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DIPTEROUS GUILDS OF SMALL-SIZED FEEDING SOURCES IN FORESTS OF HUNGARY

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Insect guilds (of Diptera and Coleoptera) on "very small-sized feeding sources" (droppings of forest animals, dead snails, tinder fungi, decaying fungi, sap of deciduous woods, *Vespa* nests, etc.) in low mountain forests in Hungary were studied from 1995 to 1998 (504 positive samples for flies, more than 20500 dipterous individuals). A small but significant fraction (about 20%) of these sources is not exploited by flies at all. The high species diversity of those that are colonized represents a majority of forest Diptera diversity in Hungary (with numerous species and genera new to Hungary and even new to science). The quality, size, persistency and place of renewal of the sources, the potential size of each dipterous population, the flies' ability to find new sources and composition of the local fauna are all important factors in determining the actual frequencies of species found on extant sources.
Although the primary texture of the forest community structure is formed by the more abundant forest species populations, those species in guilds on small-sized food sources put a colourful pattern on that texture. They are mostly rare and are probably insignificant for the main energy flow processes, but knowledge of their presence and life histories would seem to be indispensable for a complete understanding of ecosystem structures and diversity maintenance. Biomonitoring of these species, however, is a challenge because of their poorly understood ecology and fluctuating abundance. The relationships of rarity and the species colonizing these sources are discussed and the development of raritology (study of rare species) as an individual branch of ecology is predicted.

Key words: small-sized feeding sources, Diptera, species composition, diversity, raritology, Hungary

INTRODUCTION

The insect guilds found in small-sized food sources have attracted very little attention in ecology, particularly so for those sources consisting of dead organic matter. In ecology textbooks, even in the best ones, only a small portion is devoted to animals developing in droppings, carrion, etc. (cf. KREBS 1985, PRICE 1984, THOMPSON 1984). Even SZELÉNYI (1953) left them out of consideration. The most comprehensive analysis was found in BALOGH's (1953) book which, although qualitative, summarised the important literature of the time and assigned these guilds their proper importance by including them as a category in forest ecosystems. (Note that I use the term "guilds" in the sense of HAWKINS and MACMAHON (1989) rather than in its original meaning (ROOT 1967)).

Despite their importance to the understanding of the diversity of many ecosystems, comparatively few papers have dealt with insects from small-sized food sources. This is probably because: (a) Their role in the material and energy turnover of the communities is negligible; (b) Their study is difficult from a methodological point of view, and the classical methods and considerations are not usable for their study without modification (cf. SOUTHWOOD 1978); and (c) The results of previous studies reported that the species composition and frequencies of these insect populations appeared to be highly variable, almost accidental; hence entomologists – like any other natural scientists tuned to look for invariance – did not find pleasure in their long-term study. Most of the studies resulted in the publication of a list of the collected species and usually not much more.

In view of these problems, we developed new collection techniques to more effectively obtain critical data on composition and frequencies of species that comprise the guilds on small-sized food sources. We used regular sampling and simple but reliable methods (i.e., counting rather than making estimations on abundance of flies on the small-sized sources in natural conditions). With the voluminous data thus obtained we hope to answer the following questions: (a) How repeatable is the species composition of the guilds on a given type of small-sized source? (b) Based on the abundance of the dominant and subdominant species we found, may we attribute any structural characteristics (i.e., less than a true structure) to those assemblies/assemblages (there is no reason to call them communities)? (c) Is there enough commonality in the organisation of the guilds of the various small-sized sources to give them a unifying name?

Our goal for this research is to be able to estimate the contribution of these guilds to the species richness of the forest ecosystems. In additon, we also hope to increase the scientific community's awareness of the forms of rarity among insects.

MATERIAL AND METHODS

The sampling sites were selected in low mountain forests in Hungary:

1) Börzsöny Mts (central North Hungary): Verőce-Magyarkút: Keskenybükki-patak valley and the Les-völgyi-patak valley; forests along the road from Diósjenő to Kemence; two forested brook valleys (Vasfazék valley and Szénpatak valley) accessible from Királyrét;

2) Visegrádi Mts (central North Hungary): Apátkúti valley near Visegrád, on the other side of Danube;

3) Vértes Mts (NW Hungary, Transdanubia): Fáni valley.

Supplementary collections were made also in other parts of Hungary (Kőszegi Mts, Bükk Mts, Zempléni Mts).

