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Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae)

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Summary. Beetles and midges (Sciaridae and Mycetophilidae) inhabiting dead wood of three tree species were studied in 1989 in three forests of the Bornhöved Lake District (Schleswig-Holstein, Northern Germany). Logs and stumps originating from beech, alder and spruce were investigated. We found 3,956 beetles and 7,118 midges. There were 114 beetle species, 38 sciarid species, and 55 mycetophilid species reared from a total of 1.7 m^3 of dead wood. The abundance of beetles increased with the age of the wood and so did the number of beetle species and Myctophilidae. Approximately 12–13 beetle species were collected per sample. The habitat use of the different species was analysed. There was little similarity between the midge fauna of dead wood and the litter layer fauna. Mycetophilidae were predominantely found in the wood. Xylophagous beetle species inhabited the logs, whereas fungus feeders were mainly found on old stumps. Age class and water content are the major factors controlling the insect populations, whereas tree species are of minor importance.

Key words: Dead wood fauna, biodiversity, habitat use, succession, ecological forestry

Introduction

In natural forest ecosystems the different kinds of decaying wood (small or big logs, standing or lying tree trunks, stumps), are important habitats for animals (Harmon et al. 1986). The successional stages of wood decomposition provide a large number of microhabitats, in which xylophagous species (Simandl 1993) occur together with highly specialized predators and both saprophagous and microphagous species (Fog 1979a, b). The variety of habitats has a positive effect on overall species richness (Heydemann & Müller-Karch 1980; Heydemann 1982). The purpose of this study is to contribute to our understanding of the importance of decaying wood to habitat diversity in forests. The following questions need to be answered: what is the importance of tree species regarding insects inhabiting decaying wood, how do age and water content influence insects inhabiting dead wood and how do different ecological groups contribute to species composition?

Materials and Methods

The investigated area is part of the "Bornhöved Lake District" situated about 30 km south of Kiel (Schleswig-Holstein, North Germany). The beech wood originated from a 94 year-old beech stand. After tree cutting in 1983 a large number of big logs and stumps had been left on the forest floor. The

acid soil (pH = 3.5) is nutrient poor. The alder wood was collected in a forty year-old alder forest on the shore of Lake Belau. The nutrient rich peaty soil has a pH of about 5.2. The monoculture spruce forest is about forty years old and grows on an acid soil with a pH of about 3.2.
The insects were caught by means of emergence traps, which were set up in the forests. Logs were placed on a PVC film and covered by an emergence trap with 1 m^2 surface area. A seal was attached at the base of the traps to prevent both immigration and escape of insects. Stumps were covered by emergence traps with 0.25 m^2 surface area after removal of surrounding litter and roots. The traps remained on the substratum throughout the whole investigation period, which lasted from March 22 to December 12, 1989. The emergence jars were filled with formalin. Emergence traps (three replicates) were also installed on the floor of the respective forest to compare the wood samples with forest floor samples. These traps covered 1 m^2 surface area. Among the insects collected Coleoptera were identified to species except for the Staphylinidae. The families of sciaroid midges were also identified. According to the recent taxonomic classification (Schumann 1992) some former subfamilies of Mycetophilidae have family status now. For our investigation the Bolitophilidae, Diadocidiidae, Didomyiidae, and Keroplatidae were still included in the Mycetophilidae.
The emergence of wood dwelling insects is affected by various factors. Humidity increased under the emergence traps, which sometimes results in extensive growing of fungi. Occasionally the seal surrounding the base of the traps was damaged or the PVC film was destroyed by mice and had to be renewed. Spiders inhabited the opening to the sampling box to catch emerging insects. Some midges i.e., Sciaridae may have reproduced under the emergence traps (Funke 1983).
The investigated wood items were differentiated into age classes according to the classifications by Brauns (1954), Schimitschek (1952) and Szujecki (1987).
Age class 1: the bark is fixed quite firmly to the wood, the wood itself is still solid.
Age class 2: the bark is fixed only weakly to the wood, the wood itself is more or less solid.
Age class 3: the form of stumps is more or less maintained. The main part of the wood is already rotten, weak and wet.
Age class 4: the form is amorphous, several wood pieces are still maintained, but overall the wood is more or less totally rotted.
Both volume and surface area of the logs and the stumps were measured to relate the abundance of the insects emerged with the amount of wood. Surface area and volume of the logs were calculated from circumference and length. Circumference of the stumps was measured at the top and the base. Stumps were then interpreted as cones to calculate surface area and volume by circumference and height. It was difficult to define the sectional surfaces for age classes 3 and 4, which makes the estimate more or less inaccurate. In order to estimate water content samples were taken and dried at 120 °C. Water content was calculated from the difference between wet and dry weight. Wood parameters are summarized in Table 1.

Table 1. Parameters of the investigated kinds of wood (n = number of replicates, abb = abbreviations)

kind of dead wood		abb.	n	surface area (m^2)	volume (l)	water content (%)	age class
beech	old stumps	Bos	5	0.24–0.45	7.2–17.4	61–78	3–4
	young stumps	Bys	6	0.23–0.43	7.7–20.4	45–60	1
	old logs	Bol	4	1.20–2.70	89–214	70–80	2–3
	young logs	Byl	6	1.10–2.70	37–145	33–54	1
alder	old stumps	Aos	5	0.20–0.50	7.0–29.0	65–84	2–4
	young stump	Ays	1	0.40	17.2	78	1
	old logs	Aol	6	0.58–2.11	36.4–81.8	57–85	2–3
	young logs	Ayl	2	1.10–1.30	40.5–45.3	63–78	1
spruce	old stump	Sos	1	0.40	24.4	72	3
	young stump	Sys	1	0.29	14.1	56	1
	old log	Sol	1	1.57	45.9	63	3
	young log	Syl	1	1.27	41.2	51	1

Results

Species composition and abundance

Overall 11,074 insects were caught with 3,956 individuals belonging to Coleoptera, 5,894 to Sciaridae and 1,224 to the Mycetophilidae. The distributions of the species and their abundance in the different kinds of wood are listed in Appendix 1 – 3. Coleoptera were represented by 114 species, Sciaridae by 38 species and Mycetophilidae by 55 species. As the most abundant beetle family, the Staphylinidae, were not identified, the total number of beetle species will be much higher. Species richness of beetles was highest, but midges dominated by numbers.

