To make a meadow it takes a clover and a bee: the entomophilous flora of N.W. Europe and its insects

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Abstract

An analysis of the anthophilous fauna of N.W. Europe is presented, stressing the role plants play for insects. The study is based on some 29,000 relations between about 2,600 insect species and 1,300 plant species (569 genera). The data are derived from our database ("CrypTra") of biotic relations between Cryptobiota and Tracheophyta, that is based on published sources.

It is suggested that a ratio of 2 to 5 anthophilous insect species per entomophilous plant species is the rule in N.W. Europe, where other types of zoophily are virtually absent.

A small minority of the plant species/genera play a disproportionally important role as hosts to flower visitors; many of these so-called cornucopian taxa belong to the commonest entomophilous plants in the region, and occur also in moderately disturbed habitats.

There is a significant positive correlation between the commonness of a plant species and the fraction this plant represents of the trophic resources exploited by an insect species. There is, on the other hand, a significant negative correlation between the number of insect species visiting a given plant species, and the number of plant species visited by a given insect species. These two elements together demonstrate that the anthophilous fauna and the entomophilous flora of N.W. Europe as a whole form a loose system, not predominantly characterised by specialisation.

In accordance with this, factor analysis suggests that there is no ground to recognise more than three visitor types, viz., the allotropous, hemitropous, and eutropous visitors as defined by Loew. A minority of the plant taxa — essentially the cornucopian ones — can with some difficulty be associated with these three types of visitors, and a very few narrowly specialised plant taxa can be associated with more specific visitor groups. However, the large majority of plants cannot be fitted in any typology.

These results have practical implications for the nature management of the anthophilous fauna, in that the important role of the cornucopian floral element is underlined. The fact that the majority of the cornucopian species are perennial, or even woody, places constraints to agricultural practices intended to foster beneficial anthophilous insects.

Résumé

Est présentée une analyse de la faune anthophile d'Europe du nord-ouest, soulignant le rôle joué par les plantes pour les insectes. L'étude est basée sur environ 29.000 relations entre environ 2.600 espèces d'insectes et 1.300 espèces de plantes appartenant à 569 genres. Les données sont dérivées du database élaboré par les auteurs ("CrypTra") des relations biotiques entre Cryptobiontes et Tracheophytes, database s'appuyant sur des sources publiés.

On suggère que le rapport 2 à 5 insectes anthophiles par espèce végétale entomophile est de règle en Europe du nord-ouest (où d'autres types de zoophilie sont pratiquement absents).

Une faible minorité d'espèces et genres de plantes joue un rôle démesurément important en tant qu'hôtes des visiteurs des fleurs; beaucoup de ces "taxons cornucopiens" sont parmi les plantes entomophiles les plus communes de la région, présentes aussi dans des habitats modérément modifiés.

Il y a une corrélation positive significative entre l'ubiquité d'une espèce végétale et la fraction représentée par cette plante dans l'ensemble des ressources trophiques exploitées par une espèce d'insectes. Il y a, d'autre part, une corrélation négative significative entre nombre d'espèces d'insectes fréquentant une certaine espèce végétale, et nombre d'espèces de plantes fréquentées par une certaine espèce d'insectes. L'ensemble de ces deux éléments démontre que la faune anthophile et la flore entomophile d'Europe du nord-ouest forment un système lâche qui n'est pas caractérisé en premier lieu par la spécialisation.

En concordance avec ceci, l'analyse factorielle suggère qu'il n'y a pas lieu de reconnaître plus de trois types de visiteurs, à savoir les visiteurs allotropes, hemitropes et eutropes — tels qu'ils ont été définis par Loew. Une minorité de taxons végétaux (essentiellement espèces cornucopiennes) peut être associée, avec une certaine difficulté, à ces trois types de visiteurs, tandis que très peu de taxons végétaux étroitement spécialisés peuvent être associés à des groupes plus spécifiques de visiteurs. Cependant, il est impossible de ranger la grande majorité des plantes dans une certaine typologie.

Ces résultats ont des implications pratiques pour la gestion naturelle de la faune anthophile, le rôle important des éléments

floristiques cornucopiens dans ce domaine étant souligné. Le fait que la majorité des espèces cornucopiennes sont vivaces ou même ligneuses, pose certaines contraintes aux procédés agricoles ayant pour but la protection des insectes anthophiles utiles.

Motto

Die Schirmblumen

.... Denn diese Saftdrüse ist zugleich die Saftbehalter. Da nun der auf derselben befindliche Saft an der freyen Luft liegt, und durch nichts gedeckt wird, so scheint derselbe von dem Regen keineswegs geschützt zu seyn. Allein erstens ist derselbe nicht eigentlich für Bienen und Hummeln bestimmt, welche in Ansehung des Safts sehr ekel sind, und einen mit Regenwasser vermischten Saft verschmähen, da sie sich aus andern Blumen einen solchen Saft zu verschaffen wissen, der schlechterdings nicht vom Regen verdorben werden kann. Sondern derselbe ist hauptsächlich für Fliegen und andere unedlere Insekten bestimmt. Weil diese zu dumm sind, um den in andern Blumen tief versteckten und vor dem Regen völlig gesicherten Saft ausfindig zu machen; so haben sie keinen so feinen Geschmack, als die Bienen und Hummeln, sind in der Wahl desselben nicht so ekel, sondern nehmen auch mit einem durch den Regen verdorbenen Saft vorlieb. ...

C.K. Sprengel, 1793:154.

Introduction

The study of the relation between flowers and their visitors has a long tradition. Precisely 200 years ago, Christian Konrad Sprengel (1793) published his now famous book "Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen", in which he single-handedly laid down the foundations of pollination biology. This major contribution has been amply celebrated in 1893 (references in Knuth, 1893, 1898–1905) and in 1993 too there will be held at least two commemorative symposia. Sprengel's main discovery was the mutual adaptation of flowers and their pollinators (Faegri & Van der Pijl, 1979; Meeuse & Morris, 1984).

A century after Sprengel a number of workers tried, with admirable perseverance but with the limited computational tools of their time, to establish quantitatively the thesis that Sprengel had formulated qualitatively. The studies of Müller (1873–1881), De Vries (1875), Heinsius (1892), Knuth (1892–1905), Willis & Burkill (1895–1908), to mention the most important ones, brought together a wealth of factual information that awaited analysis for another century.

One more researcher is worthy of mention, viz. Julius Mac Leod. Of his studies on the anthecology of the Kempen region in Belgium, the first part appeared precisely one century ago. Mac Leod (1893–1894) wrote this masterpiece of observation and analysis because he was convinced that only a detailed, regional, study of, on the one hand, the visitors, their morphology and ethology, and on the other, the flowers with their morphology and physiology would enable a definite explanation of the functionality of flowers and their diversity. Essentially, these two papers form the documentation of an earlier one (Mac Leod, 1889) in which he introduced an innovative (Van Paemel, 1992) method in botany, which in retrospect can best be described as a graphical anova, to analyse the Belgian anthophilous fauna. Mac Leod's "graphical method" was later applied by Loew (1890) and Heinsius (1892).

