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Werner ULRICH

Nicholas Copernicus University in Toruń Department of Animal Ecology
Gagarina 9, 87-100 Toruń; Poland, e-mail: ulrichw @ cc.uni.torun.pl

THE PARASITIC HYMENOPTERA IN A BEECH FOREST ON LIMESTONE I: SPECIES COMPOSITION, SPECIES TURNOVER, ABUNDANCE AND BIOMASS

ABSTRACT: Between 1980 and 1987 a beech forest (*Fagus sylvatica*) on limestone near Göttingen (FRG) was studied using ground-photo-eclectors. 720 species of Hymenoptera were detected. 669 of the species were parasitoids, 29 phytophagous Tenthredinidae, Cynipidae and Eurytomidae, 9 ants, 4 vespids and 9 nest-building sphecids, megachilids, andrenids and bumble bees. Even after 8 years of sampling a great number of species seems to remain undetected. Estimates of extinction and immigration rates indicate species turnover rates of at least 5 to 10%. The abundance of the parasitic Hymenoptera ranged between 123 $\pm$ 23 (1981) and 1078 $\pm$ 186 (1984) ind. m^{-2} a^{-1}. The most important groups were the parasitoids of Diptera with 56 $\pm$ 15 (1981) to 936 $\pm$ 164 (1984) ind. m^{-2} a^{-1}. As judged by the sorting according to parasitoid guild, the parasitoids of gall-makers (23 $\pm$ 9 to 880 $\pm$ 163 ind. m^{-2} a^{-1}) and the egg-parasitoids (21 $\pm$ 17 to 102 $\pm$ 33 ind. m^{-2} a^{-1}) reached the highest densities. The biomass of the parasitic wasps ranged between 19 $\pm$ 5 (1981) and 170 $\pm$ 92 (1987) mg DW m^{-2} a^{-1} with a mean of 68 mg DW m^{-2} a^{-1}. In comparison with other important insect taxa this is a low value.
KEY WORDS: Hymenoptera, faunal composition, parasitoids, beech forest, density, biomass, species turnover, local extinction, local immigration.

1. INTRODUCTION

The parasitic Hymenoptera are one of the least known groups of insects in our European ecosystems. Only Thiede (1975), Ulrich (1987a, 1988) and Hilpert (1989) provided comprehensive quantitative data on species composition, abundances and biomass of the parasitoids. Thiede studied a spruce forest in the Solling (FRG) and Hilpert analyzed the parasitoid fauna of a mixed leaf forest near Freiburg (FRG). Other studies (for example Abraham 1969, König

1969, Horstmann 1970, 1988, Jones 1976a, b, Copland and Askew 1977, Aitchison 1979, Kussmaul and Schmidt 1987, Vidal 1988) only dealt with part of the Hymenoptera or were not quantitative. There are two causes for this limited knowledge: the great taxonomic difficulties and the high number of species to deal with. The Hymenoptera account for more than 1/4 of the total European insect fauna, in certain habitats for even more than half of it (Ulrich 1987a).

This paper continues previous work of Ulrich (1987a, b, 1988, 1989) and is the first in a series dealing with the parasitic Hymenoptera in a beech forest on limestone.

2. STUDY AREA AND METHODS

2.1. STUDY SITE

The studies were performed in a beech forest (*Fagus sylvatica*) on limestone near Göttingen (northern FRG). The study site is on a chalk plateau approx. 420 m above sea level (cf. Ulrich 1988, Schaefer 1990). The trees are about 120 to 140 years old, their crowns reach to a height of 30 m. Besides the dominating beech, elm (*Ulmus glabra*), oak (*Quercus robur*), ash (*Fraxinus excelsior*) and maple (*Acer pseudoplatanus* and *A. platanoides*) occur. The vegetation can be classified as a Melico-Fagetum subassociation *Lathyrus vernus*. The herb layer is well developed and consists mainly of spring geophytes (Dierschke and Song 1982, Eggert 1985) that usually disappear in summer. *Mercurialis perennis* and *Allium ursinum* dominate. Also abundant are *Anemone nemorosa*, *A. ranunculoides*, *Asarum europeum*, *Arum maculatum*, *Oxalis acetosella* and *Melica uniflora.* A distinct shrub layer is absent.

The soil is characterized by a patchy alternation of Terra fusca Rendzina (50% of the area), Rendzina (26%), and Terra fusca (14%) (Meiwes *et al.* 1981).

2.2. SAMPLING PROGRAM

All quantitative data were obtained by using ground-photo-eclectors. Ulrich (1988) gives a detailed account of the eclector program and discusses the limitations of the method.

Sampling was done with round eclectors of 1 m^2 sampling area and these were checked weekly or every 14 days. Picric acid was used as killing-liquid. In both 1981 and 1982 we used 12 one m^2 eclectors which changed place every 6 or 12 weeks. In 1983 to 1985 the traps (4 traps with a sampling area of one m^2 (1983) and 5 eclectors with 0.25 m^2 each (1984, 1985)) remained in the same place from spring to autumn and in 1986 and 1987 the traps (4 eclectors with one m sampling area each) were removed during mid July when emergences have their summer minimum. Besides these eclectors, various others were placed on experimental plots with a manipulated amount of leaf litter or predator density (Ulrich 1988, Hövemeyer 1992).

Two special habitats were included in the sampling program: areas around tree trunks and an old stump of a dead beech tree: In 1981 10 beech stems were enclosed by 4 × 4 m^2-eclectors each with a total sampling area of 3.77 m^2. They were transferred to other places at the same interval as the other traps. In 1980 one 1-m^2-eclector was placed above an about 10-year-old tree stump covered with a thick layer of mosses. Hövemeyer (1984) describes the dipterous fauna of this stump that was gathered in the same trap.

2.3. COMPUTATION OF DENSITY AND BIOMASS

To estimate abundance I added up all emergences of a species during one year and referred it to a number per square meter. Only animals that apparently or presumably had emerged were included. Wasps that probably had overwintered or had left to look for places to hibernate were excluded.

To estimate fluctuations of density, the quotient of highest and lowest density was used. In years in which a certain species was not represented in the catches, the reciprocal of the whole sampled area was considered to be the maximum density. Due to the high number of zero counts, this method underestimates the real fluctuations for many species. Except for a few abundant species it is not possible to estimate the real fluctuations of the species. Instead, the quotient gives a lower estimate of the real magnitude of density fluctuations.

To calculate the dry weight (DW), the thorax of one specimen (female) of each species was measured. The thorax volume was calculated by the formula:

V = length of (thorax + Propodeum) × max. height of thorax × width of mesoscutum

The possible statistical error, due to the measurement of only one specimen of every species, is very small if one compares the small biomass of each species with the total number of species. Usually females are slightly larger than males. But because of the fact that in almost all species many more females than males occur (Ulrich 1998a) the resulting error is very small. A regression equation was obtained by measuring specimens of 84 wasp species of all size classes (Fig. 1). The specimens were dried for one week at 100 °C and weighed with a balance (precision 10^{-6} g). The equation of the regression is:

DW (mg) = V (mm^3) 0.52493 (mg/ mm^3); $r = 0.97$; $p < 0.001$.

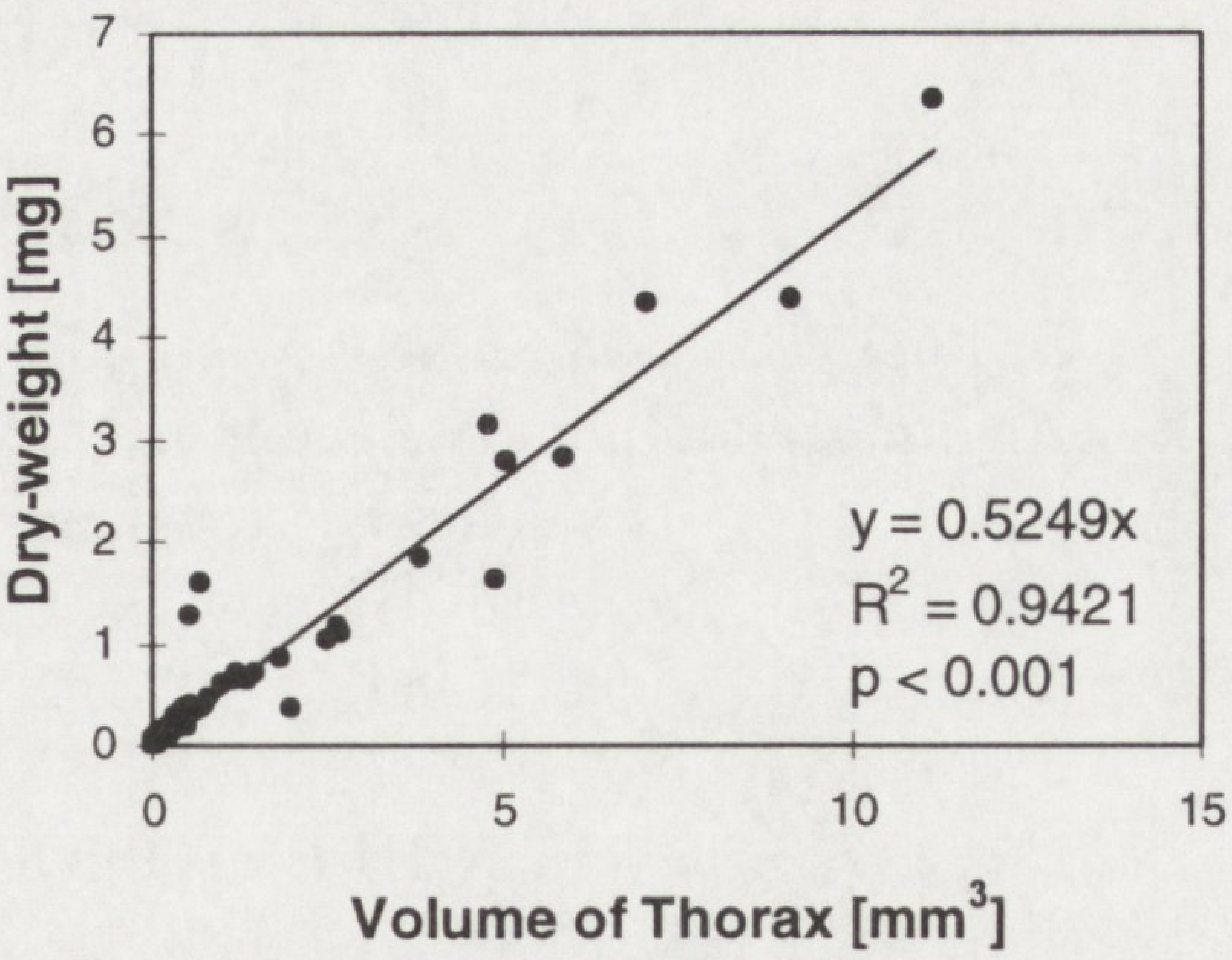


Fig. 1. Relationship between dry-weight (mg) and thorax volume (mm^3) of the Hymenoptera of the Göttingen beech forest

2.4. CLASSIFICATION OF THE PARASITOIDS INTO ECOLOGICAL GUILDS

The specimens of wasps from all study years were identified and sorted according to species. The identification of the ichneumonids was kindly done by E. Diller, R. Hinz and K. Horstmann. The Diapriidae and Serphidae were compared with the collection of H. Hilpert. The identification of all other species was done by the author. In each case a separation according to species was made and, as a rule, an identification to generic level was undertaken.

The aim of every ecological study should be to work with ecologically meaningful groups. To do so, I sorted the parasitoid species not into families or other systematic groups but into ecological guilds. As an extension of the list in Ulrich (1987a), the Hymenoptera were sorted into the following 10 guilds (the mentioned taxa represent the hosts of the parasitoids existing in the Göttingen beech forest):

1. parasitoids of mining Diptera, Lepidoptera, and Coleoptera.
2. parasitoids of gall inducing Cecidomyiidae and Cynipidae.
3. parasitoids of ectophytophagous Coleoptera, Lepidoptera, and Symphyta.
4. parasitoids of sap sucking Rhynchota and Thysanoptera.
5. parasitoids of predatory Miridae, Planipennia, Carabidae, and Staphylinidae.
6. parasitoids of saprophagous Ceratopogonidae and Brachycera.
7. parasitoids of mycetophagous Mycetophilidae and Sciaridae.
8. hyperparasitoids
9. egg-parasitoids
10. parasitoids of xylophagous Coleoptera

The classification of the wasps into these 10 guilds was mostly done according to literature (compare Ulrich 1987a, 1988). Some species (especially some Oxytorinae and Gelinae, *Aspilota* spp., *Kleidotoma psiloides* and *Basalys* spp.) were reared out of saprophagous and mycetophagous Diptera. 536 out of 669 parasitoid species could be classified into one of these guilds.

3. RESULTS

3.1. NUMBER OF SPECIES

In total 43,695 specimens were collected with ground-photo-eclectors in the area under study. This material contained as many as 720 species of Hymenoptera. (Appendix and Tables 1 and 2). Among them are 669 parasitoid species (93 %). This means that nearly 40% of the more than 1700 insect species of the Göttingen beech forest (Schaefer 1996) are entomophagous wasps.

3.2. THE NON-ENTOMOPHAGOUS HYMENOPTERA

51 species of nonparasitic Hymenoptera are represented by Tenthredinidae (20 species), Cynipidae (8), Eurytomidae (1), Formicidae (9), Vespidae (4), Sphecidae (1), Andrenidae (1), Megachilidae (1) and Apidae (6) (Table 1). All of these species only reach very low abundances (Table 1). Their total biomass is also below 1 mg DW m^{-2} a^{-1}. The densities of the *Bombus* species, the ants and nest-building-species could not be estimated exactly, but all bumble-bees and the *Dolichovespula* species were common. *Rhopalum clavipes*, *Osmia rufa* and *Andrena* spec. were found only once. They surely not belong to the local fauna.

9 species of ants were found, but only one nest of *Lasius flavus* occurred in the study-area. Of *Lasius niger* also workers were found in the traps, but no nest could be detected. All other species are represented only by immigrating males and females.

