i starodrzewach, gdzie liczba gatunków zgrupowań *Phoridae* i bogactwo gatunkowe (Fig. 15) tych klas wiekowych drzewostanów są podobne, numeryczny i gatunkowy wskaźnik mozaikowości znacznie różnią się między sobą. Wskaźniki Mn i Ms osiągają najniższe wartości w zgrupowaniach młodników, a najwyższe w zgrupowaniach starodrzewów, a więc tam, gdzie powstaje najwięcej nisz ekologicznych (Table IX).

Najważniejszy wpływ na warunki środowiskowe boru świeżego ma wiek drzewostanu sosnowego każdej z czterech klas wiekowych szeregu sukcesyjnego. W trakcie rozwoju ekosystemu borowego zmienia się organizacja układu zoocenotycznego. Rezultaty przebudowy ekosystemu mogą być także obserwowane w przebiegu zmian sukcesyjnych w odniesieniu do różnorodności gatunkowej aktualnej (H'). Wariant sukcesji jaki realizuje zgrupowanie *Phoridae* jest najbliższy wariantowi stabilizującemu. Różnice w wartościach różnorodności aktualnej dla zgrupowań *Phoridae* drągowin i starodrzewów są niewielkie (Table XI), przy znacznej różnicy w empirycznie określonej liczbie gatunków (Table X).

W zgrupowaniach *Phoridae* szeregu sukcesyjnego borów świeżych różnorodność gatunkowa potencjalna (H_{max}), podobnie jak liczba gatunków i bogactwo gatunkowe,

zmienia się skokowo (wzrost-spadek-wzrost). Wartości wskaźnika Pielou (J) dla tych zgrupowań nieznacznie różnią się między sobą (Table XI). Zaobserwowany spadek wartości wskaźnika J dla zgrupowań zadrowatych starodrzewów jest powiązany ze wzrostem organizacji wewnętrznej i ukształtowaniem się struktury dominacyjnej, charakterystycznej dla zgrupowań dojrzałych drzewostanów (Table XI, Fig. 11).

W toku sukcesji wtórnej zgrupowań *Phoridae* borów świeżych zmienia się wyraźnie udział procentowy liczebności grup fagicznych w zgrupowaniach czterech klas wiekowych borów. Spada liczebność gatunków saprofagicznych, wzrasta natomiast liczebność polifagów (Table XIII). O takim rozkładzie liczebności decydują gatunki dominujące o znanej biologii rozwoju. W uprawach jest to saprofagiczny eudominant *Megaselia brevicostalis*, w starszych klasach wiekowych dominację nasila polifag - *M. giraudii* (Appendix). Gatunki o dużej liczebności, doskonale dostosowane do środowisk wzrastającego drzewostanu sosnowego, odgrywają najważniejszą rolę w odbudowie (*M. brevicostalis* i *M. verralli*) i budowie (*M. giraudii*, *M. woodi*) ekosystemu leśnego. Gatunki te, a także pozostałe dominanty czterech klas wiekowych drzewostanów szeregu sukcesyjnego borów świeżych, są istotnymi czynnikami regulacji biocenozy. Stabilizacja liczebności w starszych klasach wiekowych drzewostanów może stanowić dobrą podstawę do badań nad funkcją jaką pełni zgrupowanie *Phoridae* w trakcie sukcesji wtórnej borów świeżych. Drugim, istotnym elementem usprawniającym funkcjonowanie ekosystemu leśnego są gatunki akcesoryczne. Ich liczba w czterech klasach wiekowych drzewostanów zmienia się skokowo, podobnie jak liczba gatunków zgrupowania. Natomiast liczba osobników grup gatunków akcesorycznych w poszczególnych klasach jest bardzo podobna (Table V). Gatunki te, stanowią rezerwę ekologiczną, która jest uruchamiana w momencie zmian środowiskowych.

Sukcesję wtórną zgrupowań zadrowatych borów świeżych Puszczy Białowieskiej cechuje wyraźna reakcja (m.in. wymiana dominantów) na zmieniające się warunki środowiskowe w trakcie wzrostu drzewostanu sosnowego. Wymienianie się podczas sezonu dużej liczby gatunków i rodzajów, obecność grupy gatunków charakterystycznych dla poszczególnych klas wiekowych, stabilizacja liczebności i różnorodności gatunkowej aktualnej (H'), przy wzroście liczby gatunków w starszych drzewostanach, a także wysoka liczebność (miara sukcesu ekologicznego) sugerują, że zgrupowanie *Phoridae* jest ściśle powiązane z procesami rozwojowymi zachodzącymi w trakcie sukcesji wtórnej borów świeżych.