Insects were collected on or near various small organic sources as listed in Table 1. Techniques were developed to determine the abundance of each species on a given source sample by

counting and not by estimation. Therefore isolators were used to capture flies and other insects actually present on these sources. The isolators are large aluminium funnels used in wine cellars and a glass aspirator used to catch mosquitoes bound with sections of bike tires (see PAPP 1985). Using a strong aspirator, I captured the smallest flies which might crawl out from under the rim of the funnel.

We constructed special traps (in a way similar to some pitfall-traps) to collect all the flies including phorids on dead snails; we then reared them to adulthood to determine the quantities and species from each source.

A new type of soil bait trap was constructed to collect adult Diptera on dead *Helix* snails (PAPP & TÓTHMÉRÉSZ in prep.). These special traps were necessary because of the special properties of the Phoridae species (the photo-eclector type traps we used at first were ineffective, since the phorids – unlike other Diptera – do quite well in complete darkness).

Some kinds of substrates were collected and taken into the laboratory where Diptera adults were reared from them. This way one can collect data on the actual quantity of the individuals and species composition developing in small-sized feeding sources such as dead *Helix* snails exposed for 48 hours and *Vespa crabro* nests (PAPP 2000). Rearing was done largely by MIHÁLYI's (1967) method.

Where the distance of the sampling points were reliably measurable, we used a Data Disto device to obtain distance data, and a map was drawn by the aid of the "Profly" software.

To find small-sized sources in a native forest is mostly a matter of good luck. One can find a good piece of tinder fungi comparatively easily, whereas one may seek all the day in vain for deer dung.

In the past we have collected extensive data on flies from wild fruits (PAPP 1992, apple bait collections) and human faeces in the same forest brook valleys (PAPP 1993), as well as on flies developing in fruiting bodies of mushrooms (ÁGNES DELY-DRASKOVITS reared 50 thousand adult Diptera of 128 species in 24 families; see DELY-DRASKOVITS 1976), but these data were not included in this project.

Statistical analysis of species richness data was done using the non-parametric analysis (Chao2 and Jack1, the first order jackknife method). The structure of our other data does not allow us to use more sophisticated methods formerly used (IZSÁK & PAPP 1994, PAPP *et al*. 1997, PAPP & IZSÁK 1999).

RESULTS

Ecological results

From April 1995 to November 1998 insects (flies and beetles) were collected on more than 500 small source samples; more than twenty thousand adult flies were captured or reared. Number of species, individuals and samples collected from 1995 to 1998 are summarised in Table 1. A separate paper was published about the flies reared from *Vespa crabro* nests (PAPP 2000).

Table 2 shows a part of our results obtained in a creek valley of the Börzsöny Mts where we applied special traps to collect flies on dead snails (*Helix pomatia*). Twenty traps were set up for 24 and 48 hours on the identical places on the same days of July and August in three consecutive years (1995–1997); flies were also

reared from the dead snails left out two days. The number and species composition of the flies on a dead snail likely depend much more on whether a snail died in the close vicinity of a fresh corpse some time earlier than on the physical or environmental factors of the micro-site.

The species numbers found on four types of sources is summarised in Table 3 and compared with species number estimation made by the Chao 2 and the first order jackknife method. When analysing data shown in Table 1, all the sources sampled are taken into consideration. The species richness calculations summarised in Table 4, however, only include the number of the adult flies captured on tinder fungi, on fox faeces, on deer faeces and on rotten or mouldy fungi.

Some faunistic results

A by-product of our studies is that dozens of species and genera were found as new for the fauna of Hungary (numerous species even new to science have been found hitherto). PAPP (1999) recorded eight genera and 15 species as new for the Hungarian fauna (*Elephantomyia edwardsi* (MEIGEN, 1818), the genera *Phalacro-*

Table 1. Number of species, individuals and samples collected from 1995 to 1998

Source	species	specimens	samples	remarks
Dead *Helix* snails	91	5013	240	see table 2
Fox dung	67	844	45	11 negative samples
Deer dung	73	569	39	
Tinder fungi	61	2708	50	
Rotten or mouldy fungi	113	1503	20	
Vespa crabro nests	19	8225	2	see PAPP (2000)
Other dung[1]	30	87	5	
Dead animals[2]	22	68	4	
Wounds of trees, bleeding stubs of trees	60	601	73	(47 + and * samples)
Apple marc	43	191+	20	(plus Drosophilidae 2571 ex.)
Other sources[3]	770	6		
Total	–	20579	504	(plus at least 91 empty samples)

*Combined samples

[1]One week old human faeces, rabbit litter thrown into a forest, wild boar dung (2), *Mustela* sp. dung

[2]Dead fox, dead frog, dead *Anguis fragilis*, owl pellet

[3]On mouldy sap of oak and hornbeam stubs (2+1), on *Meloe violaceus* (2)

Table 2. Dipterous individuals trapped during 24 hours on dead *Helix* snails combined with the numbers of flies reared from dead *Helix* snails exposed for 48 hours (20 samples each) (see also PAPP & TÓTHMÉRÉSZ, in prep.)