We present Mac Leod's (1893, 1894) data, together with the often less detailed observations of other authors, to study the quantitative relation between the floral assemblage of N.W. Europe and the diversity of its anthophilous fauna. Such a broad-based approach was chosen, because present-day anthecology is mainly directed to individual plant species that are particularly suited to unravelling specific problems. As a result, the large majority of plants which are unspecialised has received little attention. This leaves an ecologist or conservationist with no other option to support a predictive statement, than to resort to traditional typologies to register a plant as a "fly flower", "bee flower", or, vaguest of all, "beetle flower" (Kugler, 1970; Van der Pijl, 1961). This is exacerbated by the fact that supposedly inefficient pollinators, like Coleoptera and Acalyptrata, have received comparatively little attention from modern anthecology (but see e.g. Brncic, 1966; Gottsberger, 1977; Kugler, 1951, 1984; Sabrosky, 1987).

Pollination biology by its very nature concen-

trates on the role insects and other vectors play in the pollination of plants. That alternatively flowers play an important, often crucial, role in the existence of insects has been studied less often in such detail (and then mostly for bees: cf. Magers, 1970; Pellet, 1976; Probst, 1983; Westrich, 1989; but see e.g. Jervis et al., 1993; Weiss & Stettmer, 1991). Moreover, pollination biology is not often studied at a community or regional level (but see e.g. Kalin Arroyo et al., 1982; Holm, 1988; Kevan, 1972, 1973; Kevan & Baker, 1983; Kevan et al., in press; Kratochwil, 1984; Moldenke, 1976, 1979; Petanidou, 1991; Petanidou & Ellis, 1993; Ramirez & Brito, 1992; Whitehead et al., 1987).

In this paper we intend to provide a quantitative estimate of the diversity of the anthophilous fauna and its floral counterpart at a regional scale as wide as N.W. Europe, and secondly to explore the numerical patterns in the diversity of the one and the other, all the while concentrating on the insect side of the relationship. In this connection, we want to investigate whether or not it is possible to distinguish, within the flora of this region, clusters of species or genera based on the visiting pattern of the anthophilous fauna. If such clusters exist, the analyses allow predictions at the ecosystem level that have both scientific and practical value. Up to now, the existence of such clusters has, to our knowledge, not been verified, although their reality is implied by the functional classifications of floral morphologies, starting from the work of Delpino (1868–1875, summarised in Loew, 1895) and Müller (1881b), and extending to the present time (e.g. Faegri & Van der Pijl, 1979; Kugler, 1970; B.J.D. Meeuse, 1961; Proctor & Yeo, 1973).

Apart from providing some quantitative insight, the present data set enables to address two pairs of alternative hypotheses. Both revolve around a common pivot, viz. the degree to which the anthophilous fauna of N.W. Europe as a whole, together with its host flora, may be considered as a specialised system. Specialisation in this connection need not necessarily be understood as morphological and/or ethological, but may just as well be ecological or phenological. We will assume that, at least in a statistical sense, eventual specialisation will be manifest mostly in rare organisms.

The first pair of alternatives tests whether the anthophilous fauna as a whole can be regarded as specialised. It may be reasoned that common plant species receive more visitors, both by numbers of species and individuals of anthophiles, than rare ones, because common plants are more frequently encountered and are easily memorised as a search image. Now, if even rare insects were unspecialised flower visitors, they would predominantly be expected on common plants, while common insects should be expected mostly on common, and sometimes on rare plants. On the other hand, if rare insects were specialised visitors indeed, one might expect them to visit mainly rare (also specialised) plants and to find common insects mostly on common plants.

Unfortunately, we have no consistent data on the rarity of the insects, but on that of the plants we are somewhat better informed. Therefore, it is not possible to correlate directly plant rarity with insect rarity. The possibility remains, though, to correlate plants' rarities with the plants' importance for the anthophilous fauna; importance here being expressed as the share a plant species takes in the resources exploited by a given insect species. Under the assumption of a general predominance of insect specialisation, one would expect rare plants to have a great importance because they occupy a large fraction of the niche of their visitors; under the opposite assumption the importance of rare plants would be very low, not only because they are visited by a few insect species, but also because they occupy no more than a small fraction of the total niche width of these insects. In short, a specialised visitor fauna would imply a negative correlation between plant commonness and importance, an unspecialised fauna a positive correlation.

A second pair of hypotheses tests the specialisation of the entomophilous flora as a whole. It relates the number of insect visitor species recorded for a given plant, and the number of plant host species for which visits by a particular insect species have been recorded.

In the absence of specialisation at either side, one would expect rare plants to be visited by a few insect species that are sufficiently common to accidentally

find them, and that for that same reason have a large number of host plants. Alternatively, if the flora were specialised, rare plant species would receive a small number of specialised insects, themselves visiting a few plant species only. Although the distinction between the alternatives would fade away in the common plants, one might expect a positive correlation between the numbers of visitor and host species in the case of specialisation, and a negative correlation in the opposite case.

Methods

Definitions

For the purpose of this paper we need to give a precise circumscription of a few terms:

Relation: a conceptual link between a visitor species and a plant species (or genus). This link is established by at least one observation of an actual flower visit.

Presence: degree of dependence of a visitor species on a plant species, within the context of anthecology. Note that this does not imply that the plant is similarly, let alone equally, dependent on the insect species. The numerical notation will be explained below.

Importance: the fraction a plant species (genus) represents of the flower-related resources exploited by an insect species, or group of insect species.

The database

General description

The data upon which the present study is based are extracted from our database ("CrypTra") of biotic associations between cryptobiota[1] and Tracheophyta in N.W. Europe.

This database, that is based entirely on published sources, covers the geographical area from southern Scandinavia to the river Loire, and from Ireland through Germany. Data from mountain areas (> 1000 m alt.) are not included.

About 1,350 publications have been extracted so far, many of them relevant to the present paper. A selection of the most important titles is given in the references. (The well-known handbook of Knuth, 1898–1905, is not used as a source, because it is a compilation of what is available with more precision in his

[1]Cryptobiota comprises the total of the (terrestrial) invertebrate fauna and cryptogamous flora. The majority of the members of this assemblage are relatively small and short-lived, have a cryptic way of life, and population dynamics that tend to be chaotic. In general, they are poorly known taxonomically, and are little, if at all, appreciated by conservationists and by the general public.

original sources). Of the approximately 70,000 general relations covered by the database, over 29,000 are of an anthecological nature.

To be included in the database, references to insect taxa should be down to the species level, but references to plants may also be at the generic and family level. For the present study, relations concerning plant families are not taken into consideration. Relations concerning cultivated plants (both agricultural or ornamental plants) are not a priori excluded, provided that they do not concern plants grown indoors. The reason for this is twofold, a) the difficult distinction between cultivated, escaped, and fully naturalised exotic plants, and b) the fact that even cultivated or escaped species which persist only through human influence may play an important role in the ecology of the suburban landscape (Corbet & Westgarth-Smith, 1992; Jacob-Remacle, 1989a, b; Owen & Owen, 1975; Owen, 1978a, b).