Table 1. The nonparasitic Hymenoptera in the Göttingen beech forest 1981 to 1987. Densities: ind. $m^{-2} a^{-1}$

Familiy	Species	Mean densities 1981-1987	Familiy	Species	Mean densities 1981-1987
Andrenidae	*Andrena* GW1	-	Sphecidae	*Rhopalum clavipes*	-
Apidae	*Bombus hortorum*	-	Tenthredinidae	*Profenusa* GW1	< 1
Apidae	*Bombus lucorum*	-	Tenthredinidae	*Tenthredopsis nassata*	< 1
Apidae	*Bombus pascuorum*	-	Tenthredinidae	*Tenthredopsis litterata*	< 1
Apidae	*Bombus pratorum*	-	Tenthredinidae	*Tenthredopsis annuligera*	< 1
Apidae	*Bombus soeroeensis*	-	Tenthredinidae	*Tenthredo livida*	< 1
Apidae	*Bombus terrestris*	-	Tenthredinidae	*Tenthredo ferruginea*	< 1
Cynipidae	*Cynipidae* GW1	< 1	Tenthredinidae	*Tenthredo bipunctula*	< 1
Cynipidae	*Xestophanes* GW1	< 1	Tenthredinidae	*Sterictophora* GW1	< 1
Cynipidae	*Neuroterus aprilinus*	< 1	Tenthredinidae	*Pseudodineura parvula*	< 1
Cynipidae	*Andricus ostreus*	< 1	Tenthredinidae	*Phymatocera aterrima*	1
Cynipidae	*Andricus curvator*	< 1	Tenthredinidae	*Pachyprotasis rapae*	< 1
Cynipidae	*Andricus* GW2	< 1	Tenthredinidae	*Nematus fagi*	< 1
Cynipidae	*Andricus* GW1	< 1	Tenthredinidae	*Nematus* GW1	< 1
Cynipidae	*Neuroterus quercusbaccarum*	1	Tenthredinidae	*Monophadnus pallescens*	< 1
Eurytomidae	*Tetramesa longula*	< 1	Tenthredinidae	*Mesoneura opaca*	< 1
Formicidae	*Myrmica ruginodis*	-	Tenthredinidae	*Hoplocampa minuta*	< 1
Formicidae	*Hypoponera punctatissima*	-	Tenthredinidae	*Dolerus* GW1	< 1
Formicidae	*Lasius flavus*	-	Tenthredinidae	*Blennocampinae* GW1	< 1
Formicidae	*Lasius mixtus*	-	Tenthredinidae	*Aglaostigma aucupariae*	< 1
Formicidae	*Lasius niger*	-	Tenthredinidae	*Selandria serva*	< 1
Formicidae	*Lasius umbratus*	-	Vespidae	*Paravespula vulgaris*	-
Formicidae	*Leptothorax nylanderi*	-	Vespidae	*Dolichovespula saxonica*	-
Formicidae	*Myrmica lobicornis*	-	Vespidae	*Dolichovespula sylvestris*	-
Formicidae	*Myrmica rubra*	-	Vespidae	*Paravespula rufa*	-
Megachilidae	*Osmia rufa*	-			

Table 2. Densities (ind. m^{-2} a^{-1}) of abundant parasitoid species in the Göttingen beech forest 1981 to 1987

Species	Year						
	1981	1982	1983	1984	1985	1986	1987
Acoelius erythronotus	1 ± 1	2 ± 1	1 ± 1	2 ± 4	2 ± 3	5 ± 1	< 1
Anacharis eucharioides	2 ± 1	3 ± 2	1 ± 1	< 1	< 1	3 ± 2	2 ± 1
Aphelopus melaleucus	3 ± 1	5 ± 2	4 ± 3	15 ± 8	1 ± 2	2 ± 2	1 ± 1
Aspilota spec. 2	4 ± -	4 ± 2	7 ± 3	< 1	1 ± 2	27 ± 11	18 ± 9
Basalys pedisequa	2 ± 1	< 1	1 ± 1	38 ± 19	10 ± 6	9 ± 4	4 ± 3
Charitopes gastricus	2 ± 1	7 ± 2	3 ± 2	1 ± 2	-	20 ± 4	6 ± 2
Chrysocharis prodice	6 ± 2	5 ± 2	1 ± 1	1 ± 2	3 ± 4	9 ± 3	1 ± 1
Cleruchus spec.	2 ± 2	13 ± 8	1 ± 1	9 ± 24	18 ± 17	50 ± 29	10 ± 6
Eretmocerus mundus	-	4 ± 2	99 ± 43	9 ± 5	< 1	< 1	-
Eustochus atripennis	3 ± 3	4 ± 3	5 ± 6	36 ± 71	1 ± 2	9 ± 7	2 ± 2
Exallonyx quadriceps	1 ± 1	2 ± 1	< 1	-	< 1	5 ± 2	2 ± 1
Exallonyx subserratus	< 1	< 1	1 ± 1	-	1 ± 2	1 ± 1	< 1
Gastrancistrus walkeri	2 ± 3	8 ± 7	7 ± 7	39 ± 19	< 1	7 ± 5	26 ± 7
Glauraspidia microptera	4 ± 2	5 ± 2	4 ± 3	5 ± 2	2 ± 3	3 ± 3	1 ± 1
Ismarus dorsiger	< 1	-	5 ± 3	5 ± 5	2 ± 2	< 1	< 1
Lagynodes pallidus	1 ± 1	1 ± 1	-	2 ± 4	7 ± 4	1 ± 1	1 ± 1
Litus cynipseus	6 ± 9	40 ± 14	2 ± 2	18 ± 36	< 1	22 ± 10	24 ± 28
Mesopolobus spec. 1	-	-	-	6 ± 4	64 ± 21	3 ± 2	< 1
Phygadeuon ursini	1 ± 1	2 ± 1	12 ± 4	< 1	-	5 ± 2	72 ± 77
Synopeas spec. 1	1 ± 1	1 ± 1	47 ± 38	658 ± 149	77 ± 28	-	< 1
Tetrastichus brachycerus	7 ± 3	25 ± 11	17 ± 10	83 ± 57	< 1	6 ± 5	59 ± 24
Tetrastichus fageti	5 ± 2	3 ± 1	3 ± 1	12 ± 9	10 ± 6	3 ± 2	1 ± 1
Tetrastichus luteus	< 1	< 1	2 ± 2	19 ± 13	12 ± 7	8 ± 3	1 ± 1
Trichogramma embryophagum	< 1	8 ± 4	< 1	< 1	-	4 ± 5	< 1
Trichopria aequata	1 ± 1	1 ± 1	6 ± 4	1 ± 2	< 1	1 ± 1	1 ± 1
Trichopria evanescens	< 1	< 1	1 ± 2	-	-	9 ± 7	< 1

Table 3. Estimation of the propability of local extinction estimated from data on density fluctuations and collector's curves. Control areas: Surface sampled that served as a control for different experiments

Parasitoids of	No. of species in control areas	No. of species with density fluctuations > 10-fold and > 100-fold and % of control areas				Expected No. of species in 1 m^2	Expected No. of species in 30 m^2	Expected No. of species in 100 m^2	Expected No. of species with minimal densities below 0.01 and 0.003 ind. m^{-2} a^{-1} and percentage of species in 100 m^2				Expected No. of species in 200 m^2	Expected No. of species with mean densities between 0.01 and 0.005 ind. m^{-2} a^{-1}
		> 10		> 100					< 0.01 ind. m^{-2} a^{-1}		< 0.003 ind. m^{-2} a^{-1}			
		No.	%	No.	%				No.	%	No.	%		
Miners	44	9	20%	0	0%	1	32	43	2	5.2%	0	0.0%	50	7
Gall-makers	52	16	31%	4	8%	12	38	58	8	14.1%	2	2.7%	74	16
Ektophytophages	64	2	3%	1	2%	7	43	82	2	2.2%	1	0.7%	119	37
Sap-suckers	24	7	29%	2	8%	6	17	24	3	12.3%	1	2.4%	30	6
Saprophages	41	10	24%	1	2%	9	31	49	5	10.1%	1	2.0%	64	15
Mycetophages	38	1	3%	0	0%	11	29	72	1	1.6%	0	0.0%	132	60
Predators	27	10	37%	0	0%	6	26	33	3	7.9%	0	0.0%	38	5
Eggs	29	8	28%	1	3%	7	21	31	3	10.5%	1	3.2%	39	8
Parasitoids	20	1	5%	0	2%	2	15	34	1	3.6%	0	1.1%	53	19
Xylophages	1	0	0%	0	0%	-	-	-	-	-	-	-	-	-
Guild unknown	82	13	16%	1	1%	10	55	99	8	7.6%	1	0.7%	138	39
All parasitoids	422	78	18%	9	2%	71	311	525	45	8.5%	5	1.1%	709	184

3.3. THE PARASITIC HYMENOPTERA

Table 4 shows a classification of the parasitoids into their kind of host. It appears that the parasitoids of Diptera are by far the largest group (262 species). Species rich are also the parasitoids of Lepidoptera (103 species) and Coleoptera (60 species). All other Arthropod taxa harbor minor numbers of parasitoid-species.

A classification by host-guild reveals that the parasitoids of ectophytophagous hosts are the most numerous group (Table 5). It contains 108 detected species. The next species-rich guilds are the parasitoids of mycetophagous Diptera (82 species) and saprophagous Diptera and Coleoptera (63 species). Species rich are also the parasitoids of predators (41 species) and the egg-parasitoids (45 species). Parasitoids of sap sucking insects are represented by 33 species only.

Despite the large number of collected species, the entire number of Hymenoptera is still unknown. In each of the 8 years in which collections with eclectors were made, I found many "new" species. Even in the last of the 8 years, I found 72 species previously unrecognized. So, further investigation will surly extend my species list.

There are three different methods to compute the species numbers from the given data set (for a review of other methods cf. Bunge and Kirkpatrick (1993) and Solow (1994)). A combination of these computations also allows rates of immigration and extinction to be assessed.

3.4. ANNUAL NUMBER OF SPECIES

One possible way of assessing the total number of species (S) is to compute collector's curves (Pielou 1977, Ulrich 1988). The function S = f(sampled area) should asymptotically approximate the total number if such a maximum exists.

For the year 1981 it was possible to compute the total number of species that occurred in that year in the part of forest under study (Fig. 2). Ten ground-tree-photo-eclectors were placed which sampled an area of 37.7 m^2. A plot of the newly found species S as a function of the number of eclectors N shows that such a plot can readily be described by the function:

$S = 105.66\ N^{-1.0953}$; $R^2 = 0.98$; $r = 0.99$; $p < 0.001$.

From this equation one can compute the maximal number of species that could be found in that year with ground-photo-eclectors: this number is equal to the total area under the curve from 0.5 to ∞

$S = \int f(x)dx = (105.66\ 0.5^{-0.0953}) / 0.0953$

$S_{max} = 1184$ species / year

This is the maximum number of species possible. But it is, of course, too high because of the unrealistic assumption that species might have an infinitely low abundance. A more realistic assumption is that each species has a lower density limit beyond which it cannot sustain its population. This results in a lower annual number of species:

$$\sum_{0.5}^{min} f(x)$$

If one takes 1 individual / 100 m as a lower limit (100 individuals / ha) a total of 376 species per year results. For 1 ind. / 200 m^2 the total species number is 427 per year (Table 4). 289 species were actually found with the ground-photo-eclectors and it seems realistic that no more

Table 4. Abundance (ind m^{-2} a^{-1}) and biomass (mgDW m^{-2} a^{-1}) of the parasitic Hymenoptera of different host taxa in the Göttingen beech forest 1981 to 1987

Parasitoids of	No. of species	1981		1982		1983		1984		1985		1986		1987	
		ind./m^2	mg/m^2	ind./m^2	mg/m^2	ind./m^2	mg/m^2	ind./m^2	mg/m^2	ind./m^2	mg/m^2	ind./m^2	mg/m^2	ind./m^2	mg/m^2
Arachnida	3	1 ± 1	< 1	1 ± 1	< 1	2 ± 2	< 1	2 ± 3	1 ± 1	2 ± 3	< 1	2 ± 2	1 ± 1	2 ± 1	< 1
Psocoptera	1	< 1	< 1	2 ± 2	< 1	7 ± 4	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Thysanoptera	2	1 ± 2	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	6 ± 6	< 1	3 ± 3	< 1
Heteroptera	3	3 ± 2	1 ± 1	1 ± 1	< 1	3 ± 2	1 ± 1	7 ± 6	1 ± 1	4 ± 2	1 ± 1	1 ± 1	< 1	1 ± 1	< 1
Cicadina	14	9 ± 4	1 ± 1	20 ± 7	1 ± 1	9 ± 3	1 ± 1	18 ± 8	3 ± 1	1 ± 2	< 1	4 ± 3	< 1	3 ± 2	< 1
Aphidina	16	2 ± 1	< 1	2 ± 1	< 1	2 ± 2	< 1	2 ± 4	< 1	< 1	< 1	3 ± 2	< 1	30 ± 18	1 ± 1
Coccina	5	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Aleyrodina	3	< 1	< 1	4 ± 2	< 1	100 ± 43	1 ± 1	1 ± 2	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Psyllina	1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	1 ± 1	< 1
Planipennia	11	4 ± 2	1 ± 1	13 ± 4	4 ± 1	4 ± 3	1 ± 1	1 ± 2	< 1	< 1	< 1	26 ± 6	7 ± 2	8 ± 3	2 ± 1
Coleoptera	60	25 ± 17	3 ± 1	65 ± 23	5 ± 2	14 ± 7	2 ± 1	58 ± 80	1 ± 1	8 ± 7	1 ± 1	56 ± 15	5 ± 2	45 ± 28	4 ± 2
Symphyta	14	< 1	1 ± 2	1 ± 1	1 ± 2	< 1	1 ± 1	< 1	1 ± 1	< 1	< 1	< 1	< 1	< 1	< 1
Apocrita	46	2 ± 1	< 1	6 ± 3	1 ± 1	9 ± 3	1 ± 1	5 ± 5	1 ± 1	3 ± 3	1 ± 1	5 ± 3	1 ± 1	3 ± 2	< 1
Diptera	262	56 ± 15	6 ± 2	121 ± 40	11 ± 4	137 ± 41	24 ± 5	936 ± 164	33 ± 7	186 ± 38	14 ± 4	195 ± 24	39 ± 7	261 ± 83	113 ± 91
Lepidoptera	103	14 ± 4	6 ± 4	37 ± 9	11 ± 6	12 ± 4	17 ± 10	6 ± 5	8 ± 14	42 ± 14	31 ± 29	36 ± 7	34 ± 11	32 ± 35	42 ± 14
Host unknown	125	7 ± 3	< 1	30 ± 13	1 ± 1	21 ± 5	2 ± 1	42 ± 32	1 ± 1	105 ± 28	4 ± 2	96 ± 30	11 ± 7	29 ± 7	7 ± 5
Sum	669	123 ± 23	19 ± 5	301 ± 49	36 ± 8	319 ± 61	52 ± 11	1078 ± 186	49 ± 16	351 ± 50	53 ± 29	428 ± 42	98 ± 15	418 ± 97	170 ± 92

