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THE SPIDER FAUNA OF ESTONIAN MIRES*

Abundance. The numbers of spiders in the dwarf shrub layer depend on many factors, but in the first place on overwintering conditions and the character of the dwarf shrub layer. Therefore they vary considerably in different years.

Sweep-net samples, taken from early spring to late autumn enable one to describe the seasonal dynamics of the abundance and to compare different types of mires with one another and in various years (Table 7).

One can observe a very great fluctuation in the abundance of spiders in the field layer of fens in various years (in Avaste Fen, 29.4—71.4 specimens on the average in a sample). In bogs, on the contrary, one can observe a high and stable abundance in those parts of bogs which have a well-formed dwarf shrub layer (in bog pine forests 44.5—58.3 specimens on the average). The numbers of spiders are considerably lower in the dwarf shrub layer of treed bogs and treed bogs with pools (20.2—37.1 specimens on the average). Passing in a successive row from treeless bogs to bog pine forests, we observe an increase in the number of species besides an increase in the number of specimens. Through a treed bog, some spider species characteristic of a bog pine forest can pass even to a treeleess bog. According to the abundance of spiders, the treed bog forms an intermediate link between the treeless bog and the bog pine forest. Although there are some spider species common to all the three bog types, their number in different bog types is quite different.

Seasonal fluctuations in the numbers of spiders in mires are very large, but the general scheme is very similar in all mire types (Fig. 2) — there are two or three peaks. The first spiders appear in April. The high abundance in spring depends on the relatively high abundance of young individuals which were present in the community already in autumn, overwintered at the same place, but are not yet sexually mature. There are also species which overwintered in an adult stage or which reach maturity in spring. When the overwintering conditions are unfavourable, there is no increase in the numbers in spring, or it may be delayed. For instance, up to 75% of the spiders being in Avaste Fen in the autumn of 1952 perished during the winter of 1952/53. Neither was there any usual high abundance of spiders in Tähtvere Bog in the spring of the same year. The low level of the abundance in the spring of 1953 did not affect the occurrence and the size of the spider populations in autumn. One can suppose that the spiders which usually form the main mass of spiders in spring perished during the winter.

The low level of spiders in summer corresponds to the time when the species overwintering in an adult stage have disappeared from the

* For the beginning see the previous issue.

Table 7

Average number of spiders in Estonian mires

Habitat	Locality	Year	Average number of specimens	
			in a sweep-net sample (100-strokes)	in a sieve sample (1 m²)
Fen	Avaste	1951	29.4	
diel samples	„	1952	56.6	
midday samples	„	1952	71.4	11.6
Fen (flooded)	delta Emajõgi	1948	45.0	
„	„	1953	42.8	
Transitional bog				
pine forest	Sõmerpalu	1959	25.0	49.8
„	„	1960	20.8	39.2
„	Väätsa	1959	19.2	42.8
„	„	1960	28.8	18.0
„	Venevere	1959	9.3	66.0
„	„	1960	11.5	64.8
Treed transitional bog	Sõmerpalu	1959	48.3	35.3
„	„	1960	33.8	37.6
„	Väätsa	1959	27.5	26.3
„	„	1960	41.8	19.0
„	Venevere	1959	5.5	68.3
„	„	1960	7.2	41.8
Lagg zone	Tähtvere	1952	12.3	
„	„	1953	8.9	
„	Sõmerpalu	1959	19.0	47.4
„	„	1960	26.6	25.8
Bog pine forest	Endla	1948	44.5	
„	„	1950	55.2	
„	Tähtvere	1952	57.3	29.0
„	„	1953	58.3	
„	Sõmerpalu	1959	34.4	
„	„	1960	36.2	
Treed bog with pools	Endla	1948	24.9	
„	„	1950	37.1	12.9
Treed bog	Tähtvere	1952	20.2	
„	„	1953	27.4	
Treeless bog	Endla	1948—1950	5.4	6.1
„	Tähtvere	1952/53	10.7	
Drained fen	Avaste	1951	18.2	
„	„	1952	40.9	
Long-time fallow in a fen	„	1952	42.1	
rye field	„	1952	14.3	
Drained transitional bog forest	Venevere	1959	5.0	41.8
„	„	1960	9.7	21.8
Drained treed bog	Endla	1950	31.5	
„	„	1950	32.4	
Cultivated hayfield in a bog	„	1950	24.9	

community, whereas the summer and autumn species have not appeared yet or occur only as single specimens. The ratio of adults to young stages has more or less equalized by this time.