All identifications have been accepted at face value (nomenclatural changes taken into consideration), even in those cases where modern taxonomy has split up an old species. In some cases such a procedure leads to an underestimation of the number of relations of certain insect species, like *Bombus lucorum* (Linnaeus), in older literature always confounded with *B. terrestris* (Linnaeus). An exception was made in the case of the ubiquitous *Rhingia campestris* Meigen. Prior to 1920 this species was generally confounded with the rare *R. rostrata* (Linnaeus) (Drabble & Drabble, 1927). For this reason, all old citations were referred to *R. campestris*, unless explicit information to the contrary is given.

Because this paper primarily concerns the role plants play for the insects, we have not considered the pollination effectiveness of the insect visits. Cases of, e.g., nectar robbing (Inouye, 1983) are included as genuine flower visits (although notes on the behaviour of the visitor, when at all described in the literature, have been kept in the database).

However, we have narrowed the concept of flower visitors to those species that primarily use the resources offered by the plants as floral rewards (or decoys of such rewards). The few records in the literature concerning flower visits by snails or spiders (mostly Thomisidae and Salticidae) therefore were not taken into consideration. Neither are the much more numerous references to flower-dwelling larvae, like that of many Tephritidae, Geometridae, or Gelechiidae that feed on floral tissues, preferably the developing ovaria, rather than on pollen or nectar.

Nomenclature

Nomenclature for wild and naturalised plant taxa occurring in the Netherlands is based on Van der Meijden et al. (1990); for plants not occurring in the Netherlands, the Flora Europaea (Tutin et al., 1964–1983) was used, and for cultivated plants we refer to Boom (1959, 1975). For insects, various nomenclators and checklists were used, the most important ones being the lists of Aukema (1989), Kloet & Hincks (1964–1978), Lempke (1976), and the Catalogue of the Diptera of Belgium (Grootaert et al., 1991).

Insect names of the type "*Bracon* sp. *C*", and the relations based on them, are disregarded.

The names of 94 insect species mentioned in the literature could either not be found in any checklist, or could not be interpreted without ambiguity. The 210 relations connected with these names are not taken into account.

Numerical notation of the presence

Generally, the published sources give little information from which to derive a numerical estimate of the presence. Indications, when available, are recorded in the database. Both statements about the constancy, selectivity, oligotrophy etc. and about the visitation rate and abundance of the visiting species are taken into account.

Explicit references to high density or selectivity score a 2. When no indication of either was given, a default score of 1 was attributed. A relation described as occasional, etc. scores a value < 1.

Obviously, this system of scoring is subjective and prone to errors of judgement. It is of relevance, therefore, to point to the fact that these scores play a role only in the estimation of the pattern of distribution of a single insect species over its various plant hosts. The presence plays no role in the comparison between visitors or visitor categories.

Other pollination modes

Apart from anemophily and a few cases of hydrophily, the flora of N.W. Europe knows no other pollination mode but entomophily. Allegedly anemophilous or ambophilous (Stelleman, 1984) plant taxa were not a priori excluded by us.

Visitor categories

For the present study, we segregated the anthophilous entomofauna into 13 categories; they are listed below, preceded by the abbreviations that are used for them in the graphs and tables. The categories mentioned in quotes are obviously paraphyletic or polyphyletic.

RHO Rhopalocera
LEP "Lepidoptera" (Lepidoptera minus Rhopalocera)
API Apidae
APO "Apoidea" (Apoidea minus Apidae)
SYM Symphyta
ACU "Aculeata" (Aculeata minus Apoidea)
PAR "Parasitica" (Hymenoptera Apocrita minus Aculeata)
DIP "Diptera" (Nematocera + Acalyptrata + Phoridae)
CAL Calyptrata
BRA Brachycera
SYR Syrphidae
COL Coleoptera
REM Remaining visitor groups (mostly Heteroptera, but also some Mecoptera, Neuroptera, Dermaptera, etc.)

Plant rarity

Data on plant rarity for N.W. Europe as a whole are not available. As an estimate we used the data provided by the Botanical Database (1991) of the flora of the Netherlands. Because of the central position of the Netherlands, the majority of the N.W. European flora is represented in this database; records concerning plants from the periphery of the area had to be left out of some computations. From the available options we chose the species frequency classes as estimated from the oldest date (viz. 1900), because a large share of the data upon which our conclusions are based are at least that old. The rarity is expressed on a logarithmic scale from 0 to 9, based on the number of 5 × 5 km squares in the Netherlands from which the species has been recorded; the scale runs as follows:

0: 0,
1: 1−3,
2: 4−10,
3: 11−29,
4: 30−79,
5: 80−189,
6: 190−410,
7: 411−710,
8: 711−1210,
9: 1211−1677 squares.

For the purpose of an anova, the scale was condensed to five values i–v, by combining successive pairs of this scale. These rarity values will be referred to below as HSF (for "hour square frequency").

Flower parameters

As far as possible, we noted for the plant species in the database the flower colour and type of nectar accessibility (referred to further down as flower type). Data were derived from different sources, mainly regional floras and Mac Leod (1893–1894), Loew (1894), Teräs (1985), and the Botanical Database (1991).

Flower colour was noted in seven categories (as perceived by the human eye): blue, green (including transparent and brown), pink, purple, red, white, and yellow (including orange). It should be noted, however, that flower colours are difficult to fit into a tight scheme, as is evident from the various colours attributed to the same plant in different publications.

Five flower types were recognised, viz., in the conventional notation of Müller (1881b): A (flowers with fully accessible nectar), AB (with partly hidden nectar), B (with fully hidden nectar), B' (do., but flowers aggregated in capitula) and Po (flowers having no nectar). Flowers labelled in the literature as butterfly, or bee/bumblebee flowers were simply scored as "B", in order not to influence the results. It is customary to distinguish between entomophilous plants having pollen as a reward, and anemophilous plants; but it was not relevant to make this distinction here because for a visiting insect they are rather similar — both were recorded as "Po".

Plant genera, plant species

The analysis was made at two levels referring to the taxonomic level of the plant part of the relationships (as was already remarked above, all insects are identified down to the species level, but plants may be identified either to the species or to the generic level).

Before an analysis at the species level could proceed, all rela-

tions in which the plants were only known as (e.g.) *Ranunculus* sp. were deleted.

Alternatively, for an analysis at the generic level all duplicate species had to be removed; e.g., the three relations *Eristalis tenax-Ranunculus acris*, *E. tenax-R. bulbosus*, and *E. tenax-R.* sp. were collapsed to only one: *Eristalis tenax-Ranunculus*. When the relation is studied between insect species and plant genera, the maximal presence registered for any of the included plant species was taken as the score for a genus.

Parameters
insects

H_i: the number of plant species (genera) that serve as a host to insect species i.

P_{ip}: numerical estimate of the presence of insect species i on plant species (genus) p. The absence of a relation between an insect and a plant may algebraically be understood as a relation with a $P = 0$. (Where P is used to denote probability, this will be clear from the context.)