Table 5. Abundance (ind m^{-2} a^{-1}) and biomass (mgDW m^{-2} a^{-1}) of the parasitic Hymenoptera of different host guilds in the Göttingen beech forest 1981 to 1987

Parasitoids of	No. of species	1981		1982		1983		1984		1985		1986		1987	
		ind./m²	mg/m²	ind./m²	mg/m²	ind./m²	mg/m²	ind./m²	mg/m²	ind./m²	mg/m²	ind./m²	mg/m²	ind./m²	mg/m²
Miners	55	14 ± 4	3 ± 2	23 ± 5	4 ± 2	22 ± 5	15 ± 5	4 ± 5	<1	36 ± 13	3 ± 2	31 ± 6	8 ± 3	78 ± 77	85 ± 91
Gall-makers	68	23 ± 9	1 ± 1	95 ± 39	4 ± 1	86 ± 40	3 ± 1	880 ± 163	29 ± 7	167 ± 37	13 ± 4	72 ± 12	12 ± 3	121 ± 26	5 ± 1
Ectophytophages	108	6 ± 3	7 ± 4	7 ± 3	11 ± 7	8 ± 3	18 ± 10	3 ± 3	8 ± 14	7 ± 5	29 ± 29	11 ± 3	32 ± 11	32 ± 35	43 ± 14
Sap-suckers	33	9 ± 3	1 ± 1	15 ± 5	1 ± 1	110 ± 43	3 ± 1	21 ± 9	3 ± 1	1 ± 2	<1	12 ± 6	1 ± 1	37 ± 19	2 ± 1
Mycetophages	82	4 ± 3	1 ± 1	7 ± 3	4 ± 3	3 ± 2	2 ± 2	2 ± 4	<1	4 ± 3	1 ± 1	15 ± 5	5 ± 4	12 ± 4	4 ± 2
Saprophages	63	24 ± 11	2 ± 1	16 ± 10	1 ± 1	30 ± 9	3 ± 1	50 ± 20	2 ± 1	18 ± 9	1 ± 1	87 ± 19	5 ± 1	43 ± 15	3 ± 1
Predators	41	10 ± 3	3 ± 1	22 ± 6	8 ± 2	13 ± 4	4 ± 2	10 ± 7	2 ± 1	6 ± 3	1 ± 1	44 ± 8	18 ± 4	19 ± 5	15 ± 6
Eggs	45	21 ± 17	<1	94 ± 27	1 ± 1	17 ± 8	<1	65 ± 84	1 ± 1	24 ± 18	<1	102 ± 33	1 ± 1	49 ± 29	1 ± 1
Parasitoids	37	2 ± 2	<1	6 ± 3	1 ± 1	8 ± 3	1 ± 1	5 ± 5	<1	3 ± 3	1 ± 1	5 ± 2	1 ± 1	2 ± 1	<1
Xylophages	4	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Guild unknown	133	8 ± 3	1 ± 1	16 ± 5	1 ± 1	21 ± 5	3 ± 1	38 ± 22	3 ± 2	86 ± 23	4 ± 2	51 ± 9	15 ± 7	27 ± 5	13 ± 5
Sum	669	123 ± 23	19 ± 5	301 ± 49	36 ± 8	319 ± 61	52 ± 11	1078 ± 186	49 ± 16	351 ± 50	53 ± 29	428 ± 42	98 ± 15	418 ± 97	170 ± 92

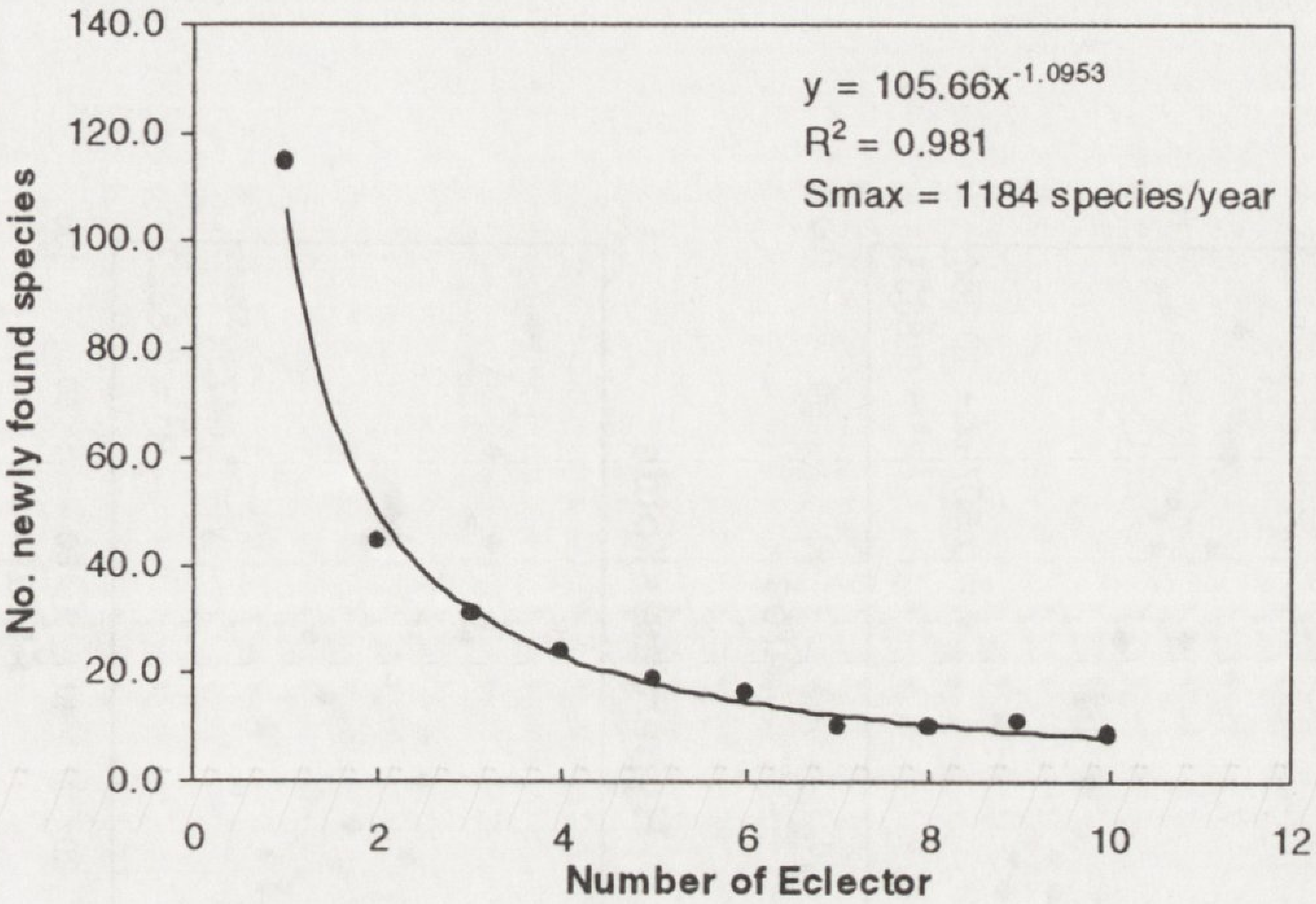


Fig. 2. Number of species found with 10 ground–photo–eclectors placed around beech trunks. Each eclector sampled an area of 3.77 m^2. Smax: Maximal number of species / year

than 500 species occurred in the part of the forest under study. It should be mentioned that this are the numbers in 1981. In other years there might be slightly different results.

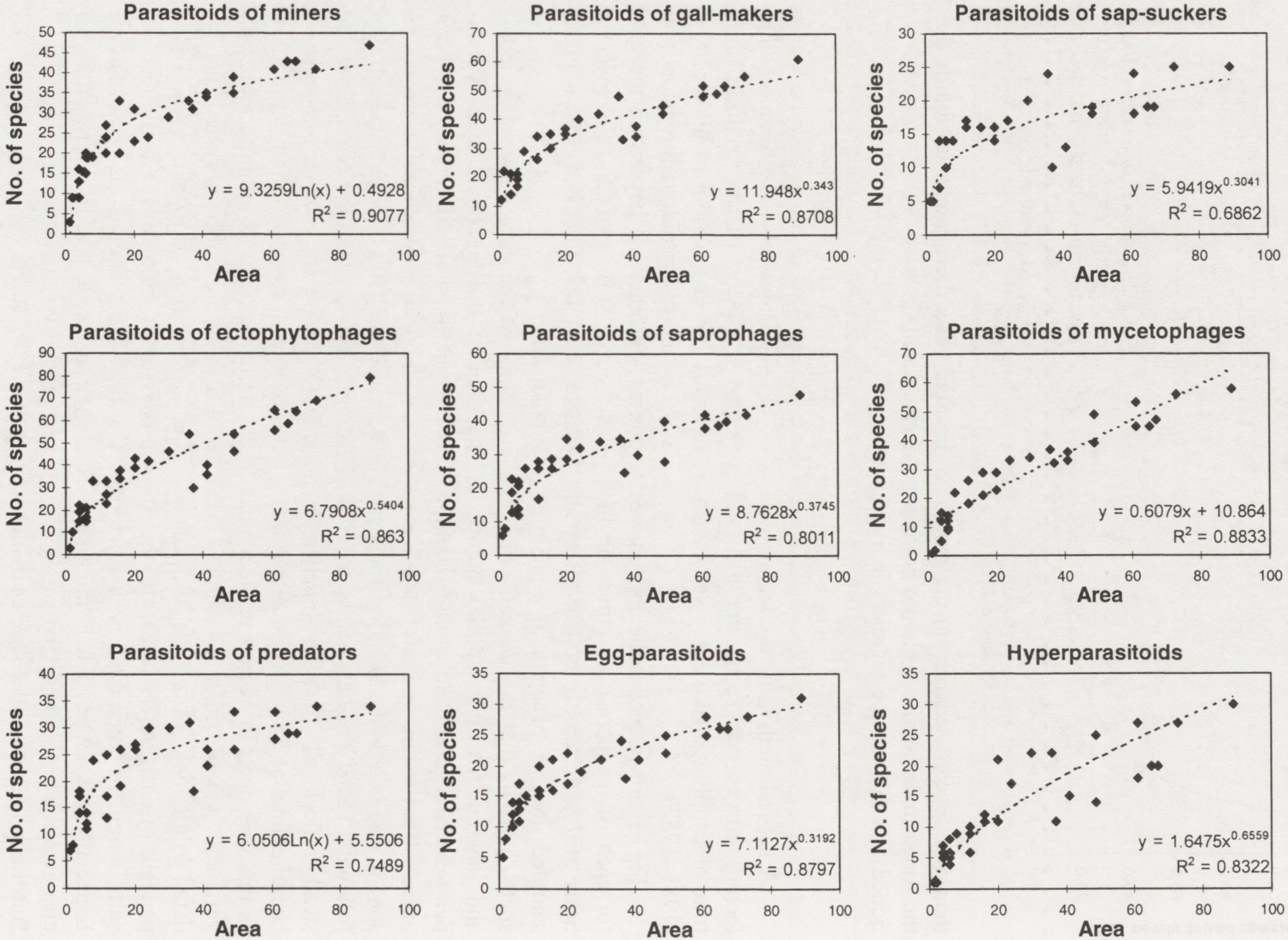
3.5. SPECIES POOL

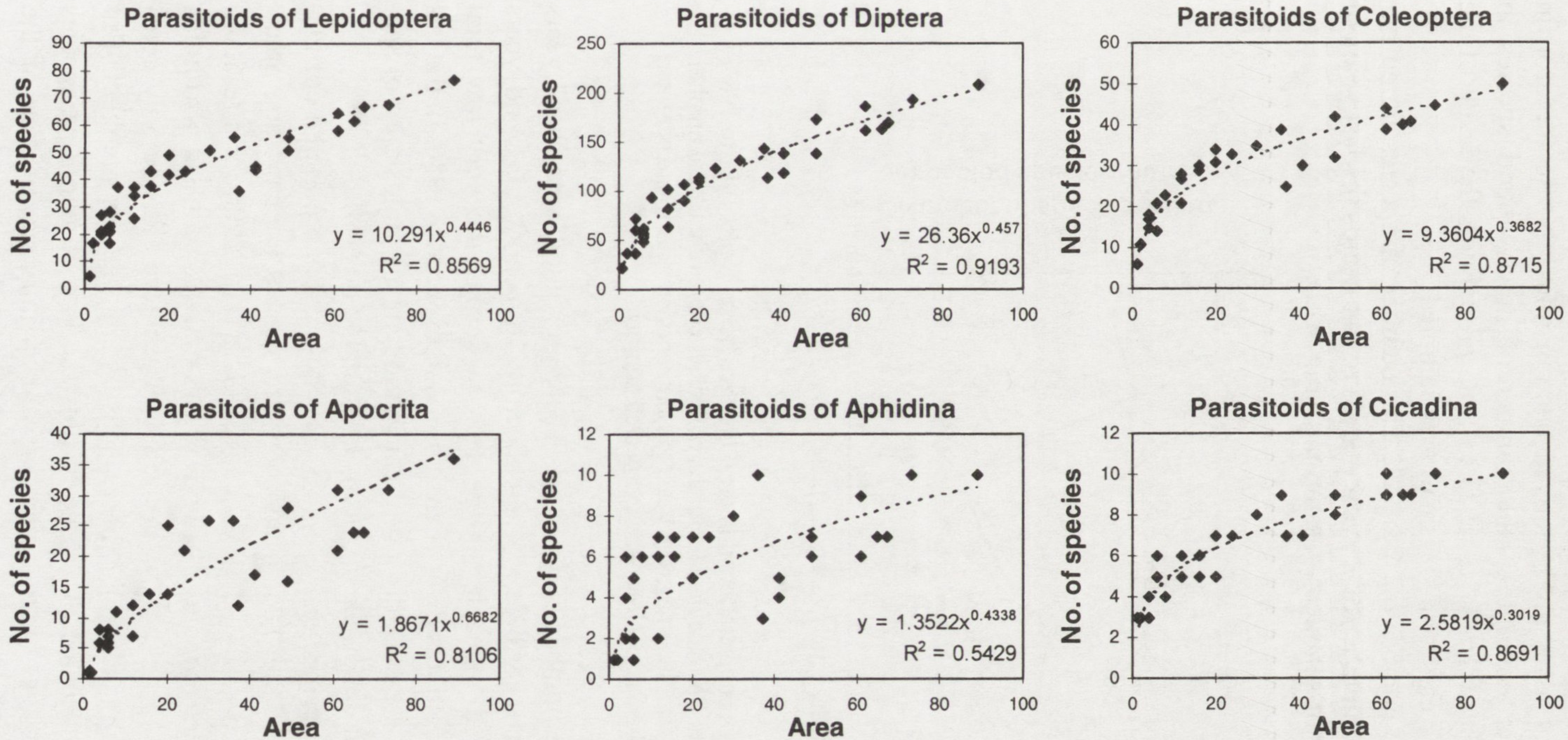
A second method is to compute collector's curves that span over the total time of sampling, that means over 7 years (1981–1987).