Maximum abundance of beetles ranged between 1,400 – 1,600 ind. · $100\,l^{-1}$ wood. Maximum abundance of midges varied between 1,500 and > 3,000 ind. · $100\,l^{-1}$ wood. The highest abundance values were recorded from old spruce logs and an old beech stump (> 3,400 ind. · $100\,l^{-1}$ wood), the lowest abundance values were found in young spruce logs (~ 90 ind. · $100\,l^{-1}$ wood). The results of the ANOVA between the different kinds of wood are shown in Table 2. The variation of abundance and number of species within the groups is remarkable. Only the old beech stumps seem to have high abundances for all the insects

Table 2: Mean abundance and species numbers of insects investigated in different kinds of wood (ind. = individuals · $100\,l^{-1}$ wood, S.E. = standard error, data marked by an * form a homogenous group at the 95% significance level, abbreviations see Table 1)

Group	n	abundance						species numbers					
		beetles		Sciaridae		Myceto-philidae		beetles		Sciaridae		Mycoto-philidae	
		ind.	**S.E.**	**ind.**	**S.E.**	**ind.**	**S.E.**	**spec.**	**S.E.**	**spec.**	**S.E.**	**spec.**	**S.E.**
Byl	**6**	135	92	312	214	49	109	9	2	7	1	4	1
Bys	**6**	306	92	304	214	33	109	10	2	6	1	1	1
Bol	**4**	172	112	150	262	56	134	*18	2	7	1	8	2
Bos	**5**	*935	100	*1089	234	*856	119	*16	2	10	1	12	1
Ayl	**2**	49	158	659	371	40	189	5	3	9	2	2	2
Ays	**1**	447		191		46		*17		8		2	
Aol	**6**	180	92	173	214	11	109	12	2	9	1	1	1
Aos	**5**	*1081	100	757	234	166	119	*17	2	9	1	5	1

Table 3. Mean abundance and species numbers of insects investigated in the differentiated age classes (ind. = individuals · $100\,l^{-1}$ wood, S.E. = standard error, data marked by * or ** form homogenous groups at the 95% significance level)

Age class	n	abundance						species numbers					
		beetles		Sciaridae		Myceto-philidae		beetles		Sciaridae		Mycoto-philidae	
		ind.	**S.E.**	**ind.**	**S.E.**	**ind.**	**S.E.**	**spec.**	**S.E.**	**spec.**	**S.E.**	**spec.**	**S.E.**
1	**15**	206	73	347	123	42	83	10	1	7	1	2	1
2	**8**	243	106	176	168	25	114	13	2	8	1	2	1
3	**6**	*521	106	389	194	**599	132	*18	2	9	1	**13	1
3.5	**4**	**1002	150	**1348	238	*281	162	*15	2	9	1	*5	1
4	**2**	**1121	212	*865	337	*239	229	*17	3	*12	2	*8	2

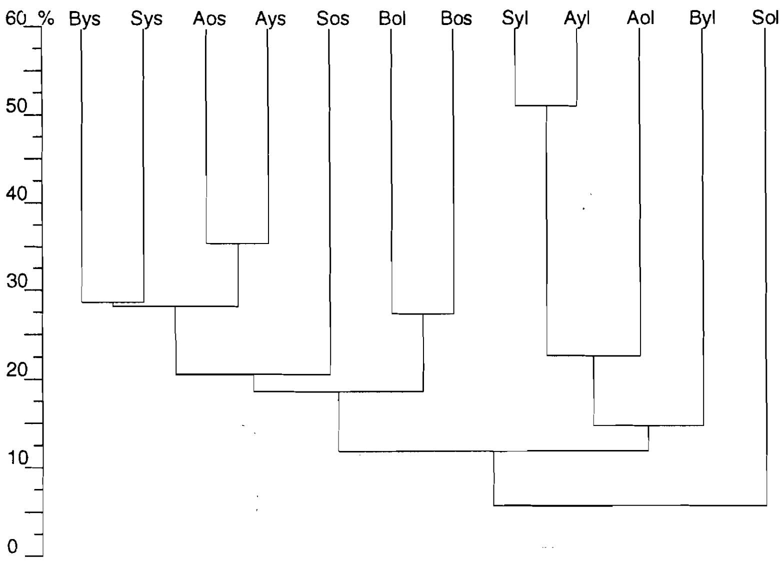

Fig. 1. Average linkage cluster analysis using the dominance similarity indices of all insects investigated (abbreviations see Table 1)

that we investigated. It is difficult to relate the number of species to the type of wood, because there is no linear relationship between the species number and the wood volume. Therefore, the number of species cannot be calculated for a definite wood volume, and the listed number of species (Table 2) refers to the samples and not to a definite wood volume. The volume of the stump samples is generally lower than that of the log samples, which leads us to suspect that the number of species in stumps would be mostly higher than in logs, if definite volumes were compared.

The ANOVA between the differentiated age classes is shown in Table 3. The abundance of beetles increased with the age of the wood. The classes 1 and 2 form a homogenous group as well as the age class 3 and the classes 3.5 and 4. For the midges the relationships between abundance and age are not as clear as for the beetles, but the highest abundances occurred in older age classes only. In the Mycetophilidae the classes 3, 3.5 and 4 are separated from the younger stages. The number of species are generally higher in older stages of decaying wood than in younger stages, which is statistically significant for the beetles and the mycetophilid midges. No significant differences were obtained for wood types of different levels of water content.

An average linkage cluster analyis using the dominance similarity index (Renkonen 1948) of all insects investigated shows no clear differentiation between the different tree species or the age classes (Fig. 1). Probably different communities live in stumps and logs, but in the case of beech wood the communities of old logs and stumps are more similar to one another than to the stumps of the other tree species. The highest similarity occurred between young logs of spruce and alder with about 50%. The similarities between the other kinds of wood are much lower (<40%) suggesting important differences between the various kinds of wood.

Habitat use of midges

The decaying wood is differentially used by the inhabiting species. As the biology of the Sciaridae and the Mycetophilidae species is not well known the midge fauna found in the different kinds of wood (Appendix 2 and 3) was compared with the litter dwelling fauna. In Figures 2 and 3 some species that occurred in all age classes of the wood are shown. Three ecological types of species can be differentiated. Some species occur both in the litter layer and the decaying wood, others were found in several kinds of wood and a third set of species was obtained only from a few kinds of wood.

The first group, species occurring in dead wood and in the litter layer, includes the sciarid species *Ctenosciara hyalipennis*, *Lengersdorfia detriticola*, *Bradysia confinis*, *Corynoptera abblanda*, *C. concinna*, *C. clinochaeta*, *Epidapus atomarius*, *E. gracilis* and *Scatopsciara vivida* as well as the Mycetophilidae *Phronia basalis*, *Corynoptera blanda*, *Macrocera stigmoides* and *Tetragoneura sylvatica*.

The wood dwelling species of the second group were not found in the litter layer. *Scatopsciara pusilla* appeared to prefer logs and young stumps (Fig. 2). *Mycomyia cinerascens* too, occurred only in various kinds of wood (Fig. 3). Contrary to the species of the first group both species were rarely found in old stumps but preferred young stumps and logs. Other species included in this group are the sciarid species *Epidapus titan*, *Lycoriella lundstroemi*, *L. solani* and *Scatopsciara calamophila* and the Mycetophilidae *Macrocera aterrima*, *M. angulata* and *Phronia tenuis*.