N_i: summation of P_{ip} for all plant species (genera) p with which insect species i is associated. N_i gives an indication of the niche width of an insect, as far as it concerns its relation to flowers.

plants

V_p: the number of insect species visiting plant species (genus) p.

s_{ip} = P_{ip}/N_i; this value estimates the importance a plant species (genus) p has for insect species i, in that it expresses the fraction a plant occupies of the insect's niche width.

S_p: summation of s_{ip} over all insect species $1..i$ that visit a plant species (genus) p; i may either comprise all insects visiting the plant taxon (S_p^t), or all insect species of a particular subset ("category") of its visitors (S_p^c). A value of $S_p = x$ may, by a rough approximation, be interpreted as the prerequisite for existence of x insect species. Note that, because of the different ways relations are filtered out in the computations based on plant species, and plant genera, S_p for a plant species and an associated plant genus will somewhat differ, even if the plant genus contains but one species. Further down we also refer loosely to S as "total importance".

z_p: z-transform of S_p: from each value of S_p the mean value (calculated over all plant species (genera) $1..p$) is substracted, and divided by the standard deviation; z may also be calculated over a summation of S-values, like z_p^{EU}, which is the z-transform of the S-values of a group of categories. The advantage of the z-transformation is that the effect of the number of insect species per category on S_p^c is removed.

Z_p: summation of z_p over all visitors (Z_p^t), or all visitors of a particular category (Z_p^c). We will use "relative importance" as an informal synonym of Z.

Data analysis
Factor analysis and statistical tests were run under the program Statistica/Mac; Kaleidagraph and MacSpin were used for visual inspection by graphing and rotation of data points. CrypTra is run under FileMaker Pro.

Results

General data

We have data on 1328 plant species (569 genera, 105 families). Table I shows a steep decline in number of visitors from the top three families (Umbelliferae, Compositae, and Rosaceae) down. This decline correlates generally with the number of species and genera per plant family, but there are striking deviations, especially when attention is given to the individual categories.

In Table II, giving the number of anthophilous species by family, the large number of families in the Coleoptera and Diptera (especially Acalyptrata) is noteworthy. This partly is an artefact of systematics, but also a reflection of the large number of anthophilous species, in particular in the Coleoptera.

To allow the reader to evaluate how the available information is distributed over the categories, Table III shows the number of relations and the number of associated plant species and genera, both when attention is focused on the plant genera, and when the analysis descends to the level of plant species.

Total and relative importance (S^c and Z^t)

The plant genera with the highest relative importance (Z^t) are given in Table IV, along with the total importances for the 13 categories (S^c) and the overall total importance (S^t); this is summarised in Table V for the twelve plant families with the highest number of genera. Similar data for the most important plant species are given in Table VI, that in addition gives the number of visitors (V_p), rarity (HSF), the flower colour and the flower type; the meaning of the columns z^{EU}, z^{AL}, and z^{HE} is explained below.

To verify the relevance of the values of the importance of the categories, we made an anova with repeated measures over the 13 categories, using both the raw data (S^c) and the standardised values (Z^c), and for both the complete data set and the two subsets (plant taxa with $Z^t > 0$ and with $Z^t < 0$). All calculations were made both for plant genera and plant species. In all cases the significance is very high ($P < 0.000000$).

Table I. The plant families with the highest total number of visiting insect species. Given are the number of visiting species per category (RHO ... REM) and the total, as well as, in the first two columns, the number of plant genera and species for which information is available. (Table arranged in descending order of the total number of visiting species.) Based upon the results of our analysis (see text), the categories are divided in three groups, viz. eutropous, allotropous, and hemitropous insects. These groups are separated by dotted lines.

plant family	gen.	sp.	RHO	LEP	API	APO	SYM	ACU	PAR	DIP	CAL	BRA	SYR	COL	REM	total
Umbelliferae	36	54	60	31	9	131	34	121	156	68	110	48	227	171	6	1081
Compositae	73	205	110	178	27	280	8	66	21	38	88	44	193	146	14	925
Rosaceae	23	77	71	47	19	198	6	49	5	26	47	37	231	216	2	836
Ranunculaceae	16	48	47	18	8	97	5	13	5	17	45	33	200	63	3	489
Labiatae	28	94	91	65	28	148		17	2	17	35	12	73	44	2	378
Cruciferae	41	72	41	39	10	110	3	13	2	16	23	17	121	46	3	364
Leguminosae	29	83	93	50	29	175		14		10	14	4	32	48	1	327
Salicaceae	2	15	16	37	9	109	8	7	1	18	21	11	94	22	2	302
Caryophyllaceae	19	58	52	111	15	75	3	13	6	14	29	17	75	19	1	267
Campanulaceae	4	19	35	12	14	133		23		7	21	5	41	15	1	260
Scrophulariaceae	15	58	39	16	23	105		16		6	19	13	47	18		247
Ericaceae	6	11	41	28	24	78		15		6	18	5	67	5	8	226
Dipsacaceae	6	17	75	31	27	77		7		3	18	7	56	22		217
Boraginaceae	14	29	57	27	22	98		4		7	11	4	48	14		208
Euphorbiaceae	2	11	16	4	3	38	4	11	2	4	6	3	96	22	3	192
Caprifoliaceae	7	14	39	42	8	11	1	11	2		3	5	80	46		167
Rubiaceae	4	14	27	8	2	8	3	6	5	9	22	12	51	36	1	155
Liliaceae	18	43	30	31	7	54		5		2	9	3	70	4		154
Geraniaceae	3	16	35	9	7	60		6		4	17	6	40	12		152
Saxifragaceae	10	18	13	31	9	39	2	9	1	11	12	3	34	24	1	145
Onagraceae	5	17	31	39	15	38	1	8		1	6	5	44	5	2	125
Valerianaceae	4	9	45	22	4	17	1	1	3	5	18	11	48	13	1	122
Convolvulaceae	3	6	18	3	5	27		4	14	3	5	3	45	6	2	114
Crassulaceae	3	11	34	3	6	56	1	2			10	2	30	3		110
Guttiferae	1	8	15	3	8	24		1			7	5	53	3		101
Polygonaceae	4	17	21	10	3	17	2	6		5	13	4	41	7		98
Rhamnaceae	2	3	17	3	7	28		29		1		1	25	6		97
Papaveraceae	8	14	4	2	12	30		1		2	1	3	36	6	1	92
Cornaceae	1	5	13			11		1			3	1	34	38		88
Primulaceae	7	20	11	1	11	17		5		3	6	9	20	9		80
Cistaceae	1	2	13	1	6	38					6		16	13		79
Resedaceae	1	4	4	1	2	34		8		1			16	8		69
Malvaceae	4	7	7	2	8	44		2		1		2	5	5	1	68
Violaceae	1	11	25	5	15	17		4		2	14	3	10	2		67
Lythraceae	1	3	43	3	12	23					1		25	1		62
Plantaginaceae	1	4	9		4	19		1			2	1	28	6		61
Orchidaceae	11	20	26	5	10	8	1	4	5	1	7	2	17	3		58
Oleaceae	5	9	34	56	5	12					5	3	20	10		55
Berberidaceae	2	2		2	3	15		3		1	4		23	4		53
Gramineae	23	28	1	1		3			2	1	6		29	11	1	53
Plumbaginaceae	4	7	25	3	8	14				2	8	2	11	2	1	48
Rutaceae	3	3			2	5		13	2		10	2	12			46
Aceraceae	1	3		6	6	26				1			6	5		44
Araliaceae	1	1	7	1	1	1		5	1	4	13		15	1		41
Tiliaceae	1	6	17	30	9	3		8			3	1	7	4		35
Solanaceae	9	16	4	8	9	12				1	1		9			32
Celastraceae	1	1				1				1	7		17	3		29
Gentianaceae	3	5	10	4	9	3					2	1	13			28
Balsaminaceae	1	4	6	1	5	1		1				1	17	2		27
Alismataceae	3	3				2		1			5		18			26
Cyperaceae	3	10			2	1					1		20	3		25
Cucurbitaceae	3	4	3		1	12		3				1	5	1		23
Asclepiadaceae	2	3	2	5	5	5		4			1	1	6			22
Hydrophyllaceae	2	2	6	1	5	4							11	2		22