Fig. 3 shows such collector's curves for each of the parasitoid guilds on the basis of 7 years and a total of 89 m^2 of sampled area. A problem of computing such curves is that the annual variation and inherent trends in species numbers per year can greatly affect the resulting curves. That means it is not possible to start in one year and add sequentially the following years. The data points given instead reflect all possible independent combinations of each given sample-area. In this way one can overcome the annual variances and obtain mean values. The data points are, of course, not independent of each other. Therefore, the results should be interpreted with caution. Especially it is not possible to infer a species-area-relationship (Pielou 1977). But it is possible to infer species numbers in a limited range of area. It is also possible to compare the curves of different guilds.

Fig. 3 shows also the functions that fit the data. Most of the resulting functions are power functions of the type $y = a x^b$. In the parasitoids of predators and miners log-functions occur and the collector curve of the parasitoids of mycetophages can be described by a linear relationship.

None of the curves allows the computation of the maximum species-number. Double-log transformations did not result in curves that reached a maximum (data not shown). It is only possible to compute the number of species in a given area. Of course, the number of species in the Göttingen forest is not unlimited. But the limited area of sampling does not allow a function to be computed that reflects the real distribution and the processes of immigration and local extinction. The functions also don't have a similar slope as had been reported for many species-area-relationships (Preston 1962 inferred a slope around 0.3 for island communities, Gaston *et al.* 1996 used a slope of 0.25 to compute species numbers of Hymenoptera in Costa


Parasitoids of miners
y = 9.3259Ln(x) + 0.4928
R² = 0.9077
Parasitoids of gall-makers
y = 11.948x^0.343
R² = 0.8708
Parasitoids of sap-suckers
y = 5.9419x^0.3041
R² = 0.6862
Parasitoids of ectophytophages
y = 6.7908x^0.5404
R² = 0.863
Parasitoids of saprophages
y = 8.7628x^0.3745
R² = 0.8011
Parasitoids of mycetophages
y = 0.6079x + 10.864
R² = 0.8833
Parasitoids of predators
y = 6.0506Ln(x) + 5.5506
R² = 0.7489
Egg-parasitoids
y = 7.1127x^0.3192
R² = 0.8797
Hyperparasitoids
y = 1.6475x^0.6559
R² = 0.8322
No. of species
Area



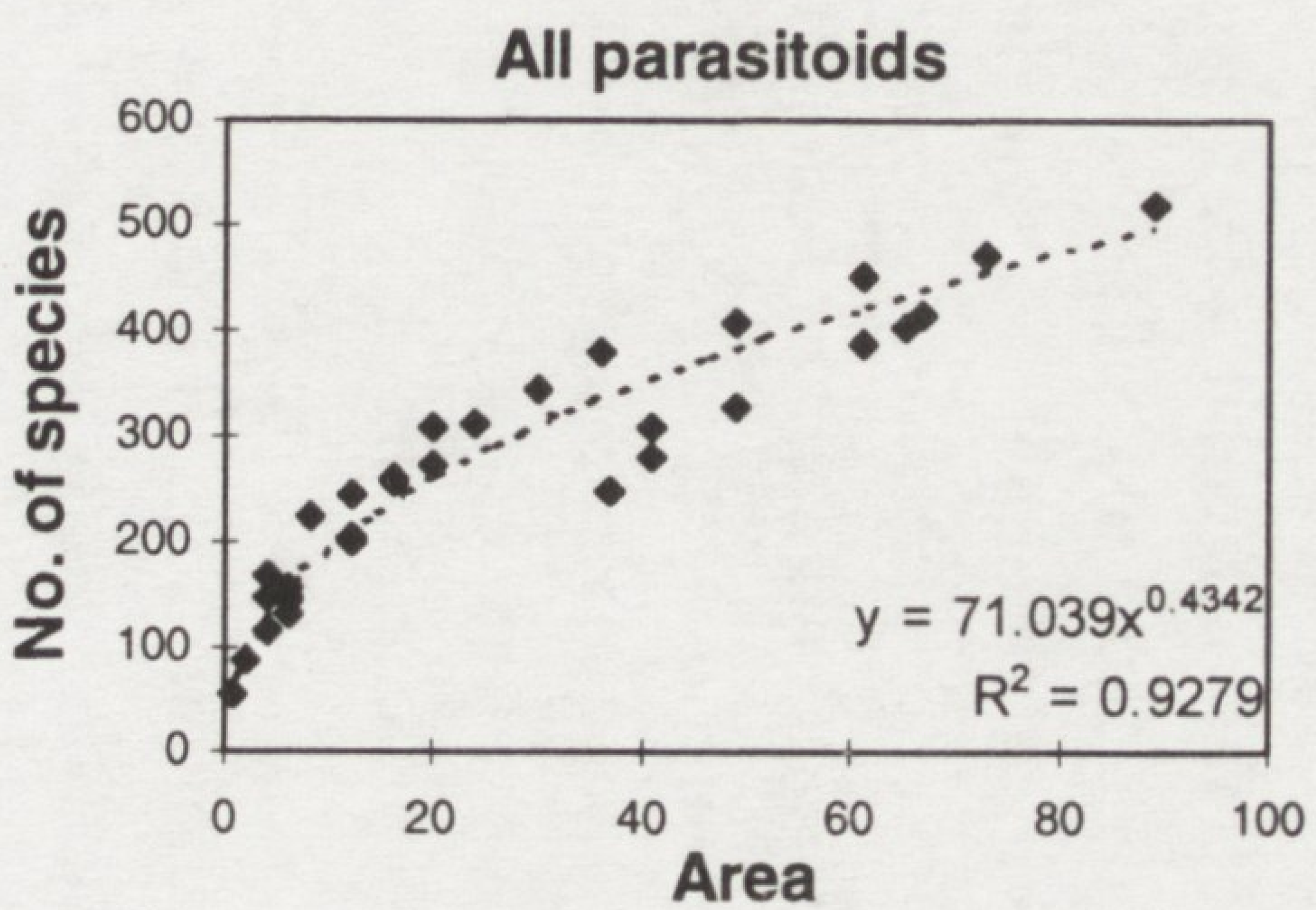


Fig. 3. Collector's curves of the parasitic Hymenoptera of the Göttingen forest. Plotted are the numbers of species against the area sampled with ground-photo-eclectors (1981 to 1987). To eliminate trends in species numbers per year, all combinations of areas sampled were included in the graph. Further details are given in the text.

Rica). Instead most of my slopes range in the order of 0.3 to 0.5. The function for all parasitoids is $S = 71.039\ X^{0.4342}$.

The next possible way of assessing the number of species is to compute curves that show the number of "new" species found in each of the years sampled. Fig. 4 gives plots of the number of species found per year and the number of species found per year per m^2 of sampled area. Fig. 5 gives a plot of the number of newly found species per year regardless of the different areas sampled in each year and a plot of the species numbers divided through the sampling area. Both functions converge to zero, but due to the limited number of years the variance-explanations are not significant at the 0.05 % level.

From Figs 4 and 5 several conclusions can be drawn:

1. In the first year of sampling (1981) about half of all species were detected. A detailed analysis showed that this trend holds for most of the parasitoid guilds.

2. The curves in part reflect the different sampling methods: 1981 and 1982 the traps were removed every 4 or 6 weeks, in 1983 to 1985 they remained in place and in 1986 and 1987 they were removed once in mid-July. So the drop in the number of newly found species in 1983 to 1985 probably is the result of the small area sampled.

3. The number of species found per year per m^2 rises towards the last years of sampling. (Fig. 4).

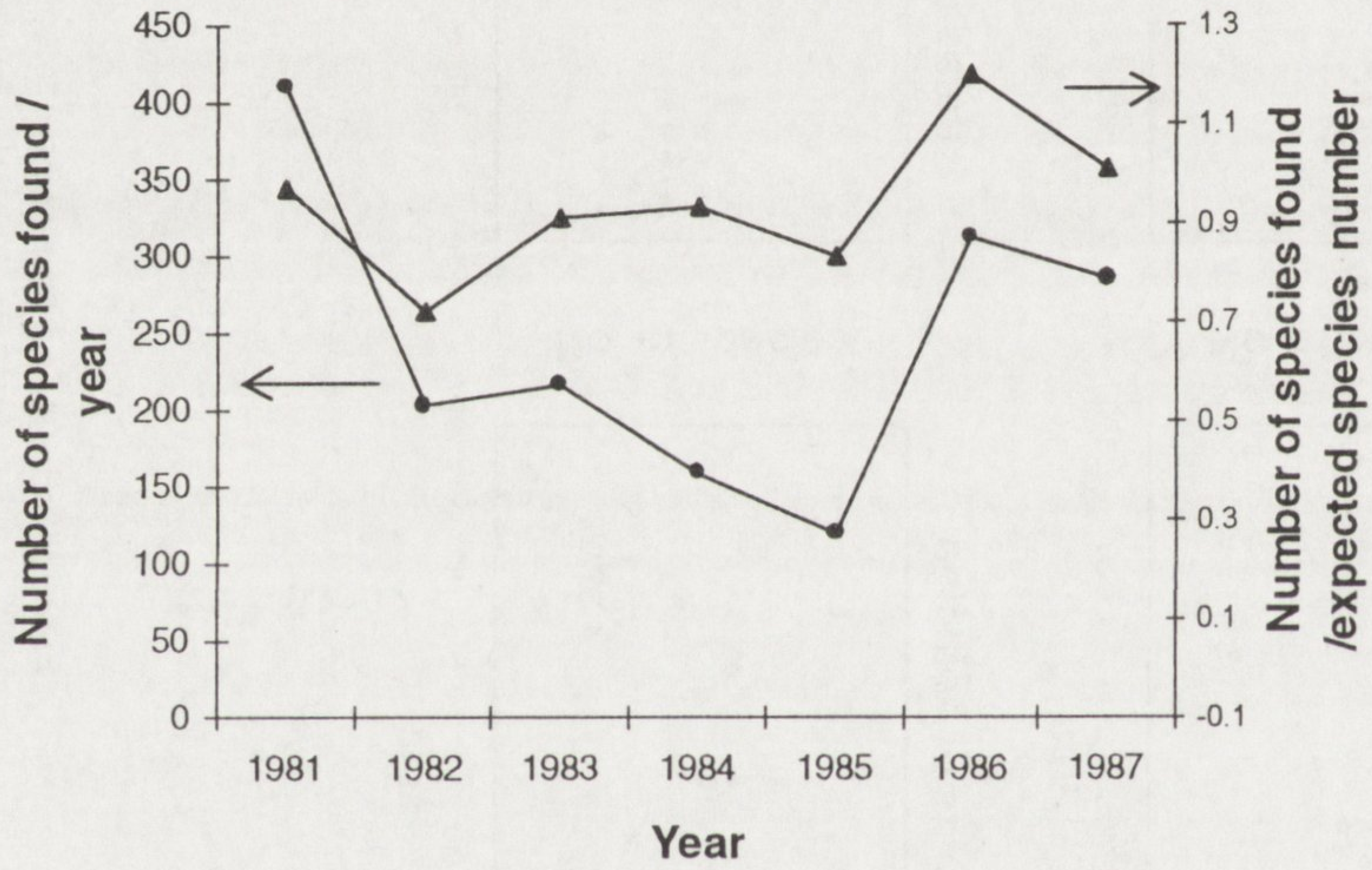


Fig. 4. Numbers of parasitic Hymenoptera found in the Göttingen beech forest 1981 to 1987. The expected number of species was calculated with the collectors curve of the total number of species (Fig. 3) and the area sampled in a given year. ●: Number of species found per year; ▲: Number of species found / expected number.

4. There are "good" and "bad" years for collecting Hymenoptera. Good years were 1981 – despite the very low total densities – and especially 1986. In the latter year in most of the guilds a lot of species were found to be new.

5. Several authors reported a correlation between species numbers and abundance (see Gaston 1996 for a review). Fig. 6 shows that such a trend also holds in the Göttingen forest if one only compares density and species numbers. But one has to take into account that species numbers are an intrinsic function of the area on which the density had been estimated and which are given by the collectors curves.