	1995	1996	1997	total
July, 1 day	254	110	424	788
August, 1st day	82	218	187	486
August, 2nd day	214	410	131	754
Flies reared	1870	338	775	2983
Altogether	2420	1076	1517	5013

Total number of species: 91; in one series max. 37 species

cera, Ditomyia, Phthinia, Ectrepesthoneura, Novakia, *Sceptonia* with one species each, the genus *Monoclona* with three species and the peculiar species *Dicranomyia ornata* (MEIGEN)). In the same paper numerous mycetophilids (in the genera *Neoempheria, Acnemia, Polylepta, Apolephthisa*) are mentioned, which are significant contributions to the collection of the Hungarian Natural History Museum.

Table 3. Non-parametric estimations of species richness. N: number of dipterous individuals captured on the source on that day, S_0: number of species actually found in that sample series; n: number of samples; L: number of single occurrences; M: number of double occurrences; Chao2: species number estimated by the Chao2 method; Jack1: species number estimated by the first order jackknife method

Locality, time (year/month/day)	N	S_0	n	L	M	Chao2	Jack1
Tinder fungus, total no of species: 61, N = 2708							
G-V,F-v., 96/05/07	374	18	6	7	8	21.1	23.8
G-V,F-v., 96/06/04	346	20	5	14	1	216	31.2
G-V,F-v., 98/05/09	318	16	7	6	5	19.6	21.1
Fox faeces, total no of species: 67, N = 844							
G-V,F-v., 95/10/31	297	11	15	5	3	15.2	15.7
G-V,F-v., 97/11/02	140	6	8	3	1	10.5	8.6
Szo,K-h., 98/09/27	102	16	7	7	1	65.0	22.0
Deer faeces, total no of species: 73, N = 569							
G-V,F-v., 97/09/28	179	31	8	16	4	63.0	45.0
Szo,K-h., 98/10/23	111	11	6	3	3	12.5	13.5
G-V,F-v., 96/09/11	52	21	4	16	5	46.6	33.0
Rotting or mouldy fungi, total no of species: 113, N = 1503							
VM,K-v., 95/10/15	502	65	4	27	14	91.0	85.3
Sze,K-v., 96/08/08	257	38	6	14	7	52.0	49.7

Some other species and genera new for the Hungarian fauna are as follow: *Keroplatus testaceus*, *Xylophagus compeditus*, *Rhaphium sp.*, *Oncopygius distans* (LOEW) (also first record of this genus), *Phaonia cincta* ZETTERSTEDT. *Xenolimosina setaria* (VILLENEUVE) represents also a separate sphaerocerid genus new to Hungary and even to the Carpathian Basin. Its only known locality in Hungary is Gánt, Fáni-valley, where it was first collected in 1992 and three years later (Oct 31, 1995). It is important to know that this species maintained its small population there.

The species of the family Phoridae play an important role in the dipterous population of almost all of the small-sized sources. We knew even in the planning phase of the project that we do not possess the taxonomic base for their study (a collection of named species, expertise, etc.). Consequently, we sorted the unnamed specimens in the HNHM into genera, identified several species and compiled a literature base. This work resulted in the publication of a list of species of the family Phoridae in Hungary (ÁDÁM & PAPP 1996) including three genera new to Hungary (*Aenigmatias, Plectanocnema* (by *P. nudipes* (BECKER)), *Woodiphora*).

The number of the rare species whose representatives were captured is very high. I would like to mention only *Sycorax silacea, Xylophagus ater, Opetia nigra, Chymomyza caudatula, Ch. fuscimana, Gigalimosina flaviceps, Anagnota bicolor*, *Steganina hypoleuca, Phyllomyza longipalpis, Fannia aequilineata*.

Sampling on wounds and bleeding stubs of trees did not result in a data set proper for quantitative analysis. A high number of wounds were found empty and this is why samples were combined (adult flies captured on several trees combined into one sample). The species composition on these wounds we found very interesting, for we discovered there are four *Aulacigaster* species in the Palearctic *(A. afghanorum* sp. n., *A. falcata* sp. n., *A. neoleucopeza* MATHIS et FREIDBERG, *A. leucopeza* MEIGEN; PAPP 1998*a*), instead of one (*A. leucopeza*). Also a species of the Drosophilidae new to science, which develop in the oozing sap, was described (*Scaptodrosophila abdita* PAPP *et al*., 1999). Another paper was published on the life-habits of the species of Periscelididae and I also captured the formerly unknown larvae of *Periscelis nigra minor* ssp. n. and *Periscelis winnertzi* EGGER.