Table II. Composition of the anthophilous entomofauna with the number of species per family (or group of families, when the number of species/family < 5). Group totals are printed in bold type.

categories / families	N.sp.
Rhopalocera	**116**
Lycaenidae	38
Nymphalidae	32
Satyridae	18
Hesperiidae	12
Pieridae	12
Danaidae, Nemeobiidae, Papilionidae	4
Lepidoptera	**377**
Noctuidae	183
Geometridae	94
Pyralidae	19
Arctiidae	13
Zygaenidae	16
Sphingidae	12
Sesiidae	9
Tortricidae	7
Incurvariidae	5
Micropterigidae	5
Glyphipterigidae, Hepialidae, Lymantriidae, Nolidae, Oecophoridae, Pterophoridae, Scythridiidae, Thyridiidae, Yponomeutidae	14
Apidae	**30**
Apidae	30
Apoidea	**351**
Andrenidae	92
Halictidae	83
Megachilidae	68
Anthophoridae	67
Colletidae	32
Melittidae	9
Symphyta	**48**
Tenthredinidae	36
Argidae	7
Cephidae, Cimbicidae	5
Aculeata	**193**
Sphecidae	85
Pompilidae	34
Eumenidae	29
Formicidae	15
Chrysididae	13
Vespidae	10
Mutillidae, Sapygidae, Scoliidae, Tiphiidae	7
Parasitica	**186**
Ichneumonidae	68
Eulophidae	49
Pteromalidae	34
Eurytomidae	7
Braconidae	6
Eucoilidae	6
Aphidiidae, Cynipidae, Encyrtidae, Eupelmidae, Figitidae, Gasteruptiidae, Leucospididae, Proctotrupidae, Pteromalidae	16
Diptera	**156**
Conopidae	20
Sphaeroceridae	18
Sepsidae	13
Bibionidae	11
Tipulidae	11
Chloropidae	9

Ephydridae	7
Tephritidae	7
Lauxaniidae	6
Sciomyzidae	5
Agromyzidae, Anisopodidae, Ceratopogonidae, Chironomidae, Coelopidae, Culicidae, Drosophilidae, Dryomyzidae, Helcomyzidae, Heleomyzidae, Lonchaeidae, Micropezidae, Milichiidae, Mycetophilidae, Opomyzidae, Otitidae, Piophilidae, Platystomatidae, Phoridae, Psilidae, Psychodidae, Ptychopteridae, Scatopsidae, Sciaridae, Thaumaleidae	49
Calyptrata	**166**
Muscidae	61
Tachinidae	44
Anthomyiidae	24
Calliphoridae	12
Sarcophagidae	10
Scathophagidae	6
Fanniidae, Rhinophoridae	9
Brachycera	**107**
Empididae	52
Stratiomyidae	15
Bombyliidae	11
Dolichopodidae	11
Tabanidae	7
Rhagionidae	5
Asilidae, Lonchopteridae, Therevidae	6
Syrphidae	**315**
Syrphidae	315
Coleoptera	**502**
Cerambycidae	68
Nitidulidae	67
Chrysomelidae	47
Curculionidae	29
Mordellidae	26
Staphylinidae	25
Elateridae	23
Bruchidae	21
Melyridae	20
Scarabaeidae	19
Oedemeridae	17
Scraptiidae	17
Cantharidae	15
Kateretidae	14
Phalacridae	12
Apionidae	11
Buprestidae	11
Dermestidae	10
Coccinellidae	8
Tenebrionidae	8
Cryptophagidae	6
Anobiidae, Anthicidae, Attelabidae, Byrrhidae, Byturidae, Carabidae, Cleridae, Dascillidae, Hydrophilidae, Lathridiidae, Leiodidae, Lycidae, Melandryidae, Meloidae, Mycteridae, Ptiniidae, Pyrochroidae, Scirtidae	28
Remaining	**40**
Miridae	15
Thripidae	7
Anthocoridae, Acanthosomatidae, Eriophyidae, Forficulidae, Lygaeidae, Nemouridae, Panorpidae, Pentatomidae, Pseudomopidae, Pyrrhocoridae, Sialidae, Stenocephalidae, Thyreocoridae, Trombidiidae	18
Grand total	**2587**

Table III. The number of relations per category, as well as the number of plant taxa and insect species involved. Because these values differ when attention is focused either on plant genera, or plant species, both sets of data are given separately.

category	genera			species		
	relations	plant genera	insect species	relations	plant species	insect species
Rhopalocera	4098	368	116	5589	803	116
Lepidoptera	1429	224	377	1488	351	344
Apidae	1458	324	30	2016	593	30
Apoidea	5145	326	351	5817	614	350
Symphyta	173	58	48	171	62	45
Aculeata	793	148	193	718	208	177
Parasitica	316	52	186	313	55	184
Diptera	457	141	156	461	190	154
Calyptrata	1327	215	166	1426	321	158
Brachycera	516	146	107	528	216	103
Syrphidae	5970	390	315	6491	692	308
Coleoptera	1727	261	502	1276	358	409
Remaining	89	59	40	88	63	39
Totals	**23498**	**569**	**2587**	**26382**	**1328**	**2417**

In the following brief discussion of the thirteen categories, the S_p values are given in parentheses. (Note that S_p values can only be compared within a category.)

The Rhopalocera have a wide choice of nectar plants. The plant genus with the highest score for Rhopalocera is *Centaurea* (4.9); at the species level *Lotus corniculatus* L. is the most attractive (3.5). Also *Cirsium* (4.3) and *Knautia* (3.9) are high-ranking genera. *Buddleja*, an ornamental that often is planted to attract butterflies, is rather low (1.2); even *Crepis* and *Erica* (both 1.3) score higher. Genera that are visited extensively by Rhopalocera are *Lotus* (3.9), *Origanum* (2.8), *Medicago* (2.6), *Scabiosa* (2.5), and *Lythrum* (2.2).