The third group was difficult to define. They occurred in a few types of wood, which may have been the result of specific habitat use or may be due to the rarity and/or the heterogenous distribution of the species. *Macrocera stigma* may have specialized on old stumps of deciduous trees. *Apolephthisa subincana* was usually found on young logs of deciduous trees (Fig. 3). *Orfelia nigricornis* and *Sciophila hirta* occurred nearly exclusively on young decaying beech logs. *Mycetophila ocellus* inhabited only old decaying beech wood, living on fungi

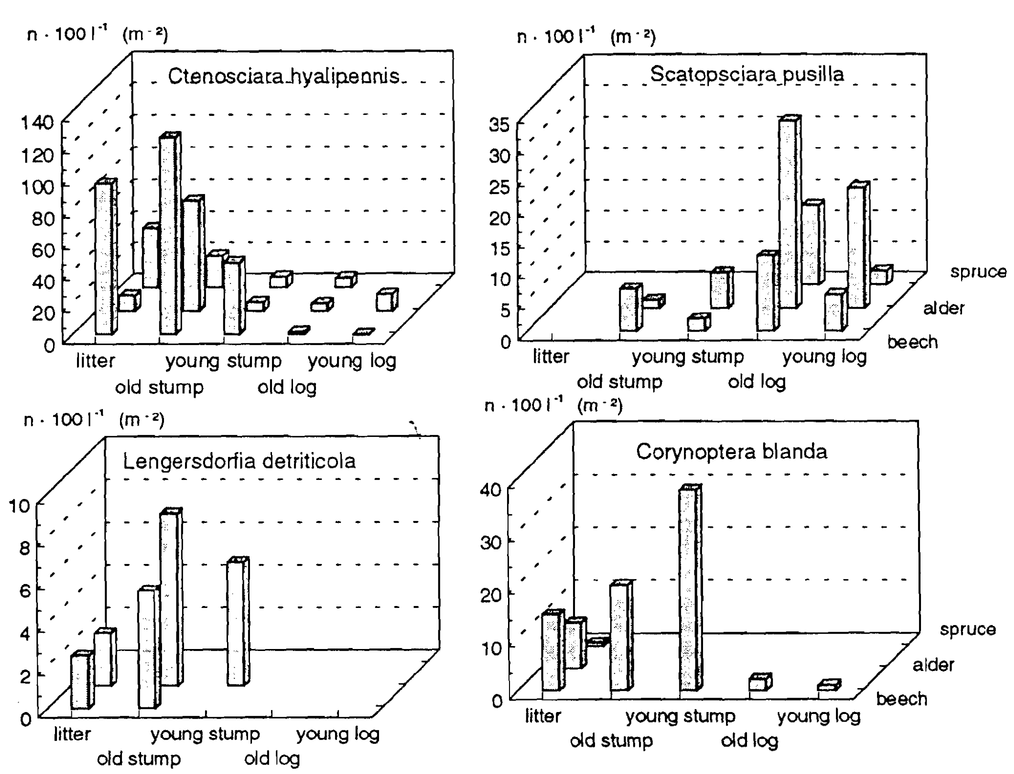

Fig. 2. Distribution of some sciarid midges on the different kinds of wood (ind. · 100 l^{-1}). Emergence of litter relates to ind. · m^{-2} (young wood: age class 1–2, old wood: age class 3–4)

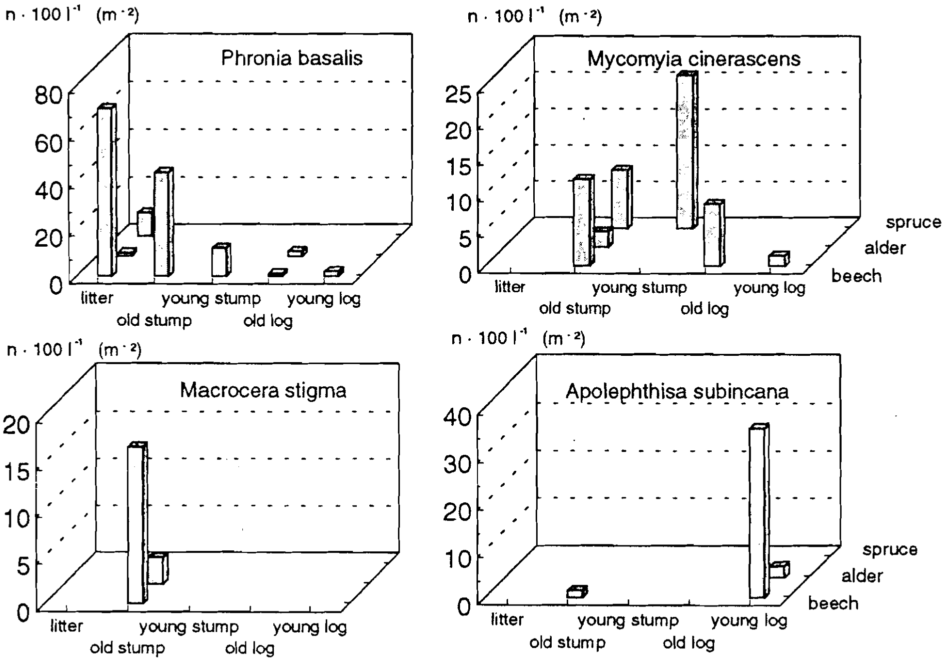

Fig. 3. Distribution of some Mycetophilidae midges on the different kinds of wood (ind. · $100\,l^{-1}$). Emergence from litter is given as ind. · m^{-2} (young wood: age class 1–2, old wood: age class 3–4)

that were growing on the wood. This species was found more frequently on stumps than on logs. Other species found mainly on beech were *Boletina flaviventris*, *Mycomyia marginata* and *Syntemna nitidula*. The larvae of *Docosia gilvipes* are known to live on fungi (Hackmann & Meinander 1979). Thus, this species was found only on old stumps of beech. *Ditomyia fasciata* occurred exclusively on alder.