Appendix. Species composition and abundance (n) of the phorid communities in the four age-classes of moist pine forest in Białowieża For-
est. n - males abundance (100 24-hour traps); zc* - zoogeographic components: C - cosmopolitan, H - Holarctic, P - Palearctic,
E - European, O - others; tg* - trophic groups: s - saprophages, f - fungivores, z - zoophages, p - polyphages; * - species in complexes since
revised (e.g. DISNEY 1999) and personal communication from Dr R. H. L. Disney.

No.	Species	zc*	tg*	Habitat							
				Plantations		Young-growth		Large pole timber		Old-growth	
				n	%	n	%	n	%	n	%
1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Anevrina curvinervis</i> (BECKER, 1901)	H		0.02	0.04	-	-	-	-	0.04	0.06
2	<i>Anevrina thoracica</i> (MEIGEN, 1804)	H		0.04	0.08	0.24	0.19	0.41	0.63	0.42	0.61
3	<i>Anevrina unispinosa</i> (ZETTERSTEDT, 1860)	P	s	0.04	0.08	0.02	0.01	0.04	0.06	0.42	0.61
4	<i>Anevrina urbana</i> (MEIGEN, 1830)	H		-	-	-	0.00	0.02	0.03	0.02	0.02
5	<i>Borophaga agilis</i> (MEIGEN, 1830)	P		-	-	-	0.00	0.13	0.20	-	-
6	<i>Borophaga carinifrons</i> (ZETTERSTEDT, 1848)	P		-	-	0.18	0.14	0.06	0.09	0.55	0.80
7	<i>Borophaga femorata</i> (MEIGEN, 1830)	P		-	-	0.06	0.05	0.02	0.03	0.25	0.36
8	<i>Borophaga irregularis</i> (WOOD, 1912)	E		-	-	0.02	0.02	0.02	0.03	0.02	0.03
9	<i>Borophaga subsultans</i> (LINNE, 1767)	H		0.05	0.11	0.95	0.76	0.55	0.85	0.15	0.21
10	<i>Conicera dauci</i> (MEIGEN, 1830)	H		0.72	1.68	0.20	0.16	0.04	0.06	0.06	0.08
11	<i>Conicera floricola</i> SCHMITZ, 1938	E		-	-	0.04	0.03	0.02	0.03	-	-
12	<i>Conicera similis</i> (HALIDAY, 1833)	H	s	-	-	0.04	0.03		0.00	-	-
13	<i>Conicera tarsalis</i> SCHMITZ, 1920	E		-	-	-	-	0.02	0.03	-	-
14	<i>Conicera tibialis</i> SCHMITZ, 1925	H	s	-	-	-	-	0.02	0.03	-	-
15	<i>Diplonevra glabra</i> (SCHMITZ, 1927)	E		0.02	0.05	-	-	-	-	-	-
16	<i>Diplonevra nitidula</i> (MEIGEN, 1830)	H	z	-	-	-	-	-	-	0.04	0.06
17	<i>Diplonevra pilosella</i> (SCHMITZ, 1927)	E	z	-	-	-	-	0.02	0.03	-	-
18	<i>Gymnoptera vitripennis</i> (MEIGEN, 1830)	E	z	-	-	0.02	0.02	-	-	-	-
19	<i>Hypocera mordellaria</i> (FALLEN, 1823)	P		0.02	0.04	-	-	-	-	-	-
20	<i>Megaselia abdita</i> SCHMITZ, 1959	H	s	-	-	0.10	0.08	-	-	0.02	0.03
21	<i>Megaselia aculeata</i> (SCHMITZ, 1919)	E		-	-	0.06	0.05	-	-	0.04	0.05
22	<i>Megaselia aequalis</i> (WOOD, 1909)	H	z	-	-	0.08	0.06	-	-	0.02	0.03
23	<i>Megaselia affinis</i> (WOOD, 1909)	E		0.16	0.37	0.40	0.32	0.12	0.19	-	-

Appendix - cont.