DISCUSSION

Difficulties in finding small-sized sources resulted in a loose data set; that is, only a few kinds of sources were found in high numbers. Those are dead snails (baiting and trapping), fox and deer faeces, tinder fungi, rotten or mouldy fungi, and wounds of deciduous trees (Tables 1 and 3).

Occurrences and frequencies

Occasionally an extremely high number of insects (flies) is found on or in a piece of the small-sized sources. For example, we reared 1295 dipterous individuals of 16 species from 4 litres volume of the debris in a wasp (*Vespa crabro*) nest, as well as 6930 specimens of 15 species from 9–10 litres of another nest (PAPP 2000). A sporophore (fruiting body) of a mushroom of c. 50 grams produces over 500 small flies (50000 mg *vs* 500×5 = 2500 mg living weight). We collected more than 7000 specimens of the staphylinid beetles from a medium-sized sporophore of a *Laetiporus sulphureus* tinder-fungus. These examples might help to understand the seemingly high abundance of numerous species in a common forest.

On the other hand, it became obvious at an early stage of our studies, that a significant part (about 20%) of those sources is empty and not exploited by any flies (Table 1). In some cases no insects were found on a seemingly proper micro-site (the empty source seemed just as good as another one that was richly occupied); even the dominant species characteristic of the given source were missing. In numerous cases the composition of the guild of one type of small-sized sources is different from site to site at a given time (as if there were no "cores" but "satellites" only; cf. HANSKI 1982). The explanation of these kind of unusual situations is that we experienced a very low representation of a minor part of the species pool instead of characteristic species in reproducible frequencies. This kind of a sample is not "typical": I would symbolise it as a small broken piece of earthenware from which the shape of the pot cannot be reconstructed. The virtual species pool is very large (cf. Table 4) if we regard all the species as members of the species pool which may appear on the given kind of small source. We can realise a part of this virtual pool by systematic collection of flies at a given site. By now we are sure that it would take years to obtain a significant part of that species pool. We can artificially improve collections by placing baits into the natural habitats. If properly done, baiting (e.g., BUCK 1994, BUCK *et al*. 1997, and also our dead snail sampling) provides useful data. However, the complete species pool of a given source with an ideal frequency vector is a fiction (as The Hyper Fox Faeces or The Hyper Dead Snail), an unattainable non-existing idealisation. I do not think that baiting or even manipulated baits would be proper tools for tests of general ecological relationships as was made by KNEIDEL (1984) and others.

The species composition, connectance (how many species would connect two kinds of small sized sources), etc., of the guilds are highly varied. The quality, size, persistency and place of renewal of the sources, the potential size of each dipterous population, their agility and ability to find new sources and composition of the local fauna (as a species pool) are the most important factors which determine actual frequencies found on extant sources. It seems that the abundant species

Table 4. Species and their total abundance in the samples of rotten fungi, fox faeces, deer faeces and tinder fungi