To estimate the proportion of species that lived exclusively in decaying wood, the occurrence of species in dead wood was compared with the occurrence of species in the litter layer. About 80% of the wood dwelling Mycetophilidae species were recorded only from decaying wood of the deciduous trees (Table 4). In total about 46% of the mycetophilid species were recorded only from decaying wood, 32% of the species were found only in the litter layers

Table 4. Species number of Mycetophilidae and Sciaridae found in the dead wood of individual tree species (total), recorded only from dead wood of one particular tree species (spec.), number of species occurring both in wood and the litter layer (litter), and number of species found also on wood of the other tree species (other). Percentages of specific species which were recorded only from the given type of dead wood but not from the litter layer are also given (spec. (%))

	total	spec.	litter	other	spec.(%)
Mycetophilidae					
beech	45	32	10	3	77
alder	21	6	3	12	86
spruce	8	1	3	4	62
Sciaridae					
beech	27	8	10	9	63
alder	31	5	11	15	65
spruce	13	1	5	7	62

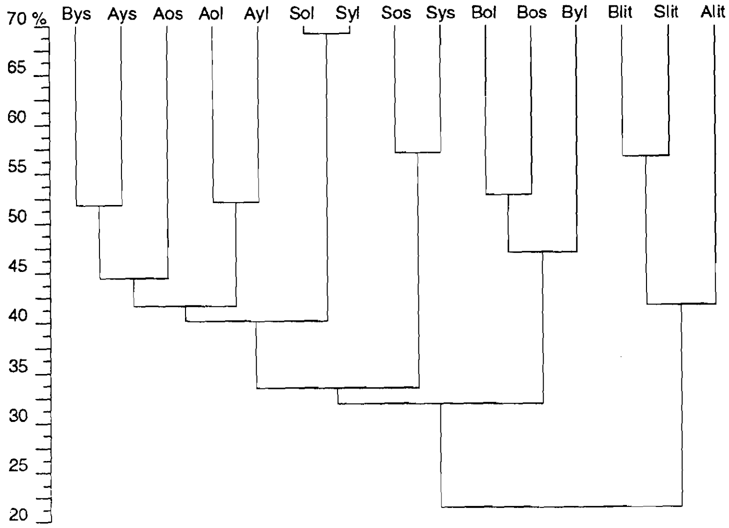

Fig. 4. Average linkage cluster analysis using species identity indices (Soerensen 1948) of the midge communities in the different kinds of dead wood and the respective litter layer (abbreviations see Table 1, lit = Litter)

while 22% occurred in both habitat types. The respective values for the Sciaridae are 30%, 45% and 25%. The Sciaridae showed the lower specialization on the dead wood of particular tree species. About 30% of the sciarid species living in dead beech wood were also found in dead wood of the other tree species. Higher specialization was found for the Mycetophilidae midges. In average about 71% of the mycetophilid species living in dead wood seem to be specialized on the particular kind of wood and only 6% of the species living in dead beech wood were also found on wood of the other tree species. The specialization on dead alder wood seems to be less strict than that on dead beech wood, because only 30% of the mycetophilid species and 16% of the sciarid species were found in dead alder wood only (Table 4).

The high differences of midge species compositions between the dead wood habitat and the litter layer is also demonstrated by a cluster analysis of the species identity indices (Soerensen 1948) (Fig. 4). The litter samples form a distinct group with a similarity of about 20% to the wood samples, whereas similarity between the wood samples is always larger than 30%. Other clusters are obtained for the dead wood of the particular tree species with exception of the young stumps of beech wood. The high similarity between the three beech samples (Bol, Bos, By) is due to the distribution of the mycetophilid species.

Habitat use of beetles

More ecological knowledge is available on beetles than on midges, so more detailed analyses of the beetles inhabiting dead wood are provided here. According to Koch (1989) about 44 species of the beetles caught are saproxylic. These species were represented by 719 individuals, which is about 25% of all individuals obtained. Only a few species inhabited young decaying wood, e.g. *Xyloterus domesticus* (Scolytidae), which was the most abundant species in young decaying beech wood. Among the rarer saproxylic species *Cicones variegatus* (Colydidae), *Sinodendron cylindricum* (Lucanidae) and *Melanotus rufipes* (Elateridae) were found on beech stumps; *Dirhagus pygmaeus* (Eucnemidae) and *Orchesia micans* (Serropalpidae) were reared from dead alder wood.

Using Koch's (1989) classification the beetles were divided into the following ecological groups; overwintering, xylophagous, mycetophagous, and omnivorous species. We expanded

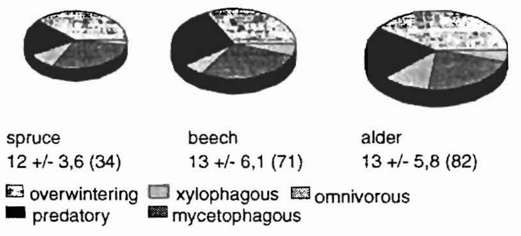

Fig. 5. Composition of wood dwelling beetles utilizing different habitats for the three investigated tree species (mean number of species per sample with std. error; total number of species in parenthesis)

this list by adding a fifth class: the predators. All species which had no food relation to the wood, i.e. Carabidae, Chrysomelidae, and Coccinellidae, but are known to overwinter under bark were classified as overwintering species.

The mean number of beetle species were evenly distributed between the dead wood of the different tree species investigated. About 12–13 species/sample (Fig.5) were recorded from beech, alder, and spruce wood. The difference between the total numbers of species collected from the different tree species is probably caused by the low number of samples for spruce. The high total number of species found on alder can be explained by the heterogenous habitation of the dead alder wood, because the number of samples for alder was lower than for beech and the mean number of species/sample was the same as for beech.

Overwintering and mycetophagous species dominated among the beetle species reared from dead wood. Only a few species were xylophagous. The high number of xylophagous species on alder compared with the wood of the other tree species is remarkable. On the other hand the percentage of mycetophagous species is higher on both spruce and beech wood.

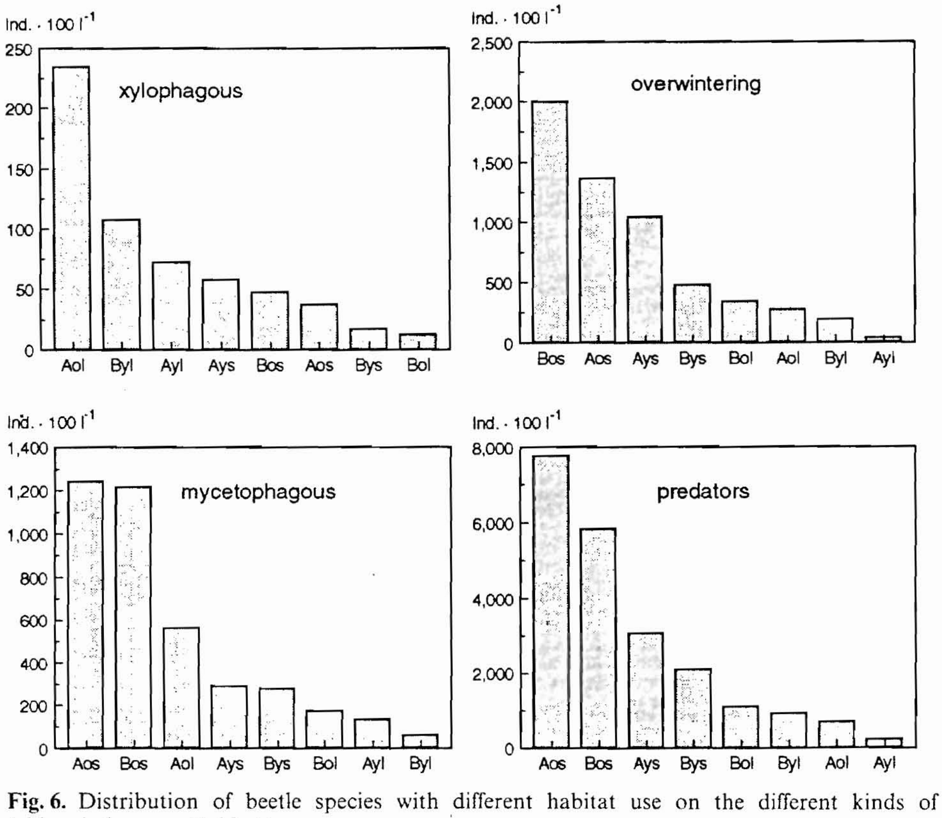

Fig. 6. Distribution of beetle species with different habitat use on the different kinds of wood (abbreviations see Table 1)