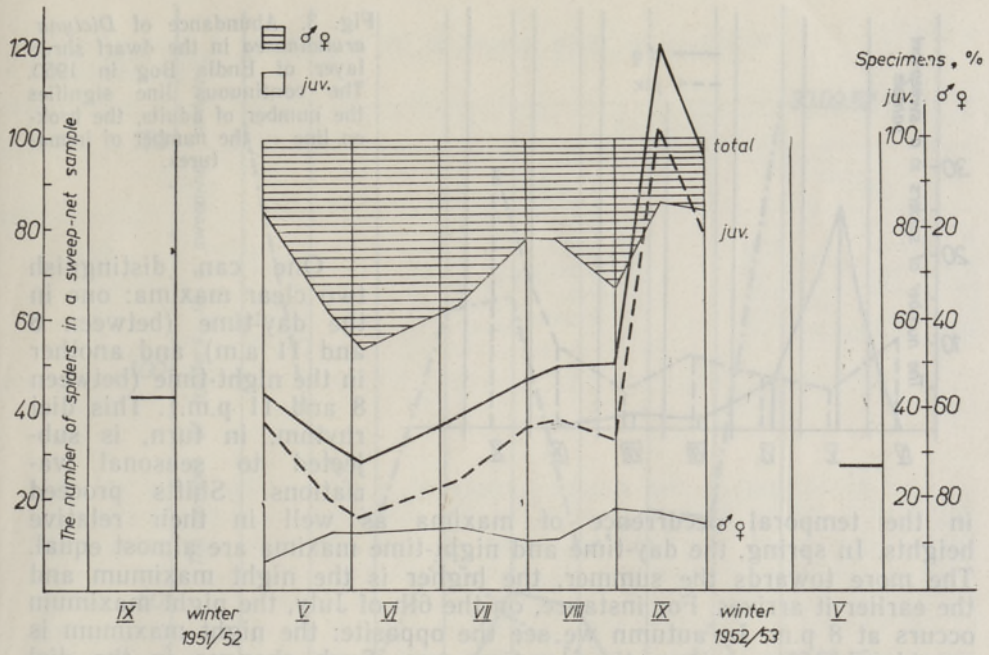

Fig. 2. Abundance (scale on the left) and distribution (scale on the right) of adult and immature spiders in the field layer of Avaste Fen in 1952. The continuous bold-face line denotes the total number of spiders, the continuous slender line — the number of adults, the broken line — the number of immatures. The hatched area represents the proportion of adults (%), the white area — the proportion of immatures (%).

The rise in numbers in summer and autumn may, on the one hand, be due to a rise in the numbers of immature stages, and on the other it may be connected with the appearance, in the community, of the species which have reached sexual maturity. The summer peak of abundance passes suddenly into an autumn peak in the middle of September, at the time of the mass hatching of young spiders from eggs. At this time the numbers of young spiders exceed the numbers of adults almost 7 times.

The abrupt decrease in the abundance in autumn is connected with a rapid deterioration of weather conditions. The influence of the climate is greatest in treeless bogs and in sparsely treed bogs, where the soil freezes more deeply. The latter phenomenon is due to the thin snow cover, which, in turn, depends on the mosaic and very weak distribution of the dwarf shrub layer (Valk, 1960). This all affects the spiders which overwinter in treeless and treed bogs, and brings about a steady low abundance of spiders in treeless bogs.

In the field layer of fens and transitional bog forests, the abundance curves of one and the same dominant or those of a few dominants may considerably affect the abundance curve of the spiders as a whole.

In bogs, the adult specimens of the dominant *D. arundinacea* affect the peak in spring, and the immature stages affect the peak in autumn (Fig. 3).

Series of the samples taken by J. Vilbaste in Avaste Fen twice a month every three hours showed that besides seasonal fluctuations in numbers one can also observe changes in samples during a twenty-four-hour day (Fig. 4).