Rotten fungi		*Tephrochlamys flavipes*	1
Psychoda sp.	7	*Suillia affinis*	4
Tinearia alternata	16	*Suillia bicolor*	5
Trichocera relegationis	1	*Suillia fuscicornis*	1
Epidapus sp.	1	*Clusiodes albimana*	3
Sciaridae sp. 1	12	*Paraclusia tigrina*	1
Sciaridae sp. 2	19	*Sphaerocera curvipes*	3
Sciaridae sp. 3	4	*Ischiolepta pusilla*	9
Cecidomyiidae sp. 1	6	*Crumomyia nigra*	1
Cecidomyiidae sp. 2	5	*Crumomyia nitida*	1
Cecidomyiidae sp. 3	3	*Alloborborus pallifrons*	1
Macrocera fasciata	1	*Coproica ferruginata*	6
Macrocera sp.	1	*Coproica hirticula*	37
Neoclastobasis sibirica	1	*Coproica vagans*	2
Dynatosoma majus	1	*Trachyopella atomus*	2
Mycetophila fungorum	1	*Trachyopella kuntzei*	3
Mycetophila sp.	8	*Gonioneura spinipennis*	1
Allodia sp.	5	*Gigalimosina flaviceps*	1
Exechia sp.	4	*Terrilimosina schmitzi*	1
Phronia sp.	1	*Paralimosina fucata*	5
Rymosia sp.	1	*Minilimosina parvula*	5
Stigmatomeria crassicornis	2	*Pullimosina heteroneura*	9
Mycetophilidae sp. 1	9	*Pullimosina meijerei*	2
Mycetophilidae sp. 2	2	*Pullimosina moesta*	5
Mycetophilidae sp. 3	4	*Spelobia (S.) manicata*	3
Mycetophilidae sp. 4	1	*Spelobia (S.) palmata*	11
Mycetophilidae sp. 5	3	*Spelobia (S.) parapusio*	171
Chironomidae sp.	23	*Spelobia (S.) rufilabris*	3
Atrichopogon sp.	4	*S. (Bifronsina) bifrons*	4
Culicoides sp.	34	*Opalimosina czernyi*	12
Forcipomyia sp.	10	*Opalimosina liliputana*	4
Holoplagia bullata	1	*Opalimosina mirabilis*	1
Apiloscatopse cochleata	1	*Telomerina flavipes*	1
Apiloscatopse flavicollis	1	*Leptocera caenosa*	5
Scatopse notata	1	*Leptocera fontinalis*	5
Coboldia fuscipes	1	*Leptocera nigra*	9
Lonchoptera furcata	1	*Asteia amoena*	3
Platypezidae sp.	1	*Leiomyza dudai*	23
Megaselia sp. 1	18	*Leiomyza laevigata*	7
Megaselia sp. 2	10	*Leiomyza scatophagina*	1
Megaselia sp. 3	4	*Leucophenga maculata*	3
Megaselia sp. 4	1	*A. (Phortica) variegata*	7
Chaetopleurophora sp.	1	*Scaptomyza (P.) pallida*	2
Gymnophora sp.	3	*Mycodrosophila poecilogastra*	37
Triphleba sp.	1	*Lordiphosa fenestrarum*	14
Nemopoda nitidula	4	*Hirtodrosophila confusa*	98

Table 4 (continued)

Hirtodrosophila trivittata	22
Drosophila buscki	2
Drosophila immigrans	65
Drosophila kuntzei	25
Drosophila limbata	3
Drosophila phalerata	170
Drosophila testacea	205
Drosophila transversa	77
Liriomyza sp.	1
Phytomyza sp.	1
Meoneura neottiophila	3
Acartophthalmus nigrinus	23
Scathophaga stercoraria	2
Pegomyia sp.	2
Fannia monilis	4
Fannia parva	120
Thricops simplex	1
Hydrotaea sp.	1
Mydaea electa	1
Mydaea sp.	1
Helina sp.	1
Coenosiini sp.	1
Total	1503

Fox faeces

Pericoma sp.	2
Trichocera relegationis	7
Sciaridae sp. 1	6
Sciaridae sp. 2	1
Cecidomyiidae sp.	1
Camptocladius sp.	38
Chironomidae sp.	1
Culicoides sp.	1
Penthetria funebris	1
Apiloscatopse sp.	2
Scatopsidae sp.	2
Megaselia sp. 1	12
Megaselia sp. 2	4
Conicera sp.	1
Diplonevra sp.	1
Gymnophora sp.	1
Triphleba sp.	1
Dryomyza flaveola	19
Neuroctena anilis	1
Oldenbergiella seticerca	485
Neoleria ruficeps	8
Tephrochlamys tarsalis	1
Sphaerocera curvipes	12
Ischiolepta micropyga	1
Ischiolepta pusilla	2
Crumomyia nitida	1
Coproica ferruginata	10
Coproica hirticula	2
Coproica vagans	7
Gonioneura spinipennis	5
Limosina silvatica	2
Gigalimosina flaviceps	1
Paralimosina fucata	8
Pullimosina heteroneura	2
Pullimosina moesta	1
Spelobia clunipes	7
Spelobia manicata	2
Spelobia palmata	2
Leptocera oldenbergi	1
Amiota (A.) alboguttata	1
A. (Phortica) variegata	6
Acartophthalmus nigrinus	2
Meoneura neottiophila	1
Adia cinerella	7
Hylemya sp.	24
Anthomyiidae sp.	6
Fannia armata	30
Fannia ornata	2
Fannia parva	45
Muscina sp.	1
Thricops diaphanus	3
Thricops simplex	1
Hydrotaea cyrtoneurina	1
Hydrotaea dentipes	4
Hydrotaea irritans	15
Morellia hortorum	1
Morellia sp.	1
Eudasyphora cyanicolor	8
Phaonia pallida	1
Mydaea corni	2
Mydaea nubila	1
Mydaea urbana/electa	1
Calliphora vomitoria	8
Lucilia caesar	1
Rhinophorinae sp.	7
Tachinidae sp.	1
Lipoptena cervi	1
Total	844