Abundances of ecological groups of beetles in different types of dead wood are shown in Fig. 6. For this comparison the staphylinids were included in the predators although some species may have entered the dead wood for overwintering or were fungus feeders. The predatory species were most abundant in all kinds of wood. The lowest abundances were found for the xylophagous species (Fig. 6). However, the age classes of decaying wood were differentially used. Abundance of xylophagous species were highest in logs and these species appeared to prefer alder, while the other types of wood dwellers appeared to prefer old stumps.

A few specialists among the predators show a different distribution. *Rhizophagus bipustulatus*, a predator of bark beetles, inhabited nearly all kinds of wood, but preferred young or wet decaying wood (Fig. 7). This correlates well with the occurrence of its prey, the bark beetle *Xyloterus domesticus*, which was found mainly in young beech wood with a water content of about 45%.

The fungus feeding species preferred old stumps. Age seemed to be of great importance, because old alder logs were more inhabited than young stumps (Fig. 6). There was no preference for wood of a particular tree species. The distribution of the mycetophagous species seemed to be controlled by both age and water content of the decaying wood. Both factors were correlated and it was impossible to differentiate which factor was the more important one. Decaying wood of age classes 3–4 with water contents lower than 60% was not represented in the sample. Abundance of *Cryptophagus pilosus* (Fig. 7) was highest in dead wood of age classes 3–4 and water contents between 60% and 80%. A similar distribution could be found for *Melanophthalma transversalis* and *Corticaria elongata*. The fungus feeding beetle *Lathridius nodifer* occurred in relatively dry wood of age classes 1–2 and relatively wet wood of age classes 2–3. *Cerylon histeroides*, another

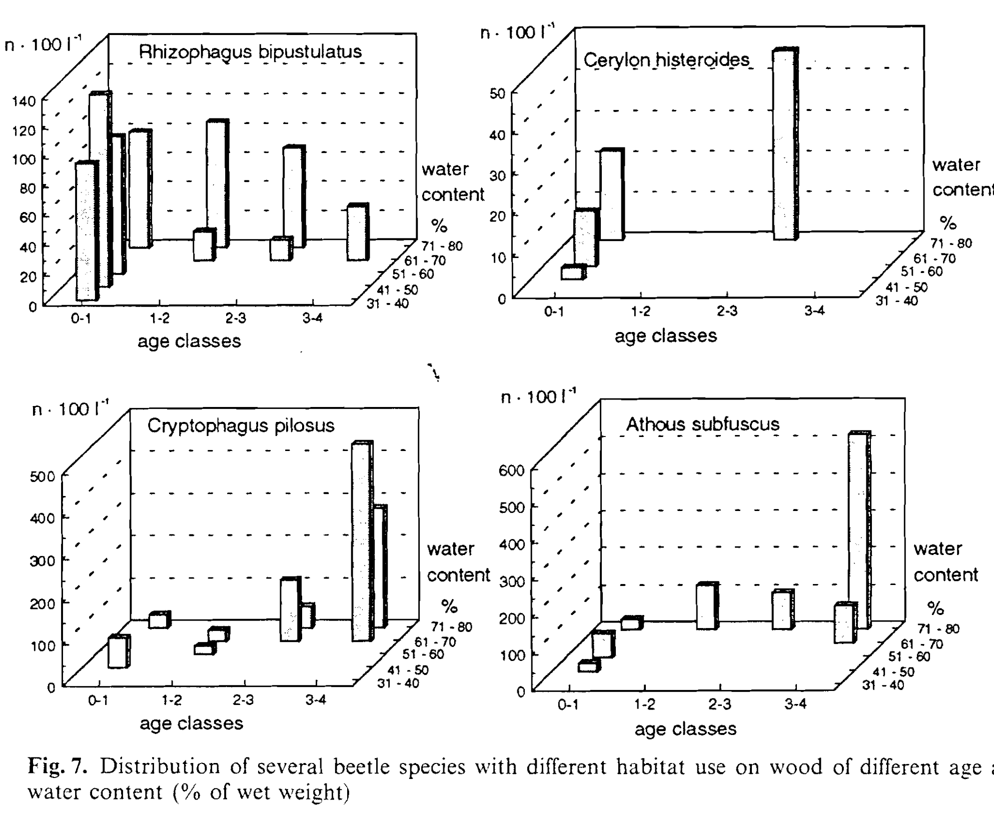

Fig. 7. Distribution of several beetle species with different habitat use on wood of different age and water content (% of wet weight)

mycetophagous species, was found in young wood with relatively high water contents. *Athous subfuscus* conspicuously preferred old and wet decaying wood. This species usually lives in the litter layer (Strey 1972). Its occurrence in old and wet wood can be explained with the increasing similarity between highly decayed wood and litter layer.

Discussion

Succession and structural breakdown of wood is influenced by so many factors, that it is difficult to find two pieces of wood with identical condition. Schimitscheck (1952) emphasized differences in the decay process of the cambium and the wood layer. Breakdown proceeds at different rates, though decomposition takes a lot of time in any case. Therefore, the succession of decay results in a temporal and spatial differentiation of ecological niches (Simandl 1993). Furthermore, many wood dwelling animal species depend on the activity of specific fungi inhabiting dead wood. Some fungi may result in higher numbers of beetle species than others (Kaila et al. 1994). This high heterogenity complicates the interpretation of the decaying wood by animals.

While quantitative studies on saproxylic species have already been published (e.g., Siitonen 1994), little information on other trophic groups associated with decaying wood is available (Palm 1959). Some publications listed high numbers of species found on dead wood. Siitonen (1994) recorded 207 saproxylic beetle species with more than 7,000 individuals from 32 m^3 of dead wood. Kaila et al. (1994) found 158 saproxylic beetle species with 15,957 individuals but the volume of wood studied is unknown. In our investigation 1.7 m^3 of dead wood were analyzed, which resulted in 44 saproxylic beetle species with 719 individuals. According to our results the saproxylic species form only a small part of the species that actually live in/on dead wood. The predatory species are of great importance for regulating the xylophagous species. Weslin (1992) showed that 83% of an *Ips typographus* population were eliminated by predators, e.g. Staphylinidae and Cleridae.