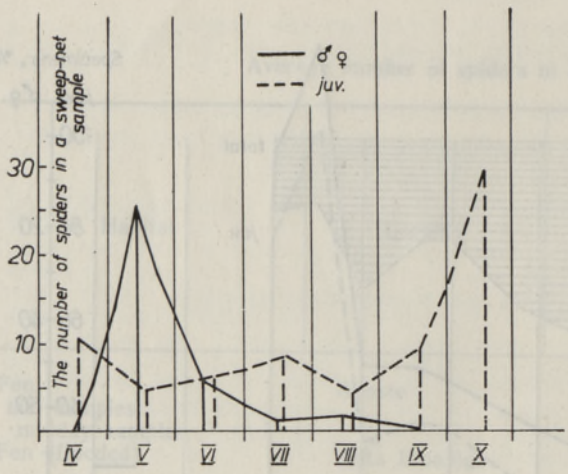

Fig. 3. Abundance of *Dictyna arundinacea* in the dwarf shrub layer of Endla Bog in 1950. The continuous line signifies the number of adults, the broken line — the number of immatures.

One can distinguish two clear maxima: one in the day-time (between 8 and 11 a.m) and another in the night-time (between 8 and 11 p.m.). This diel rhythm, in turn, is subjected to seasonal variations. Shifts proceed in the temporal occurrence of maxima as well in their relative heights. In spring, the day-time and night-time maxima are almost equal. The more towards the summer, the higher is the night maximum and the earlier it arrives. For instance, on the 6th of July, the night maximum occurs at 8 p.m. In autumn we see the opposite: the night maximum is considerably lower than the day-time one. Such changes in the diel rhythm of the abundance of spiders in the samples depend on the microclimatic conditions within the field layer (chiefly temperature and atmospheric humidity), and in particular on the changes in the distribution of warm strata (Vilbaste, 1955, 1958). When the warmest strata are in the upper part of the field layer, the animals climb upwards, and vice versa.

In addition, one must stress the importance of the catching time in the evaluation of the material and in drawing conclusions. Taking into account all the samples collected in Avaste Fen, the mean number of specimens per sweep-net sample was 56.6, whereas when we take into account only midday samples, the number was 71.4 specimens. The differences were due to midday samples which were rich in specimens in autumn.

The conditions in the moss layer are considerably stabler and therefore there are no great increases or decreases in abundance. The number of adult specimens in the moss layer is likewise considerably greater than in the field layer.

As the samples in the moss layer of fens and bogs were taken in several years and the mean values of habitats were obtained by summing up all the data, it is not possible to characterize the changes according to different years and different fens and bogs.

A comparison of the abundance of spiders in individual bog types shows that the abundance is low in such types of bogs where overwintering conditions are most infavourable: in treeless bogs (steadily low numbers) and in treed bogs with pools (low only in spring), where during the winter about two-thirds of the spiders perish in autumn. In bog pine forests, which form a connecting link between the faunas of bog and mineral land, the abundance of spiders is steadily high. Many young spiders of the field layer stay in the moss layer either permanently or temporarily. For many spiders of the field layer, the moss layer also serves as an overwintering place. Part of the animals of other bog habitats probably also overwinter in bog pine forests.