1	2	3	4	5	6	7	8	9	10	11	12
24	<i>Megaselia albicans</i> (WOOD, 1908)	E	f	-	-	-	-	0.06	0.09	-	-
25	<i>Megaselia albicaudata</i> (WOOD, 1910)	P		-	-	0.14	0.11	-	-	-	-
26	<i>Megaselia albocingulata</i> (STROBL, 1906)	H		0.05	0.11	-	-	-	-	-	-
27	<i>Megaselia alticolella</i> (WOOD, 1909)	P		0.02	0.04	-	-	-	-	0.17	0.24
28	<i>Megaselia altifrons</i> (WOOD, 1909)	P		0.14	0.34	0.84	0.67	2.41	3.72	0.08	0.12
29	<i>Megaselia analis</i> (LUNDBECK, 1920)	E		-	-	-	-	-	-	0.02	0.03
30	<i>Megaselia aquilonia</i> SCHMITZ, 1958	E		-	-	0.02	0.01	-	-	-	-
31	<i>Megaselia aristica</i> (SCHMITZ, 1920)	E		-	-		0.00	-	-	0.02	0.03
32	<i>Megaselia atrosericea</i> SCHMITZ, 1927	P		-	-	0.16	0.13	-	-	-	-
*33	<i>Megaselia badia</i> SCHMITZ, 1938	E		0.06	0.14		0.00	-	-	-	-
34	<i>Megaselia berndseni</i> (SCHMITZ, 1919)	H	f	-	-	0.08	0.06	-	-	-	-
35	<i>Megaselia bovista</i> (GIMMERTHAL, 1848)	P	f	-	-	0.04	0.03	-	-	-	-
36	<i>Megaselia brevicostalis</i> (WOOD, 1910)	C	s	6.40	15.05	0.48	0.38	0.18	0.27	0.33	0.48
37	<i>Megaselia brevior</i> (SCHMITZ, 1924)	P		0.07	0.16	0.04	0.03	-	-	-	-
38	<i>Megaselia campestris</i> (WOOD, 1908)	P		0.74	1.74	1.08	0.87	0.77	1.19	0.63	0.91
39	<i>Megaselia ciliata</i> (ZETTERSTEDT, 1848)	P	z	0.05	0.13	0.15	0.12	0.02	0.03	0.04	0.06
40	<i>Megaselia cinerea</i> SCHMITZ, 1938	E		-	-	0.06	0.05	-	-	-	-
41	<i>Megaselia cinereifrons</i> (STROBL, 1910)	E	f	-	-	-	-	-	-	0.06	0.09
42	<i>Megaselia clara</i> (SCHMITZ, 1921)	H		-	-	-	-	-	-	0.19	0.27
43	<i>Megaselia coccyx</i> SCHMITZ, 1965	H		-	-	0.14	0.11	-	-	-	-
44	<i>Megaselia coei</i> SCHMITZ, 1938	E		0.05	0.13	0.06	0.05	-	-	-	-
45	<i>Megaselia collini</i> (WOOD, 1909)	P		-	-	-	-	-	-	0.02	0.03
46	<i>Megaselia communiformis</i> (SCHMITZ, 1918)	E		-	-	-	-	-	-	0.10	0.14
47	<i>Megaselia conformis</i> (WOOD, 1909)	P		-	-	-	-	-	-	0.06	0.09
48	<i>Megaselia cothurnata</i> (SCHMITZ, 1919)	P		-	-	-	-	-	-	0.02	0.03
49	<i>Megaselia crassipes</i> (WOOD, 1909)	H		-	-	-	-	-	-	0.06	0.09
50	<i>Megaselia curvicapilla</i> SCHMITZ, 1947	P		0.05	0.11	1.10	0.88	-	-	-	-
51	<i>Megaselia dahli</i> (BECKER, 1901)	E		-	-	0.06	0.05	-	-	-	-
52	<i>Megaselia devia</i> SCHMITZ, 1936	E		-	-	0.04	0.03	-	-	-	-
53	<i>Megaselia differens</i> SCHMITZ, 1948	E		0.02	0.05	0.15	0.12	0.02	0.03	0.02	0.03
*54	<i>Megaselia dimidia</i> SCHMITZ, 1926	O		0.13	0.30	0.77	0.62		0.00	0.04	0.05

Appendix - cont.