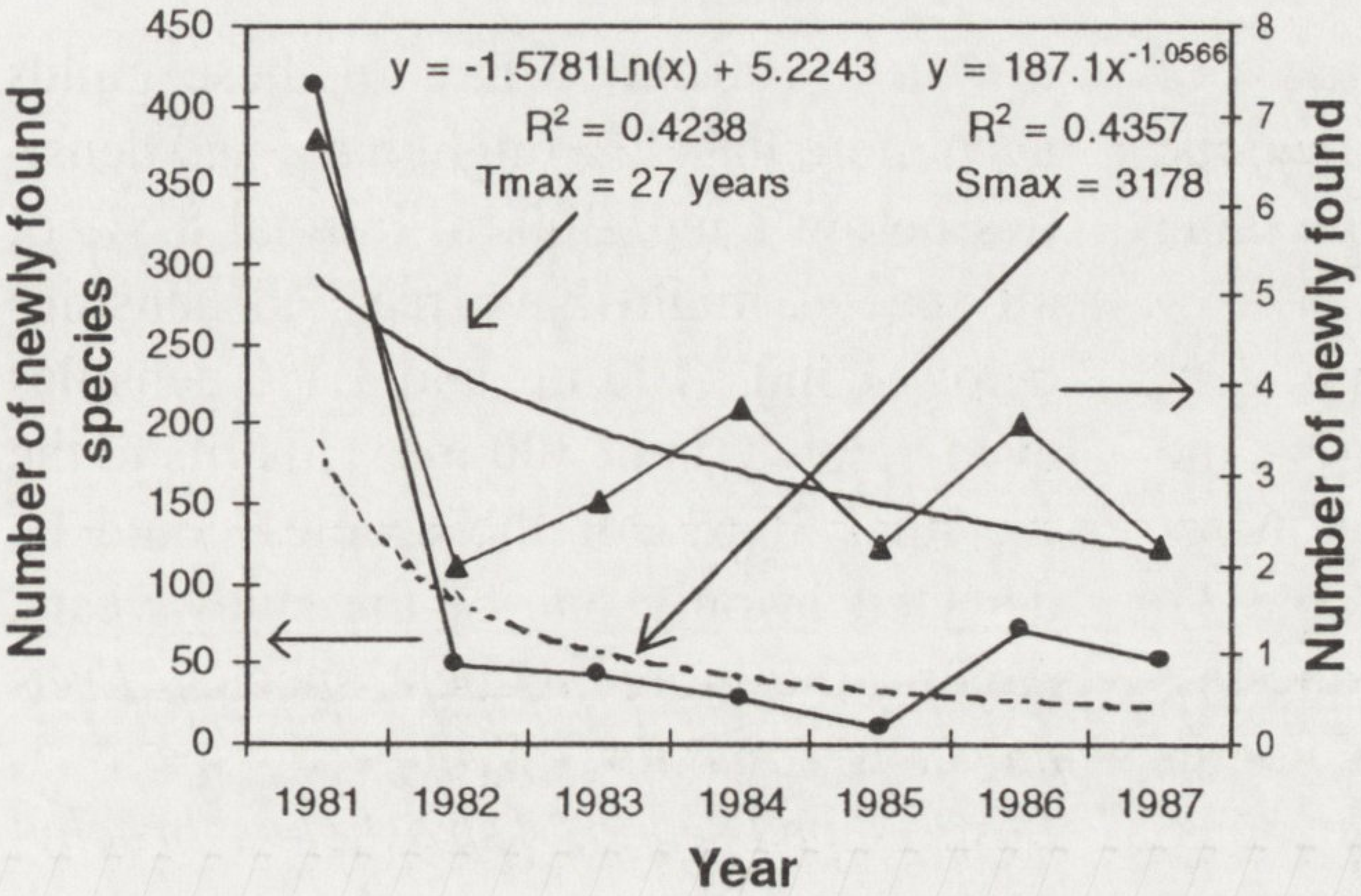


Fig. 5. Numbers of newly found species and numbers of newly found species / m^2 of the parasitic Hymenoptera in the Göttingen beech forest 1981 to 1987. Data of all ground-photo-eclectors combined. Tmax: Maximum sampling time to collect all of the species (Tmax) of the regional species pool of the Göttingen forest.
●: Number of newly found species; ▲: Number of newly found species / m^2

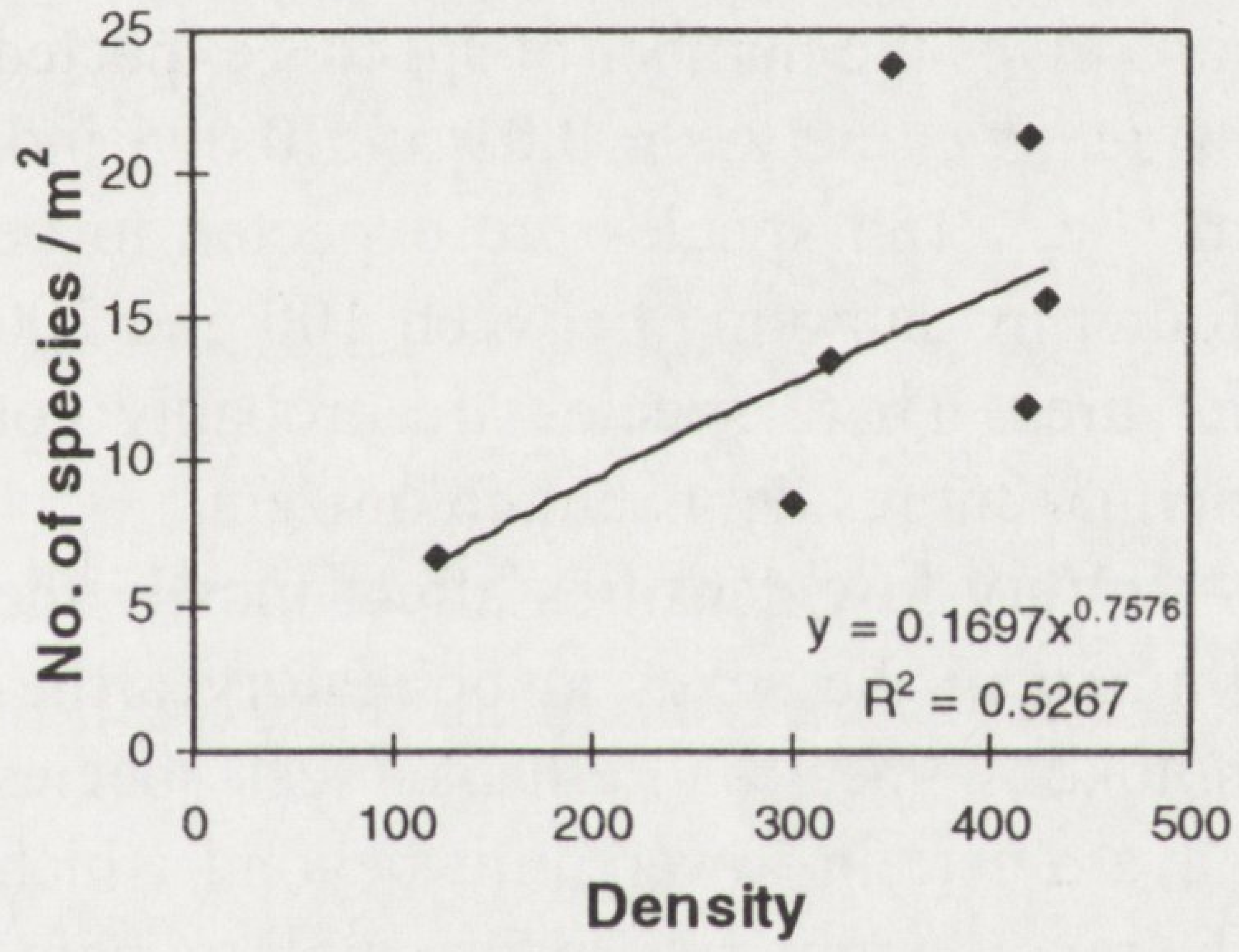


Fig. 6. Relationship between the number of parasitoid species found in the Göttingen beech forest and their total annual density (ind. m^{-2} a^{-1})

6. Of course, the forest does not contain the entire European hymenopterous fauna. After some time the sampling should reveal a maximum number of species that take part in the annual species turnover, and which have the potential to colonize a given habitat. The plots in Fig. 5 give a hint how many species can be found in the part of the Göttingen forest under study. There may be up to 3178 species able to colonize the study area and it would take 27 years to sample them.

3.6. DENSITY FLUCTUATIONS AND PROBABILITY OF LOCAL EXTINCTION

The computation of collector's curves allows a rough assessment of the probability of extinction. For this purpose Table 3 contains data about the density fluctuations of the parasitoid populations (column 3 to 6 of Table 3). It should be mentioned that these estimations are of course biased because they underestimate the real fluctuations in low density species. The following assessment gives therefore only lower limits of fluctuations and hence lower limits of local extinction rates. Column 7 to 9 of Table 3 list the estimated number of species (computed with the equations of the collector's curves, cf. Fig. 3) with mean densities between 1 and 0.01 ind. m^{-2} a^{-1}. The minimal abundances of these species are:

$$x_{min} = x_{mean} / f^{0.5}$$

with f: factor of the density fluctuation of the population. In Table 3 I used a lower density-limit of 0.01 ind. m^{-2} a^{-1}. My data give no hint that at densities below 0.02 ind. m^{-2} a^{-1} such a density-limit is reached. Analyses of the samplings in 1981 (49 m^2 sampling-area) revealed no gap between high and low density species or irregularities in the species distribution. But if one chooses even lower limits (say 1 ind. / 300 m^2) the percentages of species that reach very low densities due to density-fluctuations will be in the same order.

Given that these species with very low abundances have – on average – the same density fluctuations as the whole set of species (column 4 and 6 of Table 3), one can compute the number of species, and the percentage of the entire community, that may reach very low densities. The columns 10 to 13 show such numbers and percentages for minimal densities (x_{min} of 0.01 and 0.003 ind. m^{-2} a^{-1}). The values were computed from the above equation with mean densities of 1 ind./ m^2 to 1 ind. / 100 m^2, and factors of density fluctuations of 10 and 100. Due to the fact that, for the computations in Table 3, I used upper values for the mean abundances (0.3 ind. m^{-2} a^{-1}) but lower ones for the population fluctuations (cf. part 2, sampling program), the apparent numbers of species reaching such low densities are very probably higher.

It appears that especially in the parasitoids of sap-sucking, saprophagous, gall inducing insects, and in egg-parasitoids many species might have reached local population densities below 0.01 ind. m^{-2} a^{-1} (100 ind. / ha). In these guilds even more than 2% might have had densities below 1 ind/ 300 m. In total 8.5% of all species might have reached densities below 1 ind./ 100 m^2 and 1.1% densities even below 1 ind./ 300 m^2. This fits to the fact that 38.5% of the species could be detected in only one of the study years. Among the more frequent species, *Eretmocerus mundus*, *Synopeas* spec. 1, *Basalys pedisequa*, *Tetrastichus brachycerus* and *Litus cynipseus* had very high density fluctuations (Table 2). Table 3 also gives the number of species expected at densities between 0.01 and 0.005 ind. m^{-2} a^{-1}. 184 species are expected to be found by sampling between 100 and 200 m^2 area. These species are probably not permanent residents but colonizers.

Very low densities affect mostly the finding of the sexes in obligatory arrhenotokous species. Perhaps most species have a certain lower limit beyond which the reproduction rate is too small to maintain the population. Such low density species run a high risk of becoming extinct (cf. Krebs 1985, Den Boer 1985). Exceptions are species that are highly aggregated and have higher densities in their local patches.

3.7. DENSITY AND BIOMASS

Table 2 lists the densities of the most important species of the Göttingen forest. The other parasitoid species have mostly mean densities below 1 ind. m^{-2} a^{-1}. Table 4 gives the combined density and biomass of the parasitoids of all host taxa parasitized in the Göttingen forest. The total emergence of the entomophagous Hymenoptera ranged between 123 $\pm$ 23 (1981) and 1078 $\pm$ 186 (1984) ind. m^{-2} a^{-1}; on average they occurred with 431 ind. m^{-2} a^{-1}. The most important groups were the parasitoids of Diptera (56 $\pm$ 15 to 936 $\pm$ 164 ind. m^{-2} a^{-1}) and Coleoptera (8 $\pm$ 7 to 65 $\pm$ 23 ind. m^{-2} a^{-1}). This means that the Hymenoptera are among the most abundant arthropods of the beech forest under study (cf. Schaefer 1989, 1991).

But this is not the case if we look at the biomass (Table 4). That reached only values between 19 $\pm$ 5 (1981) and 170 $\pm$ 92 (1987) mg DW m^{-2} a^{-1}, with a mean of 68 mg DW m^{-2} a^{-1}. Other important groups of arthropods in the beech forest under study had much higher biomasses: spiders 95 (Stippich 1986), isopods

100 (Strüve Kusenberg 1987), chilopods 265 (Poser 1988), springtails 138 (Wolters 1985), Carabidae (imagines) 144 (Martius 1981), and Diptera (imagines) 400 mg DW m^{-2} a^{-1} (Hövemeyer 1985).

Interesting is the constant rise in the biomass from 1981 to 1987. This is mostly caused by the high abundance of some large Ichneumonids (*Phygadeuon ursini*, *Phygadeuon* spp., *Cratichneumon rufifrons*, *Charitopes gastricus*).

Table 5 shows the data of density and biomass of the parasitoids sorted by host guild. The parasitoids of gall-makers and egg-parasitoids reached the highest densities (23 ± 9 to 880 ± 163 and 21 ± 17 to 102 ± 33 ind. m^{-2} a^{-1}). Concerning the biomass, the wasps that lay their eggs into the larvae of ectophytophagous beetles and butterflies were in the first place (7 ± 4 to 43 ± 14 mg DW m^{-2} a^{-1}). This group is represented mostly by large Ichneumonidae and Braconidae.

3.7. TREE TRUNKS AND BEECH STUMPS

In 1980 and 1981 two important microhabitats were studied with emergence traps: the area around the tree trunks and an old stump of a dead beech tree. Tables 6 and 7 show that there are significant differences as well as identical patterns between these habitats and in comparison with the soil and herb layer distant to the trees.

With regard to the density, there are no striking differences between the emergences near tree trunks and the "normal" emergences. This applies to the total abundance and to the density of each of the parasitoid guilds (Table 6). Many more parasitoids, however, emerged out of the old tree stump studied (190 ind. m^{-2} a^{-1}). Especially the parasitoids of dipterous larvae and pupae living in soil reached a very high density (together 88 ind. m^{-2} a^{-1}). The parasitoids of miners and the egg-parasitoids, on the other hand, emerged in a lower density.