Table 4 (continued)

Deer faeces	
Psychodidae sp.	1
Trichocera relegationis	2
Trichocera sp.	2
Sciara sp.	5
Sciaridae sp. 1	18
Sciaridae sp. 2	5
Cecidomyiidae sp.	3
Camptocladius sp.	28
Chironomidae sp.	10
Ceratopogonidae sp.	2
Crossopalpus nigritella	1
Megaselia sp. 1	15
Megaselia sp. 2	2
Conicera sp.	1
Diplonevra sp.	5
Gymnophora sp.	1
Hypocera mordellaria	8
Dryomyza flaveola	41
Neuroctena anilis	1
Lyciella rorida	1
Meroplius stercorarius	1
Oldenbergiella seticerca	1
Sphaerocera curvipes	17
Ischiolepta micropyga	2
Ischiolepta pusilla	3
Crumomyia nigra	3
Crumomyia nitida	4
Coproica ferruginata	3
Coproica hirticula	1
Coproica hirtula	1
Coproica vagans	2
Elachisoma bajzae	2
Chaetopodella scutellaris	10
Limosina silvatica	2
Gigalimosina flaviceps	10
Paralimosina fucata	11
Phthitia plumosula	1
Pullimosina meijerei	2
Spelobia clunipes	6
Spelobia manicata	32
Spelobia palmata	6
Spelobia sp. female	1
Opalimosina mirabilis	1
Opacifrons coxata	2
Leptocera nigra	2
Diastata fuscula	1
Campichoeta basalis	1
Drosophila transversa	1
Meoneura sp.	1
Thaumatomyia sp.	2
Hydrophoria sp.	3
Hylemya sp. 1	43
Hylemya sp. 2	3
Anthomyiidae sp.	2
Fannia armata	6
Fannia ornata	6
Fannia parva	141
Fannia sp.	14
Azelia triquetra	2
Azelia sp.	5
Hydrotaea irritans	7
Hydrotaea sp.	5
Thricops simplex	13
Musca autumnalis	1
Neomyia cornicina	1
Morellia hortorum	1
Eudasyphora cyanicolor	17
Polietes meridionalis	4
Mydaea sp.	3
Calliphora vomitoria	2
Lucilia ampullacea	1
Pollenia sp.	1
Sarcophaga lehmanni	1
Total	569
Tinder fungi	
Trichocera sp.	1
Ptychoptera	1
Sciaridae sp. 1	23
Sciaridae sp. 2	9
Cecidomyiidae sp.	5
Chironomidae sp.	3
Ceratopogonidae sp.	1
Ditomyia fasciata	1
Acnemia nitidicollis	1
Mycetophilidae gen. 1	4
Mycetophilidae gen. 2	2
Mycetophilidae sp. 3	1
Penthetria funebris	6
Colobostema nigripenne	1
Sylvicola cinctus	1
Actina	2
Platypalpus sp.	3

Hybotidae sp.	2	*Drosophila funebris*	1
Dolichopodidae sp.	8	*Drosophila kuntzei*	3
Megaselia sp. 1	12	*Drosophila littoralis*	1
Megaselia sp. 2	7	*Drosophila phalerata*	11
Megaselia sp. 3	5	*Drosophila testacea*	14
Megaselia sp. 4	2	*Drosophila transversa*	3
Phora sp.	1	*Odinia boletina*	54
Spiniphora sp.	1	*Acartophthalmus nigrinus*	2
Platypezidae sp.	1	*M. neottiophila/lamellata*	1
Lyciella rorida	2	*Tricimba cincta*	1
Tephrochlamys flavipes	1	*Anthomyia* sp.	1
Suillia affinis	1	*Hylemya* sp.	2
Clusiodes albimana	1	*Pegomyia* sp.	3
Clusiodes apicalis	2	Anthomyiidae sp. 1	1
Limosina silvatica	1	Anthomyiidae sp. 2	2
Paralimosina fucata	1	Anthomyiidae sp. 3	2
Spelobia parapusio	1	*Fannia parva*	58
Leucophenga maculata	29	*Fannia* sp. 1	5
A.(Phortica) variegata	2	*Fannia* sp. 2	2
Scaptomyza (P.) pallida	1	*Azelia* sp.	1
Mycodrosophila poecilogastra	263	*Mydaea* sp.	1
Hirtodrosophila confusa	2125		
Hirtodrosophila trivittata	5	Total	2708

populations form the texture of the community structure. In the low mountain forests of Hungary there are also dipterous species among the dominant phytophagous species (e.g., *Mikiola fagi* in beech forests, an assemblage of several species in mixed hornbeam-oak forests). Species like *Bibio marci*, several species of *Tipula* and *Fannia*, a good number of less abundant but common species of Lauxaniidae and Sciaridae are significant or at least not negligible in the decomposition of forest litter. If compared to the former ones, species populations living on/in the small sized feeding sources are rare and disorderly ("messy"). As a consequence of their rarity they are insignificant in matter turnover and energy flow. The species in guilds of small-sized sources superimpose a colourful pattern on the texture formed by the abundant forest species.