The Lepidoptera show several conspicuous optima, the most marked being on *Senecio* (43.0, with *S. jacobaea*, 44.8), followed by *Silene* (35.8), *Salix* (30.4), *Centaurea* (24.2) and, at large distance, *Syringa* (11.2) and *Chamerion* (9.7). Also *Tilia* (9.4) is a plant genus that is to a large extent visited by Lepidoptera. The score for *Buddleja*, 6.6, is markedly higher than for the Rhopalocera but is connected with the higher number of Lepidoptera, and precisely the same standardised value (z_p = 1.9) is obtained for both categories. *Hesperis*, *Ligustrum*, *Lonicera*, and *Lychnis* score around 5.

The plant genus most favoured by the Apidae is *Trifolium* (1.5); at the specific level it is *T. pratense* L. (1.3). Because of the well-known wide range of host plants used by Apidae, the values of S_p are

relatively low. *Ballota*, *Carduus*, *Glechoma*, and *Viola* (all 0.7) and many other genera with even lower values have a preponderance of Apidae among their visitors.

Probably because of the large number of early flying *Andrena* species it receives, *Salix* holds the place of prime for the Apoidea (14.2), followed by the spring flowering *Taraxacum* (12.6). Other important genera are *Hieracium* (10.1), *Potentilla* (9.4), *Jasione* (8.9), *Campanula* (8.4), and *Trifolium* (8.0). Because many *Salix* species are difficult to identify (especially when flowering!), there is no specific willow to note as a particularly heavily visited species; the S_p = 3.1 of *S. caprea* L. probably is an underestimation. Contrary to the case of visitation by Apidae, there are but a few plant genera that are preponderantly visited by Apoidea, the most striking ones being *Campanula* (8.4), *Brassica* (5.5), and *Cichorium* (3.5).

The Symphyta are not well represented; they score highest on *Anthriscus* (6.6) and *Aegopodium* (5.5) and to a lesser extent on *Salix* (5.1).

Aculeata are somewhat more numerous than Symphyta, and like these best represented on umbelliferous plants, in particular *Heracleum* (16.2), *Aegopodium* (15.2), and *Daucus* (13.9), next to *Rhamnus* (14.3). Especially in comparison to the Symphyta, the rather low importance of *Anthriscus* (3.7) is striking. *Anethum* (6.7), *Anemone* (4.5), *Pastinaca* (3.6) and *Symphoricarpos* (3.6) belong to the plants that have a strong representation of Aculeata among their visitors.

As was noted already by Leius (1960) and Jervis et al. (1993), many Parasitica have an exceptionally strong preference for Umbelliferae, in particular the four genera that also in other categories take a prominent position: *Daucus* (39.3), *Angelica* (37.8), *Heracleum* (30.2), and *Oenanthe* (12.8). However, their fairly low representation on *Aegopodium* (7.6) and in particular *Anthriscus* (2.8) is surprising.

Both Diptera and Calyptrata are well represented on *Heracleum* (13.4, and 16.4, resp.). Diptera have also a high score on *Arum* (16.7), but that value is as exceptional as the trap flower mechanism of the host plant; most of its visitors are flies, known from no other plant. With a score of 5.0, Diptera are