The most intensively investigated beetles include only a small part of typical saproxylic species, which in our investigation amount to about 40% of the total species number of beetles found in dead wood. In other insect groups, e.g. Collembola, the portion of characteristically saproxylic species may be even lower. Springtails did not specialize on the dead wood habitat inspite of their high densities in rotten stumps (Setälä & Marshall 1994). In North American forests nearly all springtail species obtained from stumps were also found in the litter. On the other hand Sciaridae and Mycetophilidae seem to contain considerably higher amounts of saproxylic species. Among the 55 species of Mycetophilidae, 47 were saproxylic and only eight species were predators. Overall 34 saproxylic Mycetophilidae species were found on dead wood only, which amounts to 72% of the species recorded. Several midge species that were recorded as saproxylic in this study, had been shown to be specialized on dead wood by Tuomikoski (1957) either by direct observation or larval breeding, e.g. *Caenosciara alnicola*, *Trichosia caudata*, *Trichosia trochanterata*, *Scythropochroa radialis*, *Zygoneura sciarina* and species of *Xylosciara*.

Whereas the xylophagous species preferred to inhabit the young stages of decaying wood, saproxylic species were found mainly in later stages of decomposition. According to our investigations the number of species immigrating from the adjacent litter layer into the dead wood appeared to increase throughout the course of succession. As the decaying wood increased in age the wood dwelling fauna became more similar to the litter dwelling fauna. Furthermore, old stumps and logs were invaded by overwintering species, which contributed to species composition. The variety of wood dwelling species that increased as age of the dead wood increased is mainly a result of the immigration of both litter dwelling and overwintering species, whereas the xylophagous species preferred less decayed stages.

The different tree species seemed to contribute less to the species diversity of wood dwelling species. Only a few of the species recorded were typical of the wood of a particular tree species. Even *Rhagium bifasciatum* (Cerambycidae) which is known to prefer spruce wood was found on alder. *Dirhagus pygmaeus* (Eucnemidae), a rare species, is found on different tree species, but only in dead wood in a late stage of decomposition (Leiler 1976). The saproxylic species occurred on wood of nearly all investigated tree species. None of the dead wood of any one tree species supported more beetle species than the other ones.

Blab et al. (1984) estimated that about 25% of the beetle species in the FRG live in dead wood or on wood dwelling fungi. Most of the saproxylic species might be considered to be endangered. The tree pest species i.e., bark beetles cannot be labelled as endangered, because they prefer the early stages of decaying wood. Both late stages and big trunks of dead wood are most endangered, because dead wood is usually removed at an early stage of succession by forestry management. In the highly cleared forest that we investigated, we were astonished to find several species, that are listed in the "Red Area Book" of FRG (Blab et al. 1984). Among the beetles seven saproxylic species listed in the "Red Area Book" of Schleswig-Holstein (Ziegler et al. 1994) and FRG (Blab et al. 1984) were found. Dead wood is not only important for endangered sparoxylic species but also for survival of overwintering species. Although no "Red Area Books" are available for the midge families investigated owing to the lack of ecological data, a lot of midge species must also be considered to be endangered, because they are rarely recorded. Therefore, some species records must be emphasized. Recent decriptions were made for *Bradysia subvernalis*, there was only one individual found on alder wood (Heller & Mohrig 1992). Another interesting point is that numerous individuals of *Trichosia flavicoxa* were found on beech wood. This rare species has been found only in Finland (Tuomikoski 1960) and northeast Germany (Menzel et al. 1990).

Our investigations lead us to the following conclusions regarding the conservation of insect species in forests: A higher richness of saproxylic species can be achieved by conserving a large amount of dead wood in late stages of decay not just dead wood from particular trees. Some recent proposals are given by the Arbeitskreis Forstliche Landespflege (1993), who recommended the conservation of trees with low commercial value. These trees may be naturally decayed after their death.

Appendix 1. Abundance of beetles in the dead wood (ind. $100\,l^{-1}$ wood). + = abundance < 1 ind. $100\,l^{-1}$ (wood), species with maximal abundance < 2 ind. $100\,l^{-1}$ (wood) were omitted, abbreviations see Table 1)

	Bos	Bys	Bol	Byl	Aos	Ays	Aol	Ayl	Sos	Sys	Sol	Syl
Abax parallelepipedus	5	2	+	1	·	·	·	·	·	·	·	·
Carabus coriaceus	·	·	·	·	3	·	·	·	·	·	·	·
Leistus rufomarginatus	24	2	2	3	15	·	6	·	25	·	15	·
Leistus terminalis	·	·	·	·	16	6	·	·	·	7	·	·
Nebria brevicollis	17	2	+	·	·	·	+	·	·	·	·	·
Patrobus atrorufus	·	·	·	·	1	6	·	·	·	·	·	·
Pterostichus diligens	·	·	·	·	·	·	·	·	4	·	·	·
Pterostichus niger	·	·	1	+	·	·	·	·	·	7	·	·
Pterostichus oblongopunctatus	10	9	1	+	5	·	+	·	16	21	·	·
Synuchus vivalis	·	·	·	·	4	·	·	·	·	·	·	·
Grammostethus marginatus	·	2	·	·	1	·	·	·	·	·	·	·
Catops fuliginosus	·	·	·	·	5	6	·	·	·	·	2	·
Catops fuscus	29	·	1	·	25	·	1	·	·	·	2	·
Catops longulus	·	·	+	·	169	·	·	·	·	·	·	·
Catops picipes	·	·	·	·	11	·	·	·	·	·	·	·
Catops tristis	·	1	·	·	1	·	·	·	·	14	·	·
Nargus wilkini	3	24	·	·	10	·	+	·	·	·	·	·
Agathidium seminulum	·	·	·	·	8	·	·	·	49	·	2	·
Anisotoma orbicularis	2	·	·	·	4	·	·	·	·	·	·	·
Ptenidium nitidum	2	·	+	+	·	·	·	·	·	·	·	2

Appendix 1. (continued)