1	2	3	4	5	6	7	8	9	10	11	12
55	<i>Megaselia discreta</i> (WOOD, 1909)	P	f	-	-	-	-	-	-	0.06	0.09
56	<i>Megaselia diversa</i> (WOOD, 1909)	P		0.20	0.48	18.86	15.11	4.93	7.60	0.43	0.63
57	<i>Megaselia dubitalis</i> (WOOD, 1908)	P		-	-	-	-	-	-	0.02	0.03
*58	<i>Megaselia durskae</i> DISNEY, 1989	E		0.02	0.04	0.12	0.09		0.00	0.06	0.09
59	<i>Megaselia eccoptomera</i> SCHMITZ, 1927	H		-	-	0.02	0.02	0.07	0.11	0.10	0.14
60	<i>Megaselia eisfelderae</i> SCHMITZ, 1948	H	f	0.02	0.04	-	-	-	-	0.04	0.06
61	<i>Megaselia elongata</i> (WOOD, 1914)	P	z	0.02	0.04	0.18	0.14	0.24	0.37	0.04	0.05
62	<i>Megaselia emarginata</i> (WOOD, 1908)	E		0.18	0.42	0.44	0.35	0.27	0.41	0.25	0.36
63	<i>Megaselia eminens</i> SCHMITZ, 1953	E		-	-	-	-	-	-	0.04	0.06
64	<i>Megaselia errata</i> (WOOD, 1912)	E		0.05	0.13	0.12	0.10	0.02	0.03	0.08	0.11
65	<i>Megaselia fenestralis</i> (SCHMITZ, 1919)	P		-	-	-	-	0.02	0.03	-	-
66	<i>Megaselia flava</i> (FALLEN, 1823)	H		0.04	0.08	0.15	0.12	-	-	0.04	0.06
67	<i>Megaselia flavescens</i> (WOOD, 1909)	E		-	-	0.02	0.02	-	-	-	-
68	<i>Megaselia flavicans</i> SCHMITZ, 1935	P	f	-	-	-	-	0.02	0.03	-	-
69	<i>Megaselia flavicoxa</i> (ZETTERSTEDT, 1848)	E	z	-	-	0.02	0.02	-	-	0.02	0.03
70	<i>Megaselia fumata</i> (MALLOCH, 1909)	E		-	-	0.06	0.04	-	-	-	-
71	<i>Megaselia fuscovariana</i> SCHMITZ, 1933	E		-	-	0.02	0.02	-	-	-	-
*72	<i>Megaselia giraudii-complex</i> (EGGER, 1862)	C	p	0.52	1.22	15.89	12.73	16.34	25.19	16.43	23.66
73	<i>Megaselia glabrifrons</i> (WOOD, 1909)	H		-	-	0.15	0.12	-	-	-	-
74	<i>Megaselia gregaria</i> (WOOD, 1910)	E		-	-	-	-	-	-	0.02	0.03
75	<i>Megaselia groenlandica</i> (LUNDBECK, 1901)	H		-	-	0.08	0.06	-	-	-	-
76	<i>Megaselia halterata</i> (WOOD, 1910)	C	f	0.02	0.05	0.02	0.02	-	-	-	-
77	<i>Megaselia henrydisneyi</i> DURSKA, 1998	E		-	-	0.37	0.29	0.75	1.15	-	-
78	<i>Megaselia hirticrus</i> (SCHMITZ, 1918)	P		-	-	0.02	0.02	-	-	-	-
79	<i>Megaselia hortensis</i> (WOOD, 1909)	E		-	-	-	-	-	-	0.06	0.09
80	<i>Megaselia humeralis</i> (ZETTERSTEDT, 1838)	H		-	-	0.12	0.10	0.04	0.06	0.17	0.25
81	<i>Megaselia hyalipennis</i> (WOOD, 1912)	P	f	0.02	0.04	3.00	2.41	0.93	1.43	0.64	0.93
82	<i>Megaselia ignobilis</i> (SCHMITZ, 1919)	E		0.13	0.30	2.67	2.14	1.31	2.01		0.00
83	<i>Megaselia indifferens</i> (LUNDBECK, 1920)	E		-	-	-	-	-	-	0.06	0.08
84	<i>Megaselia insons</i> (LUNDBECK, 1920)	E		-	-	0.02	0.01	-	-	0.02	0.03
85	<i>Megaselia intercostata</i> (LUNDBECK, 1921)	E		-	-	-	-	-	-	0.04	0.06

Appendix – cont.