The biomass of the parasitoids near the beech trunks was higher due to higher values in the parasitoids of ectophyto-

Table 6. Density and biomass of parasitoids in a 10 year old beech stump (emergence of 1980) and near beech trunks (emergence of 1981) (ind. m^{-2} a^{-1}; mgDW m^{-2} a^{-1})

Parasitoids of	Mean density			Mean biomass		
	near beech trunks	out of an old beech stump	mean density 1981	near beech trunks	out of an old beech stump	mean biomass 1981
Miners	17 ± 3	5	14 ± 4	6 ± 2	1	3 ± 2
Gall-makers	21 ± 4	27	23 ± 9	1 ± 1	1	1 ± 1
Ectophytophages	5 ± 1	8	6 ± 3	10 ± 4	14	4 ± 4
Sap-suckers	6 ± 1	10	9 ± 3	1 ± 1	2	1 ± 1
Mycetophages	8 ± 2	45	4 ± 3	2 ± 1	11	1 ± 1
Saprophages	23 ± 4	43	24 ± 11	2 ± 1	3	2 ± 1
Predators	8 ± 2	9	10 ± 3	3 ± 1	2	3 ± 1
Eggs	14 ± 5	13	21 ± 17	1 ± 1	2	< 1
Parasitoids	1 ± 1	< 1	2 ± 2	1 ± 1	< 1	< 1
Xylophages	< 1	< 1	< 1	< 1	< 1	< 1
Guild unknown	10 ± 2	30	8 ± 3	2 ± 1	5	1 ± 1
Sum	113 ± 9	190	123 ± 23	27 ± 4	41	19 ± 5

phages. Much higher instead was the biomass of the wasps that emerged out of the beech stump (41 mg DW m^{-2} a^{-1}). Additionally to the parasitoids of ectophytophages, the pronounced emergence of larger parasitoids of mycetophages Diptera – mostly Ichneumonidae and some Belytinae – account for this fact.

Near the tree trunks there was a slight lowering of the number of species (Table 7). 255 species were found at the control sites (24 m^2 area); only 289 could be found near the trunks (37 m^2 area; in such an area about 340 species are expected). This holds especially for the parasitoids of phytophagous and saprophagous hosts. The tree stump, on the other hand, was richer in species. 57 species were detected, 48 expected. Again the parasitoids of mycetophagous and saprophagous hosts had a higher species number.

Table 7. Observed versus expected (regression of collector's curves in 1981) number of parasitoid species near tree trunks and in old beech stumps

Parasitoids of	Near tree trunks 1981; 37 m^2	Control area 1981; 24 m^2	Old beech stump; 1 m^2	
	Counted	Counted	Counted	Expected
Miners	33	32	4	1
Gall-makers	36	35	5	8
Ectophytophages	36	27	4	5
Sap-suckers	11	7	2	4
Mycetophages	38	24	10	7
Saprophages	29	30	10	6
Predators	20	13	5	4
Eggs	20	23	5	5
Parasitoids	14	12	1	1
Xylophages	-	1	-	-
Guild unknown	52	51	11	7
Sum	289	255	57	48

4. DISCUSSION

4.1. SPECIES NUMBERS

Although there are many long-term quantitative studies on other insect taxa (for example on various insects: Kendeigh 1979, on Diptera: Hövemeyer 1985, on Carabidae: Den Boer 1985, on Lepidoptera: Meinicke 1984 and the literature therein, see also the compilation of Stiling 1987 of studies on density dependence) the Hymenoptera are very poorly studied. Detailed species lists for certain families or superfamilies that had been taken over a longer and continuous period have only been provided by Weidemann (1965) (Serphidae), Abraham (1969) (Pteromalidae), König (1969) (Braconidae), Horstmann (1970, 1988) (Ichneumonidae), Copland and Askew (1977) (Chalcidoidea), Garbarczyk (1981) (Serphoidea and Scelionoidea), Sterzyński (1981) (Braconidae), Sawoniewicz (1981) (Ichneumonidae), Kussmaul and Schmidt (1987) (Ichneumonidae), Vidal (1988) (Eulophidae). Thiede (1975) published incomplete species lists as well as estimations of the abundance and biomass. He studied a spruce forest in the Solling (FRG) with the same type of eclectors used in our sampling program. More recently H i l p e r t (1989) gave a detailed account on the total hymenopterous fauna of a mixed leaf forest (Bechtal forest) near Freiburg (FRG). He also used ground-photo-eclectors.

The most striking fact which appeared in all the studies is the extraordinarily high number of parasitoid species that live in a certain habitat. In the Göttingen forest the number of potential host species is probably around 800 to 1000 species (U l r i c h 1987b) and more than 1700 species of arthropods were found during several years of study in the Göttingen forest (S c h a e f e r 1996). Therefore the parasitoids count for nearly 40% of the total arthropod fauna and are nearly as rich in species as their potential hosts (cf. U l r i c h 1989). Similar results were obtained by J a n z e n and P o n d (1975), T h i e d e (1975), M o r a n and S o u t h w o o d (1982), O w e n and S v e n s s o n (1974) and H i l p e r t (1989). They also found some hundreds of parasitoid species irrespective of the kind of habitat studied. It seems as well that a ratio of 40% is about constant for different ecosystems. The detailed analysis of U l r i c h (1987a) and H a w k i n s and L a w t o n (1987) on the relations of parasitoid to host species numbers points in the same direction.

What is the total number of parasitoid species that can be found in a beech forest? This question has no simple answer. One has to differentiate between a yearly number of species and the number of species which can potentially live and colonize a certain habitat, the species pool (E r i k s s o n 1993).

The yearly number of species in the beech forest studied is surely above 400 (in 1981 I found 407 species; Fig. 4), with a maximum of 1184 species / year (Fig. 2). Judged by collectors curves I expect an upper limit of 600 species per year at the study site, which covered a about ten ha. These values are higher than those reported by H i l p e r t (1989), who made a similar computation and found a value of only ≈ 366 species / year.

Local extinction and colonization are normal processes even in stable ecosystems like old beech forests. Therefore, every year there is some degree of species-turnover. In a study on carabid beetles, D e n B o e r (1985) reported turnover rates of up to 8% / year in an old forest habitat and mean survival rates of a species of 10 to 40 years. Hilpert reported immigration rates of 10–15% for the parasitoid fauna in the Bechtal mixed oak forest. D e m p s t e r *et al.* (1995a) reported immigration rates between 9 and 14% per year at patches of flowerheads.

What is the amount of the species-turnover in the Göttingen forest? A comparison of the species numbers per year with the species numbers over several years allows a rough assessment of immigration rates to be made. For this purpose Table 8 compares the numbers derived by the collectors curve in Fig. 2 (derived only from 1981) with the curves in Fig. 3, which are derived by combing several years. Difference in species numbers between these two estimates can have two possible causes: the immigration of species during the study period (7 years and around 16 m^2 area sampled per year) or pronounced structural changes in species composition. In a forthcoming paper (U l r i c h 1998b) I will show that the structural parameters of the populations remained rather constant during the study period. Therefore, the differences in species numbers between one year and

Table 8. Expected number of species per year and expected number during whole time of study. In the middle 16 m² per year were sampled 1981-1987

Area sampled m²	Expected number of species per year	Expected number of species during several years	Expected number of species Difference	Sampling time (16 m² area sampled /	Species turnover / year	Species turnover / year (%)	Total species turnover / yearly (%)
1	48	71	23	1	23	48%	48%
16	230	237	7	1	7	3%	3%
100	376	525	149	6	25	7%	40%
150	406	626	220	9	24	6%	54%
200	427	709	282	13	22	5%	66%
Max. No. species	1184	3178	1994	27	74	6%	168%

Data from collector's curves given in Figs 2 and 3.
The data on maximal species numbers are taken from Fig. 5.

longer periods should largely be caused by locally immigrating species.

Parasitic Hymenoptera have a high colonization ability (Dempster *et al.* 1995a) and the rates obtained in Table 8 reflect this fact. On one m² area the difference is 23 species, on 100 m² area 149 species. The resulting yearly immigration rates are surprisingly constant and range between 3 and 7% with a mean of 6% per year. That the latter number is obtained by a different method sustains the estimate.

This value is slightly lower than the values reported by other authors and is probably the outcome of the more conservative estimation technique. Dempster *et al* (1995b) using radioactive markers found colonization of patches at a distance well over 800 m up to 2.8 km.

Due to density fluctuations, at least 8,5% of the species in the study area reached densities below 1 ind. / 100 m², at least 1.1% abundances below 1 ind. / 300 m². These are densities at which the species run a high risk of extinction. It seems very probable that the yearly extinction rates due to low abundances are in the order of 5 to 10% and therefore range in the same order than the estimated yearly immigration rates.

In their model of species area-relationships Durrett and Levin (1996) obtained a similar result. A balance of immigration and extinction resulted in power functions of the type $S = a x^z$. The slope and intersect, of course depend on the initial settings, that means on the rates of extinction and immigration. In their work on nested species-area relationships, which can be attributed also to the type of collector curves I used, Leitner and Rosenzweig (1997) showed that the slope z is also a function of the abundance of a certain species and the area inhabited. To reveal the exact form of these functions further studies should concentrate on determining the spatial distribution of the species and mean abundance. In the case of the parasitic Hymenoptera more habitats have to be sampled during several years and compared. The resulting species-area-relationships, the abundances and the spatial distribution should result in more detailed theories about the relationship between species turnover and spatial distribution.

Of course, not all species of the middle European fauna colonize a beech

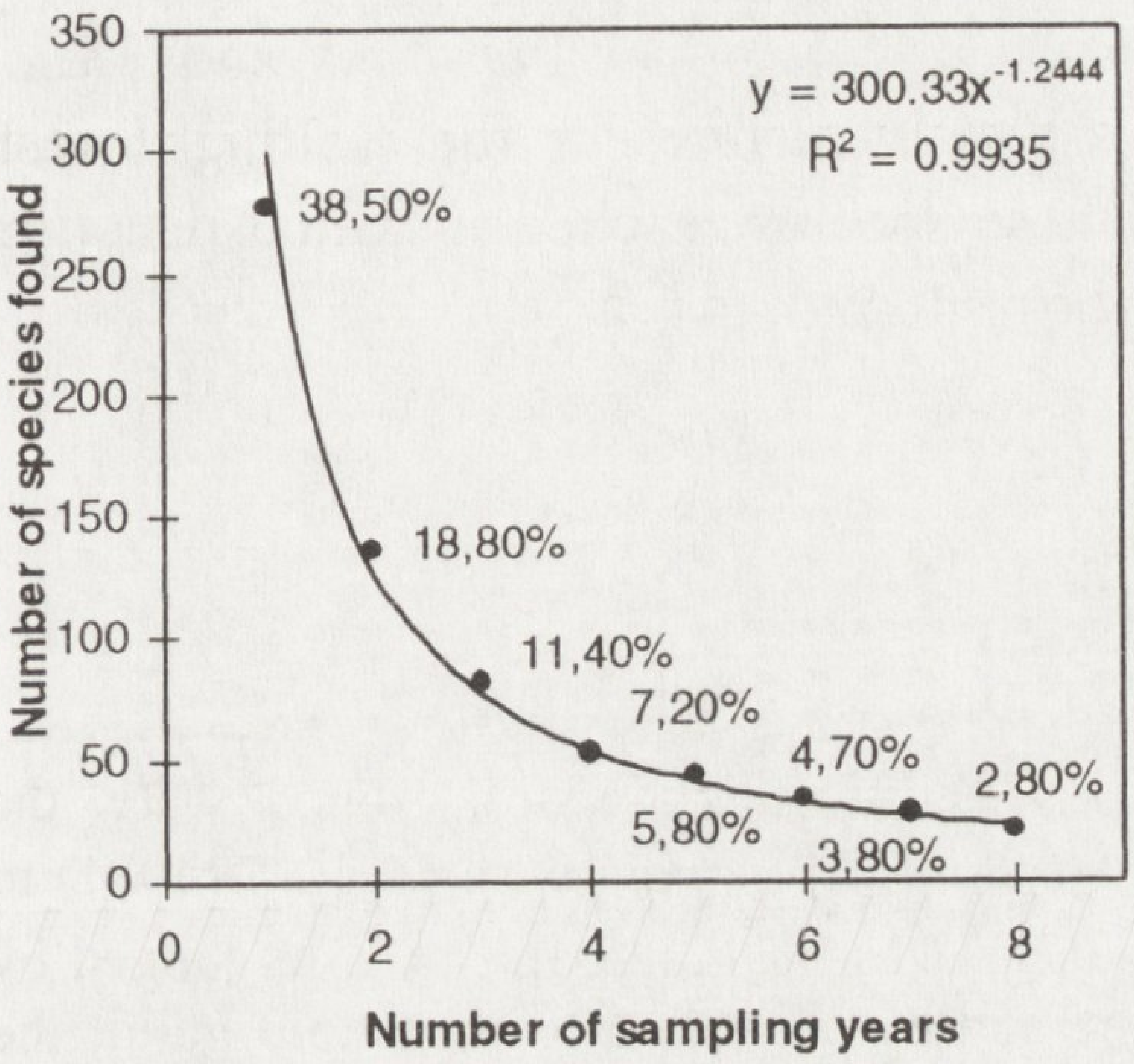


Fig. 7. Number of parasitoid species found in exactly 1, 2,...8 of the sampling years. Given are also the percentages of the total fauna

wood. There is a subset of species, a species pool (Eriksson 1993), which has the potential to colonize the ecosystem beech wood. Limiting factors are mainly the microclimate, available hosts and competitors. That means we can speak of a number of potentially indigenous species, the species who may be found at some time in a certain habitat but are not necessarily found in each year. My data indicate that for the parasitic Hymenoptera these numbers may be extraordinarily high and reach a value up to 3178 species (nearly 1/3 of the total middle European fauna of parasitic Hymenoptera), and that it would take 27 years to list them.