	Bos	Bys	Bol	Byl	Aos	Ays	Aol	Ayl	Sos	Sys	Sol	Syl
Euconnus pubicollis	·	·	·	·	·	6	·	·	·	·	·	·
Neuraphes rubicundus	4	·	+	·	·	·	+	·	·	·	·	·
Cantharis cryptica	·	·	·	·	1	6	·	·	·	·	·	·
Cantharis nigricans	·	·	·	·	3	·	·	·	·	·	·	·
Malthinus flaveolus	·	·	·	·	·	6	·	·	·	·	·	·
Rhagonycha lignosa	11	1	+	·	5	·	·	·	·	·	·	·
Cyphon padi	·	·	+	·	2	·	1	·	·	·	·	·
Cyphon phragmiteticola	·	·	·	·	29	17	·	·	·	·	·	·
Cyphon pubescens	·	·	·	·	·	·	3	·	·	·	·	·
Helodes minuta	·	·	·	·	·	6	·	·	·	·	·	·
Agriotes aterrimus	5	11	·	+	·	·	+	·	·	·	·	·
Ampedus aethiops	5	1	·	·	·	·	·	·	·	·	·	·
Athous subfuscus	9	6	·	+	30	6	1	·	25	14	·	·
Dalopius marginatus	·	2	·	+	27	6	·	·	12	7	·	·
Denticollis linearis	8	·	3	·	3	·	4	1	·	·	·	·
Melanotus rufipes	·	·	2	+	·	·	·	·	4	·	·	·
Dirhagus pygmaeus	·	·	·	·	·	6	5	·	·	·	·	·
Epuraea danica	7	4	3	1	·	·	·	·	·	·	·	2
Epuraea melanocephala	2	·	·	·	2	·	·	·	·	·	·	·
Glischrochilus hortensis	5	2	·	+	·	·	·	·	·	·	·	·
Rhizophagus bipustulatus	3	20	5	6	1	12	6	2	8	·	·	·
Rhizophagus cribratus	·	·	+	·	1	6	·	·	·	·	·	·
Rhizophagus dispar	·	4	·	+	·	·	·	·	·	·	·	·
Cerylon histeroides	1	1	+	+	·	·	·	2	8	·	·	·
Atomaria fuscata	·	2	+	·	1	·	+	·	·	·	2	·
Atomaria prolixa	·	·	+	·	2	6	·	·	·	·	·	·
Atomaria pusilla	·	·	·	·	2	·	·	·	4	·	·	2
Corticaria elongata	3	1	+	·	·	·	+	·	·	·	·	2
Enicmus minutus	·	·	·	+	·	6	·	·	·	·	·	2
Lathridius nodifer	2	6	1	2	2	·	1	·	4	·	·	·
Cryptophagus dentatus	·	2	+	1	2	6	1	·	·	·	·	·
Cryptopghagus pilosus	51	7	1	1	13	·	1	3	4	·	4	·
Melanophthalma transversalis	20	2	4	·	1	·	·	·	·	7	·	2
Mycetophagus atomarius	13	·	+	·	·	·	·	·	·	·	·	·
Adela decempunctata	·	·	+	1	·	·	+	·	·	·	2	·
Cis festivus	·	·	+	·	2	·	41	·	·	·	·	·
Anaspis rufilabris	·	·	·	·	·	·	4	·	·	·	·	·
Anaspis thoracica	3	·	·	·	·	·	13	·	·	·	2	·
Dorytomus taeniatus	·	·	·	·	3	·	·	·	·	·	·	·
Rhinosimus planirostris	·	5	+	1	·	·	+	·	·	·	·	·
Orchesia micans	·	·	·	·	·	·	·	6	·	·	·	·
Rhagium bifasciatum	·	·	·	·	·	·	1	·	·	·	·	2
Dryocoetes autographus	·	·	·	·	·	·	·	·	8	·	·	·
Xyloterus domesticus	·	2	1	11	·	·	·	·	·	·	·	·
Acalles echinatus	2	1	+	+	·	·	1	·	·	·	·	·
Ceutorhynchus erysimi	4	·	+	·	7	·	+	·	4	·	·	5
Neosirocalus floralis	37	5	9	2	1	·	4	1	8	·	·	2
Otiorhynchus singularis	·	1	+	·	4	·	+	·	·	·	·	·
Phyllobius argentatus	8	8	+	1	8	·	1	·	·	·	·	·
Rhynchaenus fagi	42	2	17	9	2	·	8	2	4	·	2	2
Strophosoma capitatum	20	7	·	·	·	·	1	·	·	14	·	·
Strophosoma melanogrammum	15	4	1	·	·	·	·	·	·	·	·	·
Staphylinidae	501	141	102	82	455	256	51	19	156	106	52	66
sum (abundance)	935	306	172	135	1081	447	180	50	385	212	144	114
sum (species)	36	35	46	32	50	17	42	9	16	9	10	11

Appendix 2. Abundance of Sciaridae in the dead wood (ind. $100\,l^{-1}$ wood) and the litter (lit: ind. m^{-2}). + = abundance <1 ind. $100\,l^{-1}$ (wood) or ind. m^{-2} (litter), species with maximal abundance <2 ind. $100\,l^{-1}$ (wood) or ind. m^{-2} (litter), were omitted, abbreviations see Table 1, Blit: beech litter, Alit: alder litter, Slit: spruce litter)

	Blit	Bos	Bys	Bol	Byl	Alit	Aos	Ays	Aol	Ayl	Slit	Sos	Sys	Sol	Syl
Bradysia aprica	·	·	·	·	·	10	·	·	·	·	·	·	·	·	·
Bradysia confinis	419	2	·	1	+	·	·	·	+	·	·	·	·	·	·
Bradysia fenestralis	+	·	·	·	·	3	·	·	·	·	2	·	·	·	·
Bradysia fungicola	1	·	·	·	30	·	·	·	2	113	·	·	·	·	·
Bradysia nocturna	·	2	·	·	·	·	54	·	·	·	·	·	·	·	·
Bradysia polonica	4	·	·	·	·	3	·	·	·	·	·	·	·	·	·
Bradysia regularis	4	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Bradysia strigata	·	·	·	·	·	4	·	·	·	·	·	·	·	·	·
Caenosciara alnicola	·	·	1	+	·	·	7	6	16	42	·	·	·	3017	2
Corynoptera abblanda	5	·	4	2	1	·	·	·	+	·	·	·	·	·	·
Corynoptera blanda	21	20	30	2	1	13	·	·	·	·	1	·	·	·	·
Corynoptera brachyptera	·	·	·	·	·	6	51	·	·	·	·	·	·	·	·
Corynoptera clinochaeata	1	·	·	·	·	9	6	·	·	·	·	·	·	·	·
Corynoptera concinna	2	3	29	+	·	1	4	·	·	·	1	·	14	·	·
Corynoptera furcifera	·	·	·	·	·	6	·	·	·	·	·	·	·	·	·
Corynoptera irmgardis	·	·	·	·	·	11	·	·	·	·	·	·	·	·	·
Ctenosciara hyalipennis	136	95	37	2	+	1	67	6	6	12	54	20	7	7	·
Ctenosciara lutea	23	·	·	·	·	·	·	·	·	·	·	·	·	2	·
Epidapus atomarius	20	33	20	3	1	1	16	·	7	3	1	4	14	30	5
Epidapus gracilis	2	196	4	·	+	14	177	52	1	·	5	·	42	15	12
Epidapus titan	·	33	20	+	1	·	40	6	4	1	·	·	42	7	2
Lengersdorfia detriticola	5	3	·	·	·	5	11	6	·	·	1	·	·	·	·
Lycoriella auripila	1	·	·	·	·	2	·	6	·	·	1	·	·	·	·
Lycoriella lundstroemi	·	2	·	·	+	·	3	·	+	·	·	·	·	·	·
Lycoriella solani	·	·	1	+	·	·	23	·	+	2	·	·	·	·	·
Plastosciara falcifera	·	2	·	·	·	+	·	·	10	·	·	·	·	·	·
Plastosciara pernitida	·	80	·	·	·	·	·	·	·	·	·	·	·	·	2
Plastosciara socialis	6	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Scatopsciara calamophila	·	10	4	+	135	·	4	·	12	16	·	4	·	·	·
Scatopsciara pusilla	·	7	1	11	5	·	3	17	23	20	·	·	·	13	2
Scatopsciara vitripennis	·	·	·	·	·	7	·	·	·	·	·	·	·	·	·
Scatopsciara vivida	6	10	47	1	34	43	54	41	4	3	22	4	7	4	·
Scythropochroa radialis	·	·	·	·	·	·	·	·	17	·	·	·	·	57	2
Trichosia caudata	·	·	·	·	·	·	·	·	21	335	·	·	·	229	61
Trichosia elegans	·	41	·	·	·	·	·	·	·	·	·	·	·	·	·
Trichosia flavicoxa	·	46	·	86	·	·	·	·	2	·	·	·	·	·	·
Trichosia pilosa	6	31	·	·	·	·	·	·	1	·	+	·	·	·	·
Trichosia subelegans	·	3	·	·	·	·	·	·	·	·	·	·	·	·	·
Trichosia trochanterata	+	·	·	·	·	·	·	·	2	·	2	·	·	·	·
Trichosia viatica	·	8	·	·	·	·	1	·	1	·	·	·	·	·	·
Xylosciara heptacantha	·	·	·	·	·	1	·	·	·	8	·	·	·	·	·
Xylosciara longiforceps	·	·	·	·	+	·	·	·	+	19	·	·	·	·	·
Zygoneura sciarina	·	·	·	·	12	·	·	·	·	·	·	·	·	·	·
sum (abundance)	665	877	233	124	150	146	651	192	149	626	92	49	134	3394	100
sum (species)	22	20	12	14	14	28	16	8	22	14	14	4	6	18	8