Since their presence/absence are incidental (that is so for several hundred species!), it is obvious that they cannot play a decisive role in the forest ecosystems. Their mere existence is a trouble for reductionists. However, if we are really concerned about the true nature of ecosystems, or about the knowledge of biodiversity on Earth (quality, quantity, evolution, etc.), they must not be neglected. In fact, their study seems indispensable for a better understanding of ecosystem structures and diversity maintenance.

Our results are not enough for a generalisation of the features of small sized source guilds, except that two basic types can be distinguished: (a) Guilds of sources that renew at places (micro-sites) year by year; for instance, tinder fungi on dead trees; (b) Guilds of sources that emerge by chance anywhere; for instance, droppings or dead snails.

It is important to note that the diversity of the two types is not different (in the mirror of the diversity index measures).

Based on our results, one of the main reasons of general rarity among insect species is that the infrequent and variable small-sized feeding sources produce a high number of rare species. Scaling must be one of the most important aspects in order to find their function. I mean, very small-sized emergence sources and extremely large sinks (the large forest area around the minute source) are to be expected.

From another aspect, the small-sized sources that are or seem to be scattered by chance at a given scale are probably found by adult Diptera only by chance as well. An overwhelming majority of those adults are lost during their searching flight. This is why the group (a) above is far more reproducible from year to year than species in guilds of group (b). This power of chance may also be a decisive experience for entomologists working on agricultural pests. In Hungary that was most characteristically expressed by Prof. T. JERMY, saying, "Do not you [theoretical ecologists] imagine too many regularities in Nature", cited by JUHÁSZ-NAGY (1986). Both sides may be right, though (cf. PAPP 1988). For example, in an earlier paper (PAPP & ÁDÁM 1996) we created a diagram of how sheep-runs are experienced by a lesser dung fly which now seems to be quite general and not just for coprophagous flies: Flies (and other insects) seek "new" sources and most of them are lost during this search. Those that have found such an object keep in contact with it via olfactory stimuli. That fact has two major consequences for the investigator: If anything bothers these flies, they fly away only a short distance so they can find this source again. Secondly, if the investigator attempts to collect all the insects that come to a source, it could take a long period of time to recruit from the environs. This could be critical in cool autumn weather when the mean recruitment period may be longer than the period of time during which a fresh piece of dung can be attractive for coprophagous flies.

Species diversity contribution of the small sized sources

We thought it important to make an estimate of the contribution of the species diversity of all the small-sized feeding sources (combined) to the diversity of forest Diptera in Hungary. Species number estimations, as for example those in

Table 3, are not good tools for this. In fact, Table 3 demonstrates how much these estimations deviate from the sample numbers necessary to judge a local subset of the species pool on that day. It is better to make a rough estimate by comparing and combining species lists (potential pool members) of all kinds of small-sized sources one by one.

Among all our collection sites, there were only two where we obtained enough data to be able to judge their contribution to the insect diversity of those low mountain forests. One of them is the Fáni-valley in Vértes Mts in Transdanubia, the other is the Keskenybükki-valley in the Börzsöny Mts in central North Hungary.

Since all the small-sized sources are dead organic matter, a key point of the estimations is the ratio of the phytophagous, predator and parasitoid species as well as those developing in dead organic materials. According to my former estimations, 16 per cent of the dipterous fauna of Hungary are phytophagous, approximately 25 per cent are predacious and parasitoid species. (All the dipterous fauna of Hungary is ca. 10000 species.) Consequently, 59 per cent belong to all those guilds which develop in dead organic materials.