1	2	3	4	5	6	7	8	9	10	11	12
86	<i>Megaselia intonsa</i> SCHMITZ, 1948	E		-	-	-	-	-	-	0.06	0.09
87	<i>Megaselia involuta</i> (WOOD, 1910)	E		0.86	2.03	1.37	1.10	0.39	0.60	0.13	0.18
88	<i>Megaselia joannae</i> DISNEY, 1998	E		-	-	0.02	0.02	-	-	-	-
89	<i>Megaselia lata</i> (WOOD, 1910)	P	f	0.40	0.94	1.66	1.33	0.06	0.09	0.04	0.05
90	<i>Megaselia latifemorata</i> (BECKER, 1901)	P		-	-	0.02	0.02	-	-	-	-
91	<i>Megaselia latifrons</i> (WOOD, 1910)	P		1.15	2.71	0.91	0.73	0.82	1.26	0.26	0.38
92	<i>Megaselia longicostalis</i> (WOOD, 1912)	P		0.02	0.04	0.20	0.16	-	-	0.12	0.17
93	<i>Megaselia longiseta</i> (WOOD, 1909)	P		-	-	0.10	0.08	-	-	-	-
94	<i>Megaselia lucifrons</i> (SCHMITZ, 1918)	E		-	-	0.02	0.02	-	-	0.06	0.09
95	<i>Megaselia lutea</i> (MEIGEN, 1830)	H		-	-	0.38	0.30	-	-	0.10	0.15
96	<i>Megaselia major</i> (WOOD, 1912)	E		0.05	0.11	0.16	0.13	0.10	0.15	0.10	0.14
97	<i>Megaselia mallochii</i> (WOOD, 1909)	E	z	0.07	0.17	0.06	0.04	0.04	0.06	-	-
98	<i>Megaselia manicata</i> (WOOD, 1910)	P		3.48	8.19	2.57	2.06	0.58	0.90	0.71	1.03
99	<i>Megaselia marekdurskii</i> DISNEY, 1998	E		0.02	0.05	0.04	0.03	-	-	-	-
100	<i>Megaselia maura</i> (WOOD, 1910)	E	f	-	-	-	-	-	-	0.02	0.03
101	<i>Megaselia meconicera</i> (SPEISER, 1925)	H	s	0.47	1.10	3.71	2.98	0.02	0.03	1.71	2.47
102	<i>Megaselia meigeni</i> (BECKER, 1901)	P		-	-	-	-	-	-	0.06	0.09
103	<i>Megaselia melanostola</i> SCHMITZ, 1942	E		-	-	0.06	0.05	-	-	-	-
104	<i>Megaselia minor</i> (ZETTERSTEDT, 1848)	P		0.55	1.29	0.05	0.04	0.06	0.09	0.06	0.09
105	<i>Megaselia nasoni</i> (MALLOCH, 1914)	H	z	0.06	0.14	0.14	0.11	0.08	0.12	0.14	0.20
106	<i>Megaselia nigra</i> (MEIGEN, 1830)	H	f	-	-	0.02	0.02	-	-	-	-
107	<i>Megaselia nigriceps</i> (LOEW, 1866)	H	s	4.35	10.23	0.73	0.58	0.21	0.33	0.18	0.26
108	<i>Megaselia obscuripennis</i> (WOOD, 1909)	E	z	-	-	-	-	0.02	0.03	-	-
109	<i>Megaselia paludosa</i> (WOOD, 1908)	P	z	-	-	-	-	-	-	0.10	0.15
110	<i>Megaselia parva</i> (WOOD, 1909)	P		-	-	0.12	0.09	0.06	0.09	0.13	0.19
111	<i>Megaselia pectoralis</i> (WOOD, 1910)	P		-	-	0.10	0.08	0.14	0.22	0.12	0.18
112	<i>Megaselia picta</i> (LEHMANN, 1822)	C		0.02	0.04	0.07	0.06	0.45	0.70	0.12	0.17
113	<i>Megaselia pleuralis</i> (WOOD, 1909)	H	s	1.88	4.42	1.25	1.00	0.54	0.84	0.28	0.40
114	<i>Megaselia plurispinulosa</i> (ZETTERSTEDT, 1860)	P	f	-	-	0.06	0.05	-	-	-	-
115	<i>Megaselia propinqua</i> (WOOD, 1909)	E		0.02	0.05	0.65	0.52	-	-	0.19	0.27
116	<i>Megaselia protarsalis</i> SCHMITZ, 1927	P		-	-	0.10	0.08	-	-	0.04	0.06