On the other hand there are very few species which are permanent or nearly permanent residents. In the Göttingen forest only 20 species of Hymenoptera (2.8%) were found in all of the study years and 47 species (6.5%) in at least 7 of the years (Fig. 7). Table 2 lists the most important of these species. Fig. 7 also shows that the species numbers found during a period of study can well be described by a power function $S = k\ T^{-a}$. Its form is dependent on the extent of sampling, the species rank order and the yearly species turnover. But is has interesting properties. More sampling-years result in higher values of k due to newly found species. But the slope is roughly constant. An analysis of all combinations of years between 5 and 8 sampling years revealed a maximum value of –1.308 and a minimum value of –1.1018. From functions with these two values one can infer that only between 0.5 to 0.1% of the yearly number of species, that means less than 5 species, can be found in every year in the part of the beech forest under study.

4.2. DENSITIES AND BIOMASS

A comparison of the abundances given in this study with those reported by Thiede (1975) and Hilpert (1989) reveals that the spruce forest studied by Thiede had much lower parasitoid densities than the Göttingen beech forest. The abundances ranged between 66 and 600 ind. $m^{-2}\ a^{-1}$, that is roughly half the value of my beech forest. On the other hand, the oak forest of Hilpert had greater parasitoid densities. He measured values between 410 and 518 ind. $m^{-2}\ a^{-1}$. The spruce forest has the least developed herb layer, the mixed leaf forest the best developed, the Göttingen forest takes the middle position. This points to the explanation that the development of the herb layer greatly affects the densities of parasitic Hymenoptera.

Despite the lower densities of the spruce forest the biomass reported by Thiede equals that of the Göttingen beech forest. The mean biomass of the parasitoids of the Solling forest was 59 ind. $m^{-2}\ a^{-1}$ (68 mg DW $m^{-2}\ a^{-1}$ in the Göttingen forest). The values ranged between 7 and 259 mg

DW m^{-2} a^{-1} (19 to 170 in the Göttingen forest). The reason for this high biomass is the greater percentage of large Ichneumonids (especially *Eusterinx oligomera, Lissonota dubia, Cylloceria melancholica, Campopex cursitans* and *Mesochorus tachypus*) in the Solling forest. These species reached maximal densities above 40 ind. m^{-2} a^{-1}.

5. SUMMARY

Between 1980 and 1987 a beech forest (*Fagus sylvatica*) on limestone near Göttingen (FRG) was studied using ground-photo-eclectors. 720 species of Hymenoptera were detected. 669 of the species were parasitoids, 29 phytophagous Tenthredinidae, Cynipidae and Eurytomidae, 9 ants, 4 vespids and 9 nest-building sphecids, megachilids, andrenids and bumble bees (Table 1). To assess the final number of species, collector's curves (Fig. 2) as well as species/ year-plots were studied (Figs 3, 4, 5). Even after 8 years of sampling a great number of species seems to remain undetected. At the same time, estimations of the frequency of extinction showed that during the sampling period in most of the parasitoid guilds more than 10% of the species reached abundances below 1 ind. / 100 m^2 (Table 3). Species with such low densities run a high risk of local extinction. An estimation of the yearly immigration of species gave values of 6%/ year (Table 8). Less than 1% of the species can be found in every year in the part of the beech wood under study (Fig. 7). The species number appeared to be positively density dependent (Fig. 6).

To compute the biomass of the wasps a regression equation was developed based on the thorax volume of the specimens (Fig. 1): DW (mg) = V (mm^3) 0.52493 (mg/mm^3); r = 0.97; $p < 0.001$.

The densities of the parasitic Hymenoptera ranged between 123 $\pm$ 23 (1981) and 1078 $\pm$ 186 (1984) ind. m^{-2} a^{-1} (Tables 2, 4, 5). The most important groups were the parasitoids of Diptera with 56 $\pm$ 15 (1981) to 936 $\pm$ 164 (1984) ind. m^{-2} a^{-1}. As judged by the sorting according to parasitoid guild, the parasitoids of gall-makers (23 $\pm$ 9 to 880 $\pm$ 163 ind. m^{-2} a^{-1}) and the egg-parasitoids (21 17 to 102 $\pm$ 33 ind. m^{-2} a^{-1}) reached the highest densities. The biomass of the parasitic wasps ranged between 19 $\pm$ 5 (1981) and 170 $\pm$ 92 (1987) mg DW m^{-2} a^{-1} with a mean of 68 mg DW m^{-2} a^{-1} . Compared with other important insect taxa this is a low value.

Quantitative samplings near the tree stems showed normal abundances whereas emergences out of an old dead tree stump were higher (Table 6). But the area around the tree stems were poorer in species (Table 7).

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Appendix . Alphabetical list of the Hymenoptera and the number of individuals (N) collected with photo-eclectors in the Göttingen beech forest near Göttingen (FRG)

Species	N	Species	N	Species	N
?lethades GW1	1	*Anaphes ?diana*	11	*Aphelinus* GW2	1
Acanosema nervosa	2	*Anaphes aries*	14	*Aphelopus holomelas*	75
Achrysocharoides cilla	69	*Anaphes dorcas*	346	*Aphelopus melaleucus*	521
Aclastus micator	166	*Anaphes* GW2	15	*Aphelopus serratus*	179
Aclastus solutus	24	*Anaphes* GW5	1	*Aphidencyrtus* GW1	1
Aclista ?analis	1	*Anaphes* GW6	9	*Aphidius ervi*	3
Aclista ?hämorrhoidalis	2	*Anaphes* GW7	1	*Aphidius* GW1	2
Aclista ?janssoni	1	*Anaphes* GW8	3	*Aphidius* GW2	1
Aclista cantianus	7	*Anaphes longicornis*	141	*Aphidius* GW3	1
Aclista GW1	2	*Ancylocentrus edentatus*	3	*Asaphes suspensus*	1
Aclista GW2	1	*Ancylocentrus* GW2	1	*Asaphes vulgaris*	11
Aclista prolongata	7	*Andrena* GW1	1	*Asobara tabida*	3
Aclista rufopetiolata	2	*Andricus curvator*	11	*Aspilota* GW"2"	1131
Aclista soror	10	*Andricus* GW1	8	*Aspilota* GW1	0
Aclista striolata	9	*Andricus* GW2	1	*Aspilota* GW11	23
Aclista subaequalis	9	*Andricus ostreus*	5	*Aspilota* GW12	0
Acoelius erythronotus	222	*Aneurhynchus longicornis*	4	*Aspilota* GW15	3
Acrolyta GW1	1	*Aneurhynchus ruficornis*	7	*Aspilota* GW16	0
Acrolyta marginata	9	*Anopedias obscurus*	2	*Aspilota* GW17	0
Acrolyta nens	1	*Anteon* GW1	1	*Aspilota* GW19	1
Acropiesta flavipes	21	*Anteris* GW1	1	*Aspilota* GW20	108
Acropiesta GW1	4	*Aoplus castaneus*	1	*Aspilota* GW21	45
Acropiesta GW2	1	*Aoplus ochropis*	39	*Aspilota* GW23	547
Acropiesta macrocera	5	*Aoplus ruficeps*	0	*Aspilota* GW26	1
Acropiesta rufiventris	29	*Apanteles* GW1	9	*Aspilota* GW27	40
Adelognathus GW1	0	*Apanteles* GW2	5	*Aspilota* GW28	8
Ademon GW1	1	*Apanteles* GW3	12	*Aspilota* GW29	2
Aegilips GW1	1	*Apanteles* GW4	7	*Aspilota* GW3	61
Aglaostigma aucupariae	4	*Apanteles* GW5	3	*Aspilota* GW30	3
Agrothereutes abbreviator	1	*Apanteles* GW6	5	*Aspilota* GW31	7
Agrypon flaveolatum	2	*Apechthis quadridentata*	6	*Aspilota* GW32	1
Alaptus GW1	244	*Apechthis rufata*	1	*Aspilota* GW33	1
Aleiodes GW1	2	*Aperileptus* GW1	4	*Aspilota* GW5	312
Aleiodes GW2	2	*Aphaereta tenuicornis*	7	*Aspilota* GW6	0
Aleiodes GW3	2	*Aphanogmus* GW1	101	*Aspilota* GW8	4
Alloea GW1	7	*Aphanogmus* GW10	5	*Astichus arithmeticus*	1
Allotropa mecrida	9	*Aphanogmus* GW11	0	*Astichus maculatus*	1
Alloxysta ?subclavata	3	*Aphanogmus* GW12	2	*Astiphromma strenuum*	1
Alloxysta GW1	1	*Aphanogmus* GW13	2	*Atractodes* GW1	58
Alloxysta victrix	53	*Aphanogmus* GW14	3	*Atractodes* GW2	4
Amblyaspis GW1	2	*Aphanogmus* GW15	1	*Aulogymnus arsames*	3
Amblyaspis GW2	17	*Aphanogmus* GW16	2	*Aulogymnus euedoreschus*	1
Amblyaspis GW3	2	*Aphanogmus* GW17	1	*Basalys abrupta*	169
Amblyaspis nodicornis	52	*Aphanogmus* GW2	7	*Basalys cymocles*	2
Amblyteles armatorius	1	*Aphanogmus* GW3	246	*Basalys parva*	22
Amitus minervae	22	*Aphanogmus* GW4	19	*Basalys pedisequa*	523
Anacharis eucharioides	208	*Aphanogmus* GW5	54	*Basalys singularis*	1
Anacharis immunis	49	*Aphanogmus* GW6	8	*Basalys tripartita*	1
Anagrus atomus	269	*Aphanogmus* GW7	11	*Basalys tuberculata*	1
Anagrus GW1	59	*Aphanogmus* GW8	2	*Bathytrix pellucidator*	33
Anagrus GW2	21	*Aphanogmus* GW9	4	*Batythrix margaretae*	1
Anagrus subfuscus	1	*Aphelinus* GW1	39	*Belyta ?filicornis*	4

Species	N	Species	N	Species	N
Belyta elegans	15	*Chorebus* GW3	1	*Dendrocerus laticeps*	2
Belyta monilineata	2	*Chorebus nerissa*	6	*Dendrocerus serricornis*	1
Belyta quadridens	2	*Chorebus phaedra*	29	*Derostenus gemmeus*	91
Blacus fischeri	10	*Chrysocharis ?laomedon*	69	*Diadegma chrysostictos*	2
Blacus GW1	28	*Chrysocharis acoris*	1	*Diadegma* GW4	7
Blacus GW2	30	*Chrysocharis nephereus*	3	*Diadegma melanius*	3
Blacus humilis	8	*Chrysocharis pilosa*	3	*Diadromus troglodytes*	7
Blacus ruficornis	1	*Chrysocharis prodice*	622	*Diaeretellus ephippium*	59
Blastothrix britannica	1	*Chrysonotomya chlorogast*	15	*Diaeretiella rapae*	65
Blennocampinae GW1	1	*Cidaphus* GW1	1	*Dibrachys cavus*	26
Bombus hortorum	0	*Cinetus ?atriceps*	1	*Dichrogaster aestivalis*	10
Bombus lucorum	0	*Cinetus* GW2	1	*Dichrogaster modesta*	11
Bombus pascuorum	0	*Cinetus* GW3	2	*Dicladocerus* GW1	1
Bombus pratorum	0	*Cinetus monilicornis*	8	*Diglyphus minoeus*	1
Bombus soeroeensis	0	*Cinetus perplexus*	6	*Diospilus rufipes*	1
Bombus terrestris	0	*Cinetus procris*	1	*Dipara petiolata*	2
Bothriothorax GW1	6	*Cirrospilus diallus*	55	*Diphyus palliatorius*	1
Bothriothorax intermedia	22	*Cirrospilus vittatus*	100	*Diplazon laetatorius*	1
Brachyserphus laeviceps	1	*Cleruchus* GW1	721	*Diplazontinae* GW1	2
Bracon GW1	5	*Cleruchus pluteus*	1	*Diplazontinae* GW2	2
Bracon GW2	3	*Coelichneumon desinatorii*	2	*Diplazontinae* GW3	40
Bracon GW3	1	*Colastes braconius*	24	*Diplazontinae* GW4	1
Bracon GW4	1	*Conostigmus* GW1	14	*Disogmus areolator*	37
Braconidae GW3	1	*Conostigmus* GW2	12	*Disogmus basalis*	8
Braconidae GW4	1	*Conostigmus* GW3	19	*Dolerus* GW1	1
Braconidae GW5	0	*Conostigmus* GW4	155	*Dolichovespula saxonica*	0
Campoletis GW1	5	*Conostigmus* GW6	3	*Dolichovespula sylvestris*	0
Campopleginae GW1	2	*Conostigmus* GW7	2	*Doryctinae* GW1	1
Campoplex hercynicus	6	*Conostigmus* GW8	1	*Dusona contumax*	4
Camptoptera aula	2	*Copidosoma* GW1	11	*Dusona oxyacantha*	3
Centistes cuspidatus	4	*Copidosoma* GW2	303	*Dyscritulus* GW1	3
Ceranisus pacuvius	86	*Corynopria solida*	10	*Earinus gloriatorius*	1
Ceraphron GW1	14	*Cratichneumon culex*	25	*Earinus thoracicus*	1
Ceraphron GW10	40	*Cratichneumon dissimilis*	2	*Ecphylus* GW1	1
Ceraphron GW11	14	*Cratichneumon fabricator*	31	*Elachertus inunctus*	2
Ceraphron GW12	1	*Cratichneumon foersteri*	5	*Embolemus antennalis*	1
Ceraphron GW13	6	*Cratichneumon luteiventri:*	1	*Encarsia* GW1	39
Ceraphron GW2	79	*Cratichneumon punctifron.*	4	*Encyrtidae* GW1	1
Ceraphron GW3	14	*Cratichneumon rufifrons*	85	*Encyrtidae* GW2	1
Ceraphron GW4	5	*Cryptoserphus aculeator*	3	*Encyrtidae* GW4	1
Ceraphron GW5	38	*Ctenichneumon funereus*	1	*Encyrtidae* GW5	3
Ceraphron GW6	20	*Cynipidae* GW1	6	*Endasys* GW1	3
Ceraphron GW7	4	*Cyrtogaster vulgaris*	16	*Endasys* GW2	1
Ceraphron GW8	13	*Dacnusa* GW1	2	*Entedon* GW1	123
Ceraphron GW9	2	*Dacnusa* GW2	2	*Entomacis perplexa*	107
Cerobelus jugaeus	8	*Dacnusa laeta*	2	*Entomacis platyptera*	2
Ceroptres arator	2	*Dapsilarthra dictynna*	2	*Ephedrus lacertosus*	329
Charitopes clausus	43	*Dapsilarthra rufiventris*	6	*Epitomus infuscatus*	2
Charitopes gastricus	444	*Dapsilarthra tenuicornis*	2	*Erdoesia tesselata*	7
Charitopes hemerobius	1	*Delopia försteri*	1	*Eretmocerus mundus*	4359
Charmon extensor	25	*Dendrocerus carpenteri*	44	*Eridolius* GW1	1
Charmon GW1	1	*Dendrocerus dubiosus*	14	*Ethelurgus sodalis*	51
Chlorocytus ultonicus	1	*Dendrocerus* GW1	9	*Euceros albitarsus*	1
Chorebus GW1	1	*Dendrocerus halidayi*	1	*Eulophus larvarum*	154
Chorebus GW2	5	*Dendrocerus laevis*	2	*Eumacepolus grahami*	178