DELY-DRASKOVITS reared 128 dipterous species from sporophores of fungi. I collected ca. 200 dipterous species on human faeces in some mountain creek valleys (PAPP 1993). I collected ca. 150 species on apple bait at the same sites (PAPP 1992: 40 spp. of drosophilids alone). There are almost no overlaps in the species composition of those guilds. The species found on tinder fungi, on sap runs of trees, on dead snails and on dead small mammals, in nests of birds and insects, and on various kinds of droppings, form an addition. And I have not mentioned the hundreds of species in dead decaying wood, which seems the richest in species (although most of them are not specific to the species of trees). We had to postpone studies on flies collectible on and developing in decaying wood, although those seem extremely important in the dipterous communities of forest ecosystems. According to an estimation of DELY-DRASKOVITS *et al.* (1991), excluding phytophagous species, this is the potential microhabitat of 80 per cent of forest Diptera. Whether this ratio is an overestimation or not, their study deserves a separate series of sampling and analysis.

Even if we hypothesise that representatives of at least 1000 at most 2000 species are present in large forests of low mountain brook valleys, the combined numbers of the species on small sized feeding sources form a majority of forest Diptera diversity in Hungary.

GENERAL SIGNIFICANCE

In response to the questions posed in the introduction *re:* repeatablilty of species composition of the guilds and structural characteristics of those assemblages, we can give a positive answer only in few cases: The drosophilid species *Hirtodrosophila confusa* is a dominant species of tinder fungi; and *Oldenbergiella seticerca* is characteristically dominant in the guild of fox faeces but only at the end of autumn. Otherwise, neither the name of the dominant species nor species composition is predictable.

When I made the project proposal for this study, I hypothesised that the data obtained from all guilds of small-sized food sources would be amenable to generalisation and that general terms would apply across guilds. In other words, are they units by the shared properties of their structure, or only by the human contemplation. Considering all the accumulated evidence, I question any claim for any kind of generalisation. Viewing the problem "from outside to inside", that is, as seen from the large-scale habitats like a beech forest, one may use names like "inclusions", "ecosystem chips", etc. However, I cannot give a proposal by which we would unite them by a general term. This agrees with a previous summary of views about this kind of generalisation (review by BALOGH 1953).

An overview of our data corroborate the opportunistic fitness guild definition by HAWKINS & MACMAHON (1989): "…guild still describes all organisms that use the same investigator-defined resource; the usefulness of the concept depends more on the investigator's acuity and care than it does on the organisms and their interactions in nature."

You may guess my answer to the question of the often-discussed relationship of diversity and ecosystem function: I do not believe that any kind of general relationships exist. And if I am right, none of the species on small-sized feeding sources are suitable for biomonitoring as a consequence of their highly variable abundance changes and largely unknown ecological background.

RARITY AND RARITOLOGY

It is no wonder that the insects that develop in small-sized sources are mostly rare species since the sources themselves are not abundant. And although rarity among insects is not always in direct relationship with the size of their breeding media, the insects we have studied seem to show all the features which characterise rare species and so their study is also relevant to rarity among living organisms in general.

In the past, most of the estimations of the ratio (or the real number) of the rare species in an ecosystem have missed their mark. These estimations work well only in the cases of sites where regular and long term studies have been performed. Otherwise, the ratio of the rare species is usually underestimated: at a given stage of studies we may know all the species of the dominant and subdominant species, but only the fore-part of the long row of rare ones. JERMY (1987) was among the first modern ecologists who re-called DARWIN's idea about the "vast number of species of all classes".

The most important lesson I derived from these studies is that we are wrong if our approach to the study of the insects found on and developing in small-sized sources is only based on our general ecological knowledge. Ecology is, by one of its definitions (DODSON *et al.* 1998), "the study of the relationships, distribution, and abundance of organisms, or groups of organisms, in an environment." This loose definition includes the study of the rare species, and they must not be neglected if we are really concerned with the knowledge of biodiversity on Earth. Needless to say, this kind of study is important for biological conservation, since all threatened species are rare.

I can corroborate the fears of former students that any study on rare species will not reveal general ecological relationships; we are still far from the realisation of general invariance rules valid for rare species.

Based on our data I was able to revise some considerations of the forms of rarity among insects (PAPP 1998*c*). I have concluded that those methods and attitudes that are usually successful and effective in ecological studies are not very successful or even usable in studies concerned with rare species. So I hypothesise the development of a new branch of ecology, namely raritology, the study of rare living organisms (PAPP 1998*b*). Those special ecologists, the raritologists, are the curious, resolute and humble researchers, who will be ready to strive after – and to spend much time for – small results without any hope of shedding light on "very important" general relationships of Nature winning the Nobel Prize. Thus, the development of raritology (study of rare species) as an individual branch of ecology is predicted (for I think, it is predictable).

In the future, studies on flies and other insects on and in small-sized feeding sources must have a perspective for the long term and be included as part of mainstream ecology instead of as a pioneer or isolated work. The delicate question will probably be who would finance this kind of long-term studies of uncertain outcome.

*

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