Appendix - cont.

1	2	3	4	5	6	7	8	9	10	11	12
117	<i>Megaselia pseudogiraudii</i> (SCHMITZ, 1920)	E		-	-	0.26	0.21	-	-	0.08	0.11
118	<i>Megaselia pulicaria-complex</i> (FALLEN, 1823)	H	p	0.42	1.00	7.03	5.63	0.85	1.31	1.81	2.61
119	<i>Megaselia pumila</i> (MEIGEN, 1830)	P		1.45	3.40	4.32	3.46	0.80	1.23	0.08	0.12
120	<i>Megaselia pusilla</i> (MEIGEN, 1830)	H		0.02	0.05	0.58	0.47	0.53	0.81	1.89	2.72
121	<i>Megaeselia pygmaea</i> (ZETTERSTEDT, 1848)	P	f	-	-	0.06	0.05	-	-	0.27	0.39
122	<i>Megaselia robusta</i> SCHMITZ, 1928	H		-	-	0.02	0.01	-	-	-	-
123	<i>Megaselia rubella</i> (SCHMITZ, 1920)	P	f	0.13	0.30	0.02	0.02	-	-	0.11	0.16
124	<i>Megaselia rudis</i> (WOOD, 1909)	E		-	-	-	-	-	-	0.02	0.03
125	<i>Megaselia rufa</i> (WOOD, 1908)	E	z	-	-	0.04	0.03	0.08	0.13	-	-
126	<i>Megaselia ruficornis</i> (MEIGEN, 1830)	H		0.02	0.04	0.32	0.26	0.65	1.00	0.32	0.47
127	<i>Megaselia scalaris</i> (LOEW, 1866)	C	p	-	-	0.02	0.02	-	-	-	-
128	<i>Megaselia scutellaris</i> (WOOD, 1909)	P	f	0.20	0.47	0.38	0.30	-	-	0.06	0.08
129	<i>Megaselia sepulchralis</i> (LUNDBECK, 1920)	P		-	-	0.85	0.68	0.30	0.46	2.67	3.85
130	<i>Megaselia serrata</i> (WOOD, 1910)	E		-	-	-	-	-	-	0.06	0.09
131	<i>Megaselia setulipalpis</i> SCHMITZ, 1938	E		0.02	0.04	0.02	0.02	-	-	0.10	0.14
132	<i>Megaselia simplex</i> (WOOD, 1910)	E		-	-	-	-	-	-	0.04	0.05
*133	<i>Megaselia sinuata</i> SCHMITZ, 1926	E		-	-	0.02	0.01	-	-	-	-
134	<i>Megaselia sordida</i> (ZETTERSTEDT, 1838)	H		-	-	1.06	0.85	-	-	-	-
135	<i>Megaselia spinicincta</i> (WOOD, 1910)	E	f	-	-	0.22	0.17	0.04	0.06	0.06	0.09
136	<i>Megaselia spinigera</i> (WOOD, 1908)	P		-	-	0.04	0.03		0.00	0.06	0.08
137	<i>Megaselia stigmatica</i> (SCHMITZ, 1920)	E		-	-	0.04	0.03	-	-	-	-
138	<i>Megaselia styloprocta</i> (SCHMITZ, 1921)	P		0.04	0.08	0.04	0.03	0.02	0.03	-	-
139	<i>Megaselia subnudipennis</i> (SCHMITZ, 1919)	E		0.14	0.32	0.10	0.08	-	-	0.12	0.17
140	<i>Megaselia subpleuralis</i> (WOOD, 1909)	H		0.05	0.11	0.04	0.03	-	-	-	-
141	<i>Megaselia subtumida</i> (WOOD, 1909)	P		-	-	-	-	-	-	-	-
142	<i>Megaselia superciliata</i> (WOOD, 1910)	P		-	-	-	-	-	-	0.06	0.08
143	<i>Megaselia sylvatica</i> (WOOD, 1910)	P	f	-	-	0.04	0.03	-	-	0.02	0.03
144	<i>Megaselia tarsalis</i> (WOOD, 1910)	E		-	-	0.04	0.03	-	-	0.02	0.03
145	<i>Megaselia tarsella</i> (LUNDBECK, 1921)	E		-	-	0.02	0.02	-	-	-	-
146	<i>Megaselia teresamajewskae</i> DISNEY, 1998	E		0.02	0.05	-	-	-	-	-	-
147	<i>Megaselia trojani</i> DISNEY, 1998	E		-	-	0.02	0.02	-	-	-	-