Species	N	Species	N	Species	N
Eupelmus urozonus	1	*Holcaeus calligetus*	1	*Mesoneura opaca*	2
Euplectromorpha laeviscui	14	*Holcaeus* GW1	8	*Mesopolobus dubius*	0
Euryproctini GW1	1	*Holcaeus* GW2	3	*Mesopolobus* GW1	388
Eusterinx alpigenus	1	*Holcaeus stenogaster*	4	*Mesopolobus* GW2	1
Eustochus atripennis	613	*Holcopelte* GW1	1	*Mesopolobus* GW3	4
Eustochus GW1	13	*Holcopelte obscura*	12	*Mesopolobus tibialis*	3
Exallonyx ater	93	*Homolobus annulicornis*	9	*Metanopedias lasiopterae*	1
Exallonyx brevicornis	16	*Homotherus varipes*	2	*Metaphycus* GW1	2
Exallonyx longicornis	12	*Hoplocampa minuta*	1	*Meteorus colon*	1
Exallonyx microcerus	40	*Hyperimerus pusillus*	13	*Meteorus jaculator*	3
Exallonyx minor	14	*Hypoponera punctatissima*	0	*Meteorus vexator*	3
Exallonyx quadriceps	230	*Hyposoter citrofrontalis*	0	*Microctonus* GW1	58
Exallonyx subserratus	133	*Hyposoter* GW2	3	*Microctonus* GW2	15
Exallonyx trichomus	109	*Ichneumon albiger*	1	*Microlycus heterocerus*	8
Exallonyx trivoveatus	2	*Ichneumon stramentarius*	8	*Microplitis mediator*	2
Exeristes ?longiseta	2	*Ichneutes reunitor*	1	*Microterys* GW1	23
Exochus GW1	2	*Idiotypa nigriceps*	2	*Monophadnus pallescens*	4
Exotela obscura	1	*Iphitrachelus lar*	3	*Mymar pulchellum*	1
Gastracanthus pulcherrim	16	*Isadelphus inimicus*	4	*Myrmica lobicornis*	1
Gastrancistrus autumnalis	114	*Ismarus dorsiger*	134	*Myrmica rubra*	4
Gastrancistrus GW1	30	*Itoplectis alternans*	5	*Myrmica ruginodis*	2
Gastrancistrus GW2	2	*Kleidotoma* GW1	6	*Necremnus leucarthros*	1
Gastrancistrus GW3	2	*Kleidotoma psiloides*	115	*Nematus fagi*	6
Gastrancistrus GW4	3	*Kleidotoma tetratoma*	3	*Nematus* GW1	5
Gastrancistrus GW6	65	*Labolips innupta*	1	*Netelia* GW2	4
Gastrancistrus walkeri	1129	*Laepserus dentifer*	2	*Netelia latungula*	4
Gelinae GW7	11	*Lagynodes pallidus*	229	*Netelia testacea*	1
Gelis albipalpus	1	*Lasius flavus*	0	*Neurateles* GW1	16
Gelis areator	13	*Lasius mixtus*	7	*Neurateles* GW2	2
Gelis brassicae	2	*Lasius niger*	10	*Neurateles* GW3	1
Gelis GW1	10	*Lasius umbratus*	1	*Neuroterus aprilinus*	1
Gelis GW2	5	*Leiophron basalis*	21	*Neuroterus quercusbaccar*	331
Gelis GW5	3	*Leiophron fascipennis*	28	*Olesicampe* GW1	20
Gelis longicauda	5	*Leptacis tipulae*	4	*Omphale aetius*	115
Gelis sulcata	15	*Leptothorax nylanderi*	1	*Omphale* GW1	85
Glauraspidia microptera	498	*Lissonota biguttata*	4	*Omphale* GW2	463
Glypta GW1	20	*Lissonota* GW1	2	*Omphale* GW5	3
Gnaptodon pumilio	69	*Litus cynipseus*	1679	*Omphale* GW7	8
Gonatocerus litoralis	1	*Mastrus deminuens*	1	*Omphale versicolor*	52
Gregopimpla inquisitor	1	*Mastrus varicoxis*	3	*Ooctonus vulgatus*	8
Gryon GW1	1	*Medophron* GW1	7	*Ophion minutus*	4
Grypocentrus GW1	1	*Megastigmus dorsalis*	3	*Ophion mocsaryi*	3
Fabrocytus GW1	8	*Megastylus cruentator*	53	*Opius caudatus*	2
Habrocytus GW2	1	*Megastylus* GW1	8	*Opius* GW1	7
Habrocytus GW3	1	*Melanips opacus*	37	*Opius* GW2	2
Habronyx GW1	1	*Merismus megapterus*	1	*Opius* GW3	3
Hadrodactylus GW1	1	*Merismus nitidus*	2	*Opius* GW4	2
Halticoptera aenea	4	*Mesochorus* GW1	2	*Opius* GW6	1
Helictes GW1	10	*Mesochorus* GW2	4	*Opius* GW7	1
Helorus ruficornis	3	*Mesochorus* GW3	3	*Opius* GW8	1
Hemigasterini GW1	1	*Mesochorus* GW4	1	*Oresbius* GW1	2
Hemigasterini GW2	1	*Mesoleius aulicus*	6	*Ormyrus rufimanus*	1
Hemiptarsenus fulvicollis	4	*Mesoleius* GW1	3	*Orthizema triannulatum*	1
Hemiptarsenus unguicellus	4	*Mesoleptus* GW1	1	*Orthocentrinae* GW1	8
Hercus fontinalis	19	*Mesoleptus scrutator*	2	*Orthocentrus* GW2	12

Species	N	Species	N	Species	N
Orthocentrus GW3	13	*Phygadeuon* GW4	30	*Pseudodineura parvula*	1
Orthocentrus GW5	24	*Phygadeuon* GW5	17	*Pseudomesocrina* GW1	1
Orthocentrus GW6	14	*Phygadeuon* GW6	17	*Psilus caecutiens*	1
Orthocentrus GW7	1	*Phygadeuon* GW7	1	*Psityrus bohemicus*	0
Orthocentrus GW8	1	*Phygadeuon* GW8	82	*Pteromalidae* GW1	3
Orthocentrus GW9	1	*Phygadeuon* GW9	4	*Pteromalus* GW1	22
Orthostigma GW1	5	*Phygadeuon trichops*	3	*Pteromalus* GW2	6
Orthostigma GW2	11	*Phygadeuon ursini*	797	*Pygostolus sticticus*	24
Osmia rufa	0	*Phymatocera aterrima*	0	*Rhembobius perscrutator*	1
Oxylabis bisulca	2	*Phytodietus* GW1	3	*Rhopalum clavipes*	1
Oxylabis thomsoni	1	*Phytodietus* GW2	2	*Rhyssalus clavator*	85
Oxytorinae GW5	5	*Picrostigeus* GW1	105	*Saphonecrus connatus*	10
Oxytorinae GW8	1	*Picrostigeus* GW3	4	*Scambus* GW1	1
Pachyneuron formosum	15	*Picrostigeus* GW4	5	*Seladerma breve*	10
Pachyneuron grande	1	*Piestopleura flavimanus*	36	*Seladerma* GW1	20
Pachyprotasis rapae	4	*Pimpla* GW1	35	*Selandria serva*	1
Panstenon oxylus	1	*Pimpla melanacrias*	10	*Semiotellus* GW1	1
Pantoclis ?ruralis	1	*Pimpla turionellae*	3	*Skleroceras clavigerum*	6
Pantoclis GW2	1	*Pirene chalybea*	1	*Spalangia erythromera*	3
Pantoclis mese	1	*Pirene conjungens*	1	*Spaniopus amoenus*	24
Pantoclis scotica	1	*Pirene varicoxis*	3	*Spilomicrus ?annulicornis*	1
Pantoclis similis	30	*Platygaster* GW1	126	*Spilomicrus integer*	2
Pantoclis sulcata	1	*Platygaster* GW10	3	*Spudastica robusta*	3
Pantolyta ?GW2	92	*Platygaster* GW11	4	*Stenichneumon culpator*	1
Pantolyta ashmeadi	2	*Platygaster* GW12	1	*Stenomacrus* GW1	58
Pantolyta atrata	4	*Platygaster* GW13	2	*Stenomacrus* GW2	41
Pantolyta GW1	1	*Platygaster* GW2	404	*Stenomacrus* GW3	1
Pantolyta GW5	29	*Platygaster* GW3	4	*Stenomalina gracilis*	7
Pantolyta parvula	4	*Platygaster* GW4	2	*Sterictophora* GW1	3
Paravespula rufa	0	*Platygaster* GW5	5	*Stictomischus* GW1	3
Paravespula vulgaris	0	*Platygaster* GW6	9	*Stilbops vetula*	6
Paroxylabis semirufa	13	*Platygaster GW7*	4	*Stilpnus* GW1	85
Paroxylabis spinifer	0	*Platygaster* GW8	24	*Stilpnus* GW2	3
Pediobius alcaeus	84	*Platygaster* GW9	10	*Sussaba cognata*	1
Pediobius cassidae	2	*Platylabus histrio*	3	*Susteraia acerina*	9
Pediobius foliorum	15	*Plectiscidea* GW1	5	*Sympiesis gordius*	3
Pentapleura GW1	25	*Plectiscidea* GW2	3	*Sympiesis* GW1	1
Peridesmia congrua	2	*Plectiscidea* GW3	1	*Sympiesis sericeicornis*	33
Perilissus sericeus	1	*Plectiscus* GW1	3	*Sympiesis xanthostoma*	9
Peristenus GW1	104	*Pleolophus vestigialis*	4	*Symplecis* GW1	1
Peristenus GW2	121	*Plutothrix scenicus*	10	*Synacra* GW1	1
Phaedroctonus transfuga	64	*Plutothrix trifasciatus*	14	*Synergus albipes*	4
Phaenocarpa GW1	3	*Pnigalio* GW1	1	*Synopeas decurvatus*	1
Phaenocarpa GW2	1	*Pnigalio pectinicornis*	1	*Synopeas* GW1	4174
Phaenocarpa GW3	2	*Pnigalio soemius*	9	*Synopeas* GW2	42
Phaenoglyphis stricta	9	*Polyaulon paradoxus*	19	*Synopeas* GW3	22
Phaenoglyphis villosa	18	*Polynema fumipenne*	26	*Synopeas* GW4	5
Phaneroserphus calcar	34	*Polynema* GW1	1	*Synopeas* GW5	30
Phobocampe crassiuscula	2	*Polynema* GW2	4	*Synopeas* GW6	2
Phobocampe GW1	34	*Praon* GW"1"	41	*Synopeas* GW7	1
Phobocampe GW3	1	*Probles microphtalmus*	1	*Synopeas mamertes*	1
Phygadeuon cheilosiae	5	*Probles nigriventris*	8	*Syntretus* GW1	10
Phygadeuon GW10	2	*Proclitus* GW1	5	*Syntretus* GW2	4
Phygadeuon GW12	1	Proclitus GW2	3	Syntretus GW3	1
Phygadeuon GW3	40	Profenusa GW1	8	Syrrhizus GW1	1

Species	N	Species	N	Species	N
Syrrhizus GW2	1	*Torymus fulgens*	31	*Trioxys bicuspis*	79
Tates heterocera	51	*Torymus* GW1	2	*Trioxys* GW1	4
Telenomus GW1	304	*Torymus persicariae*	37	*Trio* xys GW2	1
Telenomus GW2	2	*Toxares* GW1	0	*Trioxys macroceratus*	7
Teleopterus GW1	1	*Tranosema rostrale*	2	*Trissolcus* GW1	1
Tenthredo bipunctula	1	*Tretoserphus laricis*	9	*Trybliographa melanopter*	23
Tenthredo ferruginea	1	*Trichacis pisis*	23	*Tryphoninae* 1	3
Tenthredo livida	1	*Trichionotus flexorium*	20	*Tyndarichus ?navae*	1
Tenthredopsis annuligera	1	*Trichogramma embryopha*	162	*Woldstedtius flavolineatus*	19
Tenthredopsis litterata	2	*Trichogramma* GW1	3	*Xenomerus ergenna*	13
Tenthredopsis nassata	1	*Trichomalus* GW1	18	*Xestomnaster chrysochlor*	7
Tetramesa longula	8	*Trichomalus* GW2	1	*Xestophanes* GW1	1
Tetrastichus ?charoba	233	*Trichopria aequata*	232	*Xorides securicornis*	6
Tetrastichus brachycerus	2648	*Trichopria cameroni*	14	*Xyalaspis* GW1	2
Tetrastichus fageti	440	*Trichopria evanescens*	103	*Zele deceptor*	5
Tetrastichus GW1	213	*Trichopria* GW2	30	*Zygota claviscapa*	4
Tetrastichus GW2	7	*Trichopria inermis*	1	*Zygota ruficornis*	30
Tetrastichus GW3	3	*Trichosteresis glabra*	1		
Tetrastichus GW4	13	*Triclistus* GW1	1		
Tetrastichus GW5	1	*Trimorus* GW1	16		
Tetrastichus intermedius	11	*Trimorus* GW2	7		
Tetrastichus luteus	392	*Trimorus* GW3	1		
Thriptoctenoides gaussi	2	*Trimorus* GW4	1		
Thymaris contaminatus	1	*Trimorus* GW5	1		
Torymidae GW1	1	*Trimorus* GW6	2		
Torymus auratus	0	*Trimorus* GW7	1		

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