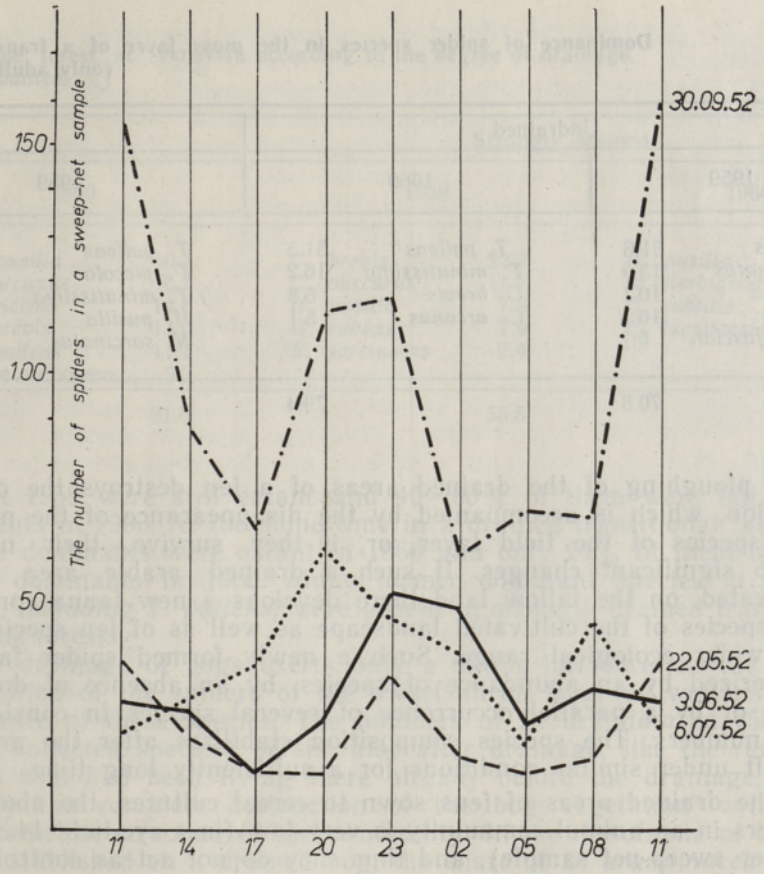

Fig. 4. Diel dynamics of spiders in the field layer of Avaste Fen in 1952.

The spider fauna of transitional bog forests reflects their heterogeneous nature and diverse genesis. More than in any other mire type, the numbers of spiders depend on the type of the transitional bog. In some transitional bog pine forests the abundance of spiders increases by the autumn up to five-fold (up to 120 specimens per m^2) and the ratio of adults to young specimens increases to 1.2/1 in favour of adults by the time of the appearing of overwintering species.

Drainage. The effect of drainage on the spider fauna can be followed on the basis of the materials collected in the field layer of Avaste Fen (1951 and 1952), Endla Bog (1950) and those of the field and the moss layer of Sõmerpalu, Väätsa and Venevere transitional bog forests (1959 and 1960).

The percentage of spiders in the mesofauna of mires diminishes in accordance with the degree of the intensity of transformation of these territories by man.

After the digging of a system of drains, the marginal areas of a fen begin to overgrow with brushwood. The number of spider species increases on the margin of arable land at the expense of the species of mineral land. The number of spider specimens increases in the marginal areas of fens (up to 94.2 specimens per sweep-net sample).

Dominance of spider species in the moss layer of a transitional (only adults have

Undrained				Drai	
1959		1960		1959	
T. pallens	31.6	*T. pallens*	51.3	*T. pallens*	30.8
N. sarcinatus	13.9	*T. minutissima*	16.2	*P. piccolo*	23.0
H. pusilla	10.1	*C. brevis*	6.8	*T. minutissima*	13.8
C. brevis	10.1	*C. arcanus*	5.1	*H. pusilla*	9.2
H. rubrofasciate	5.1			*N. sarcinatus*	6.2
	70.8		79.4		86.0

The ploughing of the drained areas of a fen destroys the original vegetation, which is accompanied by the disappearance of the previous spider species of the field layer, or, if they survive, their numbers undergo significant changes. If such a drained arable area is left uncultivated, on the fallow land there develops a new fauna consisting of the species of the cultivated landscape as well as of fen species having a wider ecological range. Such a newly formed spider fauna is characterized by an abundance of species, by an absence of dominant species, or by a parallel occurrence of several species in considerably higher numbers. The species composition stabilizes after the area has been left under similar conditions for a sufficiently long time.

In the drained areas of fens sown to cereal cultures, the abundance of spiders in an animal community is very low (in a rye-field 14.3 specimens per sweep-net sample), and thus they do not act as controllers of the natural balance among various animal groups.

The influence of drainage on the spider fauna of transitional bog forests was followed in the Venevere transitional bog in 1959 and 1960, in three different degrees of drainage.

The spider fauna of the field and dwarf shrub layers of transitional bog forests at Venevere has been steadily poor in species as well as in the numbers of specimens, and changes after drainage have been insignificant. Only the numbers of the species *Xysticus ulmi* and *Evarcha arcuata* are somewhat more numerous in all habitats. However, of all the transitional bog forests studied, the fauna of the moss layer is richest in specimens, and the changes under the action of drainage are much greater.