Appendix - cont.

1	2	3	4	5	6	7	8	9	10	11	12
148	<i>Megaselia uliginosa</i> (WOOD, 1909)	E	f	-	-	0.08	0.06	-	-	-	-
149	<i>Megaselia unguicularis</i> (WOOD, 1909)	E		-	-	-	-	-	-	0.02	0.03
150	<i>Megaselia unicolor</i> (SCHMITZ, 1919)	P		0.06	0.14	10.40	8.34	2.51	3.86	0.80	1.16
151	<i>Megaselia valvata</i> SCHMITZ, 1935	E		-	-	-	0.00	0.02	0.03	0.13	0.19
152	<i>Megaselia variana</i> SCHMITZ, 1926	P		-	-	-	0.00	-	-	0.02	0.03
153	<i>Megaselia verna</i> SCHMITZ, 1932	E		-	-	0.06	0.05	-	-	-	-
154	<i>Megaselia verralli</i> (WOOD, 1910)	P		9.56	22.46	0.63	0.50	0.06	0.09	0.06	0.08
155	<i>Megaselia woodi</i> (LUNDBECK, 1922)	P		0.45	1.06	18.43	14.77	8.58	13.22	17.89	25.78
156	<i>Megaselia xanthozona</i> (STROBL, 1892)	P		0.50	1.18	0.12	0.10	0.06	0.09	0.12	0.18
*157	<i>Megaselia zonata</i> (ZETTERSTEDT, 1838)	P		2.19	5.14	0.62	0.50	0.04	0.06	0.02	0.03
158	<i>Menoziola obscuripes</i> (SCHMITZ, 1927)	E		-	-	-	-	0.06	0.09	0.12	0.17
159	<i>Metopina braueri</i> (STROBL, 1880)	E		-	-	-	-	-	-	0.02	0.03
160	<i>Metopina heselhausi</i> SCHMITZ, 1914	P	s	0.11	0.26	0.09	0.07	0.02	0.03	0.06	0.09
161	<i>Metopina oligoneura</i> (MIK, 1867)	E	s	0.91	2.13	0.16	0.12	0.08	0.12	0.10	0.15
162	<i>Obscuriphora sheppardi</i> DISNEY, 1986	E		-	-	-	-	0.02	0.03	-	-
163	<i>Phalacrotophora berolinensis</i> SCHMITZ, 1920	E	z	-	-	0.27	0.21	0.31	0.48	0.42	0.60
164	<i>Phalacrotophora fasciata</i> (FALLEN, 1823)	E	z	0.02	0.04	0.84	0.67	1.06	1.63	0.22	0.31
165	<i>Phora artifrons</i> SCHMITZ, 1920	E		0.09	0.21	3.52	2.82	2.22	3.42	1.60	2.30
166	<i>Phora atra</i> (MEIGEN, 1804)	H	s	-	-	-	-	0.04	0.06	-	-
167	<i>Phora convallium</i> SCHMITZ, 1928	P		-	-	-	-	0.24	0.37	0.06	0.09
168	<i>Phora dubia</i> (ZETTERSTEDT, 1848)	P		-	-	0.26	0.21	1.11	1.72	0.22	0.31
169	<i>Phora holosericea</i> SCHMITZ, 1920	H	z	0.02	0.04	0.08	0.06	1.21	1.86	2.87	4.13
170	<i>Phora indivisa</i> SCHMITZ, 1948	P		-	-	0.08	0.06	0.32	0.49	0.02	0.03
171	<i>Phora michali</i> DISNEY, 1998	E		-	-	0.02	0.01	-	-	-	-
172	<i>Phora obscura</i> (ZETTERSTEDT, 1848)	E		0.07	0.17	1.36	1.09	2.34	3.61	7.13	10.27
173	<i>Phora penicillata</i> SCHMITZ, 1920	P		0.04	0.08	6.37	5.10	5.02	7.73	0.78	1.12
174	<i>Phora praepandens</i> SCHMITZ, 1927	E		-	-	0.04	0.03		0.00	0.06	0.09
175	<i>Phora pubipes</i> SCHMITZ, 1920	O		-	-	0.02	0.01	2.00	3.08	0.02	0.03
176	<i>Phora tinctoria</i> SCHMITZ, 1920	P		-	-	-	-	-	-	0.35	0.51
177	<i>Poloniphora bialoviensis</i> DISNEY, 1998	E		0.06	0.14	0.04	0.03	-	-	-	-
178	<i>Pseudacteon formicarum</i> (VERRALL, 1877)	E	z	-	-	-	-	-	-	0.08	0.11