genus	family	RHO	LEP	API	APO	SYM	ACU	PAR	DIP	CAL	BRA	SYR	COL	REM	S^t	z^{EU}	z^{AL}	z^{HE}	Z^t
Heracleum	Umbelliferae	0.8	0.3	0.1	3.6	4.2	16.2	30.2	13.4	16.4	3.4	10.5	5.8	0.4	105.3	0.7	14.6	4.0	73.1
Salix	Salicaceae	0.5	30.4	0.3	14.2	5.1	1.7	1.3	6.3	8.2	2.6	15.4	7.2	2.0	95.2	10.0	4.0	5.5	64.1
Anthriscus	Umbelliferae	0.3	5.4	0.0	3.0	6.6	3.7	2.8	5.6	5.7	6.0	6.4	10.1	1.7	57.3	1.6	4.3	4.9	48.5
Ranunculus	Ranunculaceae	1.4	0.4	0.0	4.9	1.9	0.4	3.2	1.8	5.3	9.1	21.3	14.2	1.0	64.8	1.2	2.1	9.5	47.7
Daucus	Umbelliferae	0.5	0.0	0.0	5.4	0.9	13.9	39.3	1.9	1.8	1.7	4.2	6.3	0.5	76.4	1.0	10.5	2.4	38.7
Aegopodium	Umbelliferae	0.8	0.2	0.0	2.6	5.5	15.2	7.6	0.8	1.6	3.5	8.9	4.6	0.1	51.4	0.5	5.4	3.3	37.9
Cirsium	Compositae	4.3	4.0	1.0	6.9	0.0	5.0	2.4	2.3	3.2	1.9	3.9	7.3		42.3	3.4	2.1	2.5	34.1
Senecio	Compositae	1.6	43.0	0.2	5.6		0.7	2.1	3.1	3.3	2.7	1.9	1.1	0.9	66.3	11.2	1.5	1.1	33.4
Calluna	Ericaceae	1.0	7.9	0.5	5.5		1.2		0.8	2.8	1.2	2.6	1.0	6.3	30.9	3.1	0.6	2.1	33.0
Achillea	Compositae	1.7	3.6	0.0	7.2	0.5	8.9		1.9	4.3	3.4	2.0	10.1	1.1	44.6	2.5	2.6	3.2	31.0
Rubus	Rosaceae	1.9	3.0	0.5	6.9	0.3	5.4	0.4	2.8	2.6	2.0	9.8	10.0		45.4	2.5	1.9	4.4	30.1
Centaurea	Compositae	4.9	24.2	1.1	5.2		0.1		1.4	0.3	0.6	1.2	0.4	0.3	39.6	7.7	0.1	0.2	28.1
Angelica	Umbelliferae	0.7	3.0	0.1	1.7	0.5	3.1	37.8	3.0	4.4	0.3	3.6	0.8	0.2	59.2	0.9	8.8	0.7	27.7
Taraxacum	Compositae	1.1	1.7	0.9	12.6	0.4	0.4	1.5	0.5	3.0	1.4	8.3	6.1	0.3	38.2	3.4	0.8	3.1	27.7
Crataegus	Rosaceae	0.2	3.3	0.0	2.9				0.5	0.6	2.4	11.9	43.3		65.2	1.1	0.0	12.1	27.5
Potentilla	Rosaceae	0.8	0.3	0.0	9.4	0.1	1.0	0.2	2.6	2.1	5.4	8.7	2.0		32.7	2.1	0.9	3.1	23.1
Knautia	Dipsacaceae	3.9	4.4	1.0	5.9		0.9		0.2	2.9	1.1	1.5	2.4		24.3	3.1	0.5	0.7	22.8
Euphorbia	Euphorbiaceae	0.3	1.0	0.1	1.9	1.8	3.6	1.2	0.5	0.5	0.3	9.6	7.7	2.3	30.7	0.4	1.2	3.9	21.3
Trifolium	Leguminosae	2.7	2.5	1.5	8.0		0.5		0.9	0.5	0.1	0.4	1.4		18.4	3.0	0.1	0.0	19.7
Hieracium	Compositae	1.7	1.2	0.2	10.1	0.2	0.2		1.6	1.4	0.8	2.8	6.6	1.0	28.0	2.7	0.4	2.1	19.1
Leucanthemum	Compositae	1.9	1.2	0.0	1.2	1.7	1.3	4.1	0.1	4.2	0.8	1.3	7.5	1.0	26.3	0.6	1.9	1.9	18.9
Thymus	Labiatae	2.3	3.9	0.6	5.3		1.8	0.2	1.4	2.7	0.9	0.9	2.2		22.0	2.4	0.9	0.5	17.1
Galium	Rubiaceae	0.6	1.5	0.0	0.4	0.5	2.4	2.0	1.9	2.8	1.9	2.6	9.0	1.0	26.3	0.2	1.5	2.8	16.2
Pimpinella	Umbelliferae	0.3	0.6	0.0	0.5	1.4	0.1	4.0	3.7	4.1	2.7	4.1	2.0	0.1	23.4	-0.1	2.2	1.5	16.2
Silene	Caryophyllaceae	0.2	35.8	0.2	0.5		0.2		0.1	1.1	0.6	0.6	0.6	1.0	40.7	8.0	0.0	0.2	15.4
Jasione	Campanulaceae	0.5	1.9	0.1	8.9		7.2		1.7	2.5	0.3	1.0	2.0		26.2	2.3	1.9	0.4	15.2
Veronica	Scrophulariaceae	0.6	1.3	0.2	7.9		1.4		0.4	2.6	3.8	1.8	1.5		21.6	1.9	0.6	1.2	15.2
Lotus	Leguminosae	3.9	2.3	0.4	7.2		0.2		0.1	0.1		0.0	1.7		15.9	2.8	-0.2	0.0	12.5
Carum	Umbelliferae	0.0	0.3		0.2	2.8	1.9		1.6	2.7	0.9	0.3	4.5	0.5	15.8	-0.2	1.4	1.0	12.2
Rhamnus	Rhamnaceae	0.5	0.8	0.1	2.8		14.3		0.5		0.0	1.4	1.7		22.1	0.6	2.5	0.3	12.0
Prunus	Rosaceae	0.3	4.1	0.0	4.0	0.3	0.3		0.4	0.7	0.7	6.9	10.6		28.3	1.6	0.1	3.6	11.7
Spiraea	Rosaceae	0.1	3.8	0.0	0.8	0.2	2.8		0.9	0.8	0.7	1.1	15.6	0.6	27.3	0.7	0.6	3.5	11.7
Arum	Araceae									16.7					16.7	-0.4	2.8	-0.4	11.4
Echium	Boraginaceae	1.2	3.9	0.8	6.1		0.4		0.4			1.6	1.8		16.1	2.4	-0.1	0.4	11.0
Leontodon	Compositae	1.0	0.9	0.4	4.4	0.0	0.2		0.3	1.0	0.1	4.0	2.3	0.7	15.3	1.2	0.0	1.2	10.5
Stellaria	Caryophyllaceae	0.3	0.9	0.0	2.7	0.4	0.3	4.2	3.8	1.1	1.4	3.5	0.9		19.5	0.5	1.6	0.9	10.4
Myrrhis	Umbelliferae	0.0			0.0	1.9	1.0		3.9	2.3	2.0	0.3	1.4		12.7	-0.3	1.4	0.4	10.1
Chaerophyllum	Umbelliferae	0.1	1.0		0.7	2.2	1.3	2.4	1.0	1.3	0.1	5.6	2.9		18.5	0.1	1.3	1.5	10.0
Chamerion	Onagraceae	0.5	9.7	0.3	2.0	0.3	1.4		0.0	0.1	1.1	0.4	0.9	0.7	17.6	2.5	0.1	0.3	9.9
Sambucus	Caprifoliaceae	2.4	3.5		0.1	0.0		1.3		0.0	0.4	4.0	10.0		21.9	1.0	0.0	2.8	9.5
Origanum	Labiatae	2.8	2.5	0.4	1.6				1.4	1.0	0.2	0.5	0.6	0.1	10.9	1.3	0.2	-0.1	9.3
Sorbus	Rosaceae	0.1	1.0	0.0	0.5		0.9		0.4	0.2	1.5	3.9	15.3		23.8	0.0	0.0	4.1	8.8
Tanacetum	Compositae	0.5	2.7	0.0	2.8	0.1	1.2		0.1	1.2	1.2	1.1	1.1	1.1	13.8	1.0	0.2	0.8	8.3
Scabiosa	Compositae	2.5	0.7	0.6	2.9				0.5			0.8	0.5		8.5	1.2	-0.1	-0.1	8.2
Caltha	Ranunculaceae	0.1		0.0	0.0				0.1	1.7	2.4	8.8	2.5		15.7	-0.3	0.1	2.6	8.1
Valeriana	Valerianaceae	1.0	2.3	0.0	0.4	0.0	0.1	1.8	1.3	2.6	1.4	1.9	1.7		14.6	0.5	0.8	0.7	7.9
Vaccinium	Ericaceae	0.1	1.7	0.6	3.4		1.5			0.1	0.2	1.0		1.0	9.5	1.0	0.0	0.1	7.8
Solidago	Compositae	1.3	4.1	0.1	2.1		1.4	1.0	0.0	2.0	0.2	1.2	1.3	0.1	14.9	1.4	0.6	0.2	7.5
Mentha	Labiatae	0.7	2.0	0.1	0.6		0.3		2.7	1.5	0.4	2.0	4.8	0.1	15.1	0.4	0.6	1.2	7.3
Campanula	Campanulaceae	0.3	0.8	0.2	8.4					0.2	1.1	0.9	2.6	0.1	14.5	1.9	-0.2	0.7	7.3
Viola	Violaceae	0.5	0.4	0.7	1.5		0.7		1.1	2.5	0.2	0.1	0.2		7.8	0.3	0.5	-0.2	7.3
Matricaria	Compositae	0.3	0.8	0.0	1.3		0.5	0.5	1.6	1.0	1.2	2.3	5.4	0.3	15.2	0.2	0.4	1.6	7.1
Oenanthe	Umbelliferae	0.0		0.0	0.7	0.5	1.3	12.8	0.5	1.1	0.8	0.2	2.2		20.0	-0.2	2.7	0.3	7.1
Chrysosplenium	Saxifragaceae					0.3	0.3	1.0	3.4	0.4	0.2	0.1	7.5	1.0	14.1	-0.4	0.8	1.5	7.0
Geranium	Geraniaceae	0.9	2.9	0.0	2.5		1.4		0.6	0.7	0.7	2.6	3.4		15.8	1.1	0.3	1.1	7.0
Medicago	Leguminosae	2.6	6.2	0.0	2.6		1.7		0.2		0.1	0.0	0.2		13.7	2.3	0.1	-0.3	6.8
Succisa	Dipsacaceae	0.8	0.6	0.6	1.6		0.3			0.9	0.8	1.3	0.7		7.7	0.5	0.0	0.2	6.7
Erica	Ericaceae	1.3	0.4	0.5	1.3		0.1		0.6	0.1		0.6	0.4	0.7	5.9	0.5	-0.1	0.0	6.3
Vicia	Leguminosae	1.7	1.3	0.3	3.1		0.3		0.0	0.0	0.1	0.1	4.4		11.4	1.1	-0.2	0.6	6.0
Carduus	Compositae	0.6	2.4	0.7	2.0		0.0		0.2	0.1	0.0	0.2	1.8		8.0	0.9	-0.2	0.1	5.5
Hypochaeris	Compositae	0.3	0.1	0.0	2.7	0.0	0.2	0.5	0.0	2.0	1.5	2.3	0.8		10.5	0.4	0.3	0.6	5.2
Lythrum	Lythraceae	2.2	1.1	0.3	2.3					0.1		0.6	1.0		7.6	1.0	-0.2	0.0	5.1
Pastinaca	Umbelliferae	0.1			0.7		3.6	0.3	1.0	1.6	0.1	4.7	0.2		12.3	-0.2	1.0	0.7	5.1
Tilia	Tiliaceae	0.4	9.4	0.2	0.2		2.0		0.1		1.0	0.1	1.2		14.6	2.0	0.1	0.1	5.0
Sedum	Crassulaceae	1.0	0.1	0.1	4.2	0.0	0.1			1.3	0.4	0.9	1.5		9.5	0.9	0.0	0.2	4.9
Stachys	Labiatae	1.1	0.8	0.4	2.1		0.1			0.0		0.6	3.7		8.7	0.7	-0.2	0.6	4.3
Anemone	Ranunculaceae	0.1		0.0	0.1		4.5		0.6	0.4	0.5	2.7	3.2		12.0	-0.3	0.8	1.0	4.2
Ajuga	Labiatae	0.9	0.7	0.6	1.7		0.1					0.3	0.3		4.7	0.6	-0.2	-0.2	4.2
Brassica	Cruciferae	0.3	0.0	0.1	5.5			0.3	0.5	0.6	0.0	2.0	1.2	0.2	10.6	1.0	0.0	0.4	4.2
Eupatorium	Compositae	1.7	5.4	0.0	0.5		1.1		0.1	0.2	0.2	0.4	1.1	0.1	10.8	1.4	0.0	0.0	4.1
Sinapis	Cruciferae	0.4	1.0	0.0	3.2		0.3		0.3	0.0	0.1	1.0	1.2	1.0	8.3	0.7	-0.2	0.4	4.0