The digging of draining ditches has a small effect on the numbers of spider species and on their species composition (Table 8). Drainage exercizes a considerably greater influence on the abundance of spiders (as result of draining it diminishes up to four times) and it is of a still greater effect on the relations between the abundance of spider species (dominants vary in different years, differences between the abundance of spider species are small since there exist no species whose percentage would exceed the percentage of others many times over). The most abundant species is *Tapinocyba pallens* — a species which is dominant also in several other forest types.

When we observe the preservation of the dominant spider species of 1959 in the community of the moss layer in 1960, we see that in an undrained bog pine forest 100% of the spider species which had domin-

Table 8

bog pine forest at Venevere according to the degree of drainage been counted, %)

ned		Strongly drained			
1960		1959		1960	
H. pusilla	16.7	*C. brevis*	22.2	*H. pusilla*	23.8
C. arcanus	16.7	*C. obscurus*	11.1	*M. herbigradus*	14.3
P. piccolo	14.8	*H. pusilla*	7.4	*C. subtilis*	9.5
C. brevis	13.0	*G. rubens*	7.4	*C. laevitarsis*	9.5
T. pallens	11.1	*N. sarcinatus*	7.4		
T. minutissima	9.3				
	81.6		55.5		57.1

ated in 1959 were still extant and 40—80% of them were left among dominants in 1960. At the same time in a drained transitional bog forest 80% of dominants were extant in 1960 and only 20% of them belonged to the dominants in 1960. Many former dominant species of drained forests, including *T. pallens,* were absent in strongly drained transitional bog pine forests.

The drainage of bogs exerts only a slight influence on the species composition of the spiders of the dwarf shrub layer as well as on the abundance of these species. The numbers of *D. arundinacea* (53.4% of all the collected species) persist also after drainage, like the remaining species who had been living there already before the drainage.

Only the complete destruction of the bog vegetation will cause changes in the structure of the community. In the mesofauna of the field crops established on a drained bog, the share of *D. arundinacea* became very insignificant. In the cultivated hayfield established in the drained parts of Endla Bog, *Pachygnatha degeeri* predominated in 1950, whereas in the following year it was most probably replaced by some other spider species.

The relationship of the fauna of mires to that of the neighbouring areas

One may suppose that the fauna of such treeless open habitats as flooded meadows, flooded fens and fens (of the latter such ones that are steadily suffering from excessive moisture) are quite similar in their spider fauna.

Flooded fens represent a transition from flooded meadows to fens, while transitional bogs represent a transition from fens to bogs.

Flooded meadows and flooded fens are characterized by a very similar abundance of spiders in the years under consideration: in the flooded meadow of the Pedja River there were 42.8 (1961) and 43.7 (1962) specimens per sweep-net sample, and in the flooded fen of the delta of the River Emajõgi 45.0 (1948) and 42.8 (1953). The species composition is more different. There are no common species among dominants; among influents *Xysticus ulmi* and *Tatragnatha extensa* are common.

In the spider fauna of flooded fens and fens, there is one common dominant species (*Tibellus maritimus*) and there are two common influent species (*Xysticus ulmi* and *Dictyna arundinacea*). It is rather

difficult to compare the abundance of spiders, since in Avaste Fen the abundance of spiders in the two years of investigation was very different. It seems that both the years were quite exceptional — 1951 was a year with an extraordinarily low abundance (29.4) and 1952 was a year with an extraordinarily high abundance (71.4 specimens per sweep-net sample).

The increase of bog elements in the vegetation of fens is a natural process that alters the fens to transitional bogs. This process is accompanied by an increase in the dominance of bog species, and especially that of *Dictyna arundinacea* in the community. While in our fens (which are mostly treeless or characterized by sparse birches, chiefly *Betula pubescens*) the life conditions are relatively uniform, in transitional bogs man's influence has been greatest and life conditions have been most variable. This variability has also influenced the fauna. The spider fauna of transitional bog forests is greatly of a local character, depending more than in other mire habitats, on the way how a particular transitional bog and the fauna of the neighbouring area have established themselves. This becomes especially evident when we compare the spider fauna of transitional bog forests at different geographical points. It appears that the spider faunas of two different transitional bog habitats at one geographical point (e.g., a transitional bog pine forest and a sparse transitional bog forest at Sõmerpalu) are closer to each other (Sørensen's index QS=50%; Renkonen's index PS=57%) than the faunas in two physiognomically very similar, but geographically remote areas (e. g., in transitional bog pine forests at Sõmerpalu and at Väätsa — QS=46%; PS=31%). This means that even if the species composition is somewhat similar, the dominance values of the common species are quite different.