Appendix 3. Abundance of midge families belonging to Mycetophilidae s.l. in the dead wood (ind. $100\,l^{-1}$ wood) and the litter (lit: ind. m^{-2}). + = abundance < 1 ind. $100\,l^{-1}$ (wood) or ind. m^{-2} (litter) were omitted, abbreviations see Table 1, Blit: beech litter, Alit: alder litter, Slit: spruce litter)

	Blit	Bos	Bys	Bol	Byl	Alit	Aos	Ays	Aol	Ayl	Slit	Sos	Sys	Sol	Syl
Bolitophilidae															
Bolitophila cinerea	·	25	3	·	·	·	·	·	·	·	·	·	·	·	·
Diadocidiidae															
Diadocidia ferruginosa	+	·	·	·	·	·	7	·	+	·	·	·	·	·	·
Diadocidia spinulosa	·	·	·	·	·	·	3	·	·	·	1	·	·	2	10
Ditomyiidae															
Ditomyia fasciata	·	·	·	·	·	·	3	·	3	35	·	·	·	·	·
Keroplatidae															
Macrocera anguluta	·	2	·	·	·	·	1	·	·	·	·	·	·	·	·
Macrocera aterrima	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·
Macrocera centralis	+	2	1	·	·	·	3	·	·	·	·	·	·	·	·
Macrocera parva	·	·	·	·	·	·	3	·	·	·	·	·	·	·	·
Macrocera stigma	·	15	·	·	·	·	1	·	·	·	·	·	·	·	·
Macrocera stigmoides	4	3	·	·	·	·	·	·	·	·	+	·	·	·	·
Macrocera vittata	·	·	·	·	·	+	·	·	·	·	·	·	·	2	·
Macrorrhyncha flava	·	·	·	·	·	·	3	·	·	·	+	20	·	4	·
Mycetophilidae															
Acnemia nitidicollis	·	·	·	1	+	1	·	·	·	·	·	·	·	·	·
Apolephthisa subincana	·	2	·	·	27	·	·	·	·	2	·	·	·	·	·
Boletina flaviventris	·	·	·	6	·	·	·	·	·	·	·	·	·	·	·
Boletina trivittata	2	2	·	·	·	+	·	·	·	·	·	·	·	·	·
Docosia fuscipes	·	13	·	+	·	·	·	·	·	·	·	·	·	·	·
Docosia gilvipes	+	204	·	3	1	·	·	·	·	·	+	·	·	·	·
Docosia sciarina	·	2	·	·	+	·	·	·	·	·	·	·	·	·	·
Ectrepesthoneura hirta	·	8	·	2	1	·	4	·	+	·	·	·	·	·	·
Exechia fusca	1	·	·	·	·	2	·	·	·	·	3	·	·	·	·
Mycetophila ocellus	·	242	·	11	·	·	·	·	·	·	·	·	·	·	·
Mycetophila spectabilis	·	11	·	·	·	·	·	·	·	·	·	·	·	·	·
Mycomyia cinerascens	·	13	·	6	1	·	1	·	·	·	·	8	21	·	·
Mycomyia marginata	·	5	·	·	·	·	·	·	·	·	·	·	·	·	·
Neoempheria lineola	·	21	·	1	·	·	·	·	·	·	·	·	·	·	·
Neoempheria pictipennis	·	11	·	·	·	+	·	·	·	·	1	·	·	·	·
Neoempheria winnertzi	·	5	·	·	·	·	1	·	·	·	·	·	·	·	·
Orfelia fasciata	+	5	·	+	+	+	·	·	·	·	·	·	·	·	·
Orfelia nigricornis	·	·	·	+	2	·	·	·	·	·	·	·	·	·	·
Orfelia unicolor	·	3	·	1	·	·	6	·	+	·	·	·	·	7	·
Palaeodocosia janickii	7	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Phronia annulata	·	3	·	+	·	·	·	·	·	·	·	·	·	2	2
Phronia basalis	100	42	11	1	2	2	·	·	3	·	14	·	·	·	·
Phronia johannae	·	11	·	+	·	·	·	·	·	·	·	·	·	·	·
Phronia nitidiventris	·	2	·	+	·	·	·	·	·	·	·	·	·	·	·
Phronia tenuis	·	2	·	·	·	·	·	6	·	·	·	·	·	·	·
Polylepta guttiventris	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·
Synapha vitripennis	·	157	·	1	·	1	97	·	·	·	+	16	·	·	·
Syntemna nitidula	·	3	·	·	·	·	·	·	·	·	·	·	·	·	·
Tarnania fenestralis	·	·	·	·	·	·	1	·	·	·	·	·	·	2	·
Tetragoneura sylvatica	8	3	25	·	·	3	24	29	·	·	1	·	·	·	·
sum (abundance)	137	851	42	40	37	20	188	46	10	40	27	49	28	24	15
sum (species)	28	30	5	23	13	23	15	2	7	3	17	3	1	6	2

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