Appendix - cont.

1	2	3	4	5	6	7	8	9	10	11	12
179	<i>Triphleba crassinervis</i> (STROBL, 1910)	E		0.05	0.13	-	-	-	-	-	-
180	<i>Triphleba distinguenda</i> (STROBL, 1892)	E		-	-	0.02	0.02	-	-	-	-
181	<i>Triphleba hyalinata</i> (MEIGEN, 1830)	E	s	-	-	0.02	0.02	-	-	-	-
182	<i>Triphleba lugubris</i> (MEIGEN, 1830)	H	z	0.11	0.25	0.11	0.09	0.04	0.06	0.08	0.12
183	<i>Triphleba luteifemorata</i> (WOOD, 1906)	E		-	-	0.14	0.11	0.24	0.37	0.23	0.33
184	<i>Triphleba minuta</i> (FABRICIUS, 1787)	E	f	0.06	0.14	0.06	0.05	-	-	-	-
185	<i>Triphleba nudipalpis</i> (BECKER, 1901)	E	s	-	-	0.02	0.02	-	-	0.04	0.06
186	<i>Triphleba opaca</i> (MEIGEN, 1830)	P	s	2.02	4.76	0.11	0.09	0.11	0.17	0.34	0.49
187	<i>Triphleba smithi</i> DISNEY, 1982	E		-	-	-	-	-	-	0.02	0.03
188	<i>Triphleba trinervis</i> (BECKER, 1901)	H		0.27	0.63	0.48	0.38	0.08	0.12	0.10	0.14
189	<i>Trucidophora ewardurskae</i> DISNEY, 1990	E	z	-	-	-	-	0.04	0.06	0.10	0.15
190	<i>Veruanus oldenbergi</i> (SCHMITZ, 1927)	E		-	-	0.04	0.03	-	-	-	-
191	<i>Megaselia</i> sp. A			0.02	0.04	0.02	0.02	0.02	0.03	0.02	0.03
192	<i>Megaselia</i> sp. B			-	-	0.02	0.02	0.02	0.03	0.02	0.03
193	<i>Megaselia</i> sp. C			-	-	0.02	0.02	-	-	0.02	0.03
194	<i>Megaselia</i> sp. D			-	-	-	-	-	-	0.02	0.03
195	<i>Megaselia</i> sp. E			-	-	-	-	-	-	0.02	0.03
196	<i>Megaselia</i> sp. F			-	-	-	-	-	-	0.02	0.03
197	<i>Megaselia</i> sp. G			-	-	-	-	-	-	0.02	0.03
198	<i>Megaselia</i> sp. H			-	-	-	-	-	-	0.02	0.03
199	<i>Phora</i> sp. A			-	-	0.02	0.02	0.04	0.06	-	-
200	<i>Triphleba</i> sp. A			-	-	-	-	0.04	0.06	-	-
201	Genus new to science			-	-	-	-	0.22	0.34	-	-
	abundance-sum			42.55	100.00	124.78	100.00	64.87	100.00	69.41	100.00
	number of species			76		138		86		131	