Among bog habitats, the bog pine forest lying on the margins of bogs has the most heterogeneous spider fauna. It consists of the spider species which have come from habitats of mineral grounds as well as from the bog and its lagg zone. Due to that circumstance, the species composition of the spider fauna of different bog pine forests is very variable, depending on the species composition of the fauna of the neighbouring habitats. Contrary to other mire habitats, the distribution of dominants in the dwarf shrub layer of bogs is very stable. *D. arundinacea* is here, at the highest stage of paludification, absolutely prevalent and renders the structure of the spider community in bogs entirely different from that of other mire habitats. *D. arundinacea* has probably passed to bogs together with the most important bog shrubs. It is therefore equally well thriving on the margins of sandy heath areas as well as on the margins of bogs and bog pine forests. The other species accompanying *D. arundinacea* on sandy heath areas are also known from bogs.

If we compare the spider fauna of a bog pine forest with that of a sandy heath area situated on the margin of the Tähtvere Bog, it appears that in respect to their number of species (in the bog pine forest 25, in the heath 23 spider species) as well as in respect to the abundance of spiders (in the bog pine forest 57.3 (1952) and 58.3 (1953); in the heath area 41.8 (1952) and 61.4 (1953) per sweep-net sample), these areas are quite similar. The comparison of the species composition yields similarity indices QS=33%; PS=42%. At the same time one must estimate the percentage of similarity (PS), which takes into account the dominance values of the species common to both areas, to be quite high. And yet one cannot characterize the spider community of bogs only on the basis of the spiders of the dwarf shrub layer; the latter are assigned a charac-

teristic «bog» appearance according to certain bog species occurring there in single specimens.

The intrusion of faunal elements of the mineral ground and the great importance of the faunal elements of the bogs render the faunas of the moss layers of transitional bog pine forests and of bog pine forests closely related to each other (the predominant spider species there are *Tapinocyba pallens, Hahnia pusilla, Ceratinella brevis, Centromerus arcanus*).

Summary. Over 35 000 spider specimens have been collected from Estonian mires. They belong to 301 spider species (Tables 1 and 2).

Spiders constitute an essential component in the field layer of fens (up to 25%), transitional bog forests (up to 17%) and in the dwarf shrub layer of bogs (up to 30%) (Table 3). In the moss layer the percentage of spiders is still higher, with seasonal fluctuations considerably lower than in the field layer.

The spider fauna of all the habitats inconsiderably influenced by human activities, as well as the spider fauna of mires is characterized by the fact that there exist small amounts of dominants which, however, contain the predominant part of specimens (Fig. 1). The majority of species belong to recedents, making up one-third of the specimens. The influents occupy a position between these two groups.

In the structure of the spider community of the field layer of fens and transitional bog forests, there occur changes in the composition of dominant species from year to year (Table 4), but each year the spider community includes some species whose percentage considerably exceeds that of others. The species composition in the field layer changes more considerably in the moss layer.

The structure of the spider community of the dwarf shrub layer of large bogs (Table 6) is quite different: the predominance of *Dictyna arundinacea* in bogs is very stable (over 50% of the specimens), also in different years (Fig. 3). Further species characteristic of the dwarf shrub layer are *Heliophanus dampfi, Araneus adiantus, Clubiona trivialis, Evarcha laetabunda, Oxyopes ramosus* (Tables 4 and 5).

Of the species active in the moss cover of bogs, the most abundant are *Pardosa sphagnicola* appearing in marginal areas and *Pardosa hyperborea* living in treeless bogs.

The abundance of spiders varies greatly in various habitats (Table 7). Seasonal fluctuations (Fig. 2) are great, but similar in their general pattern (with 2 or 3 peaks) in all mire types. Diel fluctuations in samples are also extensive (Fig. 4), varying during the growing period according to seasons.

Drainage reduces the role of spiders in the habitat. In the structure of the spider community, there become evident such changes as an increase in the number of species, absence of dominant species, or a parallel occurrence of several species having a considerably higher dominance. After ploughing the original fauna perishes completely. A new fauna is formed from the species inhabiting mires and mineral soils.

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EESTI SOODE ÄMBLIKEFAUNA

Eesti soodelt on kogutud üle 35 000 ämbliku 301 liigist. Puhmarinde mesofaunast moodustavad ämblikud madalsoodes kuni 25%, siirdesoodes kuni 17% ja rabades kuni 30%. Samblarindes on ämblike osatähtsus veelgi suurem, selle aastaajaline kõikumine aga tunduvalt väiksem kui rohurindes.

Enamik rohurinde ämblikuisendeid kuulub väikese hulga liikide, dominantide hulka. Enamik liike kuulub retsedentide hulka.

Madalsoode ja siirdesoometsade rohurindes on ühel aastal valdavad ühed, teisel aastal teised ämblikuliigid, kuid igal aastal on koosluses mõni liik, mille osatähtsus ületab tunduvalt teiste liikide oma.

Dictyna arundinacea valdavus suuremates rabades on stabiilne — üle 50% isendeist ka erinevatel aastatel. Rabade puhmarindes on iseloomulikud liigid *Heliophanus dampfi, Araneus adiantus, Clubiona trivialis, Evarcha laetabunda, Oxyopes ramosus.*

Rabade sammalkattel tegutsevatest liikidest on kõige arvukamad *Pardosa sphagnicola* rabaservades ja rabasaarte ümber kitsal *Sphagnum*-mättalisel alal ning *P. hyperborea* lagerabal.

Arvukuse sesoonsed kõikumised (joon. 2) on ulatuslikud, kuid üldskeemilt kõigis sootüüpides sarnased — kas 2- või 3-tipulised. Arvukuse ööpäevased kõikumised püükides on suured ja muutuvad sesoonselt.

Maade kuivendamise tagajärjel väheneb ämblike osatähtsus koosluses, liikide arv suureneb, domineerivad liigid puuduvad või esineb paralleelselt mitu märgatavalt suurema arvukusega liiki. Ümberkünd hävitab esialgse fauna täielikult. Uus fauna formeerub nii soo- kui ka mineraalmaa liikidest.

Аста ВИЛЬБАСТЕ

ФАУНА ПАУКОВ ЭСТОНСКИХ БОЛОТ

На болотах Эстонии собрано свыше 35 000 особей пауков, относящихся к 301 виду. В мезофауне травяного яруса пауки составляют на низинных болотах до 25%, в лесах переходного болота до 17% и на верховых болотах до 30%. В моховом ярусе удельный вес пауков еще больший, но сезонное колебание его значительно меньше, чем в травяном ярусе.

Часть пауков травяного яруса относится к небольшому числу видов — к доминантам. Большинство видов принадлежит к рецедентам.

В травяном ярусе низинных болот и в лесах переходных болот доминируют в разные годы различные виды пауков, но каждый год в сообществе обнаружен какой-то вид, удельный вес которого значительно превышает удельный вес других видов.

Доминирование вида *Dictyna arundinacea* в более крупных верховых болотах стабильно также в разные годы — свыше 50% от всех особей. В травяном ярусе верховых болот характерными являются еще *Heliophanus dampfi, Araneus adiantus, Clubiona trivialis, Evarcha laetabunda, Oxyopes ramosus.* Из видов, живущих на поверхности мохового покрова, более многочисленными являются *Pardosa sphagnicola* на узком кочковатом поясе по краям болот и вокруг минеральных островов болот и *Pardosa hyperborea* на безлесном болоте.

Сезонные колебания численности пауков схожи по всем типам болот и имеют 2—3 пика.

При осушении болот удельный вес пауков в сообществе уменьшается, количество видов увеличивается. Доминирующие виды отсутствуют или встречаются одновременно несколько видов со значительно высокой численностью. Распахивание болот полностью уничтожает первоначальную фауну их. Новая фауна формируется из видов как с болота, так и с минеральной почвы.