Table V. Summary of the values of S^c, S^t and Z^t (for genera) for the plant families with the highest number of included genera. Both sums and average values are presented.

	RHO	LEP	API	APO	SYM	ACU	PAR	DIP	CAL	BRA	SYR	COL	REM	S^t	z^t
Sums															
Boraginaceae	2.7	4.6	1.6	8.1		0.5		1.6	0.8	0.5	3.3	5.7		29.5	-18.9
Caryophyllaceae	3.0	44.7	0.5	4.8	0.4	2.5	4.5	5.7	4.6	4.0	5.8	3.0	1.0	84.4	-9.8
Compositae	34.8	98.9	6.8	93.0	3.0	23.3	12.4	17.3	35.4	17.8	46.8	67.6	9.9	466.8	113.2
Cruciferae	3.0	10.3	0.3	18.5	1.3	2.5	1.7	4.3	4.3	3.7	13.4	20.5	1.7	85.4	-82.0
Gramineae	0.0	1.0		0.4			0.6	0.1	0.9		1.5	5.5	1.0	11.0	-75.9
Labiatae	11.6	20.4	5.2	22.7		2.7	1.2	5.7	5.9	1.9	5.5	30.2	0.5	113.6	11.1
Leguminosae	16.9	15.3	3.3	36.9		4.1		3.4	2.0	0.3	1.1	25.4	0.7	109.3	4.0
Liliaceae	0.9	7.0	0.1	3.9		1.4		0.2	1.0	0.6	5.2	0.9		21.3	-55.9
Ranunculaceae	1.9	3.5	0.2	5.9	1.9	5.2	3.2	4.8	7.8	12.0	33.7	20.4	1.6	102.3	16.1
Rosaceae	4.8	18.9	1.1	29.4	1.6	14.0	1.0	9.5	9.1	13.9	53.3	122.9	1.6	281.2	95.6
Scrophulariaceae	1.7	3.8	1.6	9.9		2.8		1.5	3.5	4.4	2.6	12.0	0.1	43.8	-11.9
Umbelliferae	4.2	11.0	0.2	23.1	29.5	76.1	139.5	42.2	49.4	24.7	60.7	44.9	4.1	509.5	239.2
All 569 genera	116.0	377.0	30.0	351.0	48.0	193.0	186.0	155.0	166.0	109.0	314.9	492.1	39.0	2577.0	0.0
Average values															
Boraginaceae	0.2	0.3	0.1	0.6		0.0		0.1	0.1	0.0	0.2	0.4		2.1	-1.4
Caryophyllaceae	0.2	2.5	0.0	0.3	0.0	0.1	0.2	0.3	0.3	0.2	0.3	0.2	0.1	4.7	-0.5
Compositae	0.5	1.3	0.1	1.2	0.0	0.3	0.2	0.2	0.5	0.2	0.6	0.9	0.1	6.1	1.5
Cruciferae	0.1	0.3	0.0	0.5	0.0	0.1	0.0	0.1	0.1	0.1	0.3	0.5	0.0	2.1	-2.0
Gramineae	0.0	0.0		0.0			0.0	0.0	0.0		0.1	0.2	0.0	0.5	-3.2
Labiatae	0.4	0.7	0.2	0.8		0.1	0.0	0.2	0.2	0.1	0.2	1.1	0.0	4.1	0.4
Leguminosae	0.6	0.5	0.1	1.3		0.1		0.1	0.1	0.0	0.0	0.9	0.0	3.9	0.1
Liliaceae	0.0	0.3	0.0	0.2		0.1		0.0	0.1	0.0	0.3	0.0		1.1	-2.8
Ranunculaceae	0.1	0.2	0.0	0.3	0.1	0.3	0.2	0.3	0.4	0.7	1.9	1.1	0.1	5.7	0.9
Rosaceae	0.2	0.9	0.1	1.3	0.1	0.6	0.0	0.4	0.4	0.6	2.4	5.6	0.1	12.8	4.3
Scrophulariaceae	0.1	0.3	0.1	0.7		0.2		0.1	0.2	0.3	0.2	0.8	0.0	2.9	-0.8
Umbelliferae	0.1	0.3	0.0	0.6	0.8	2.0	3.7	1.1	1.3	0.6	1.6	1.2	0.1	13.4	6.3
All 569 genera	0.2	0.7	0.1	0.6	0.1	0.3	0.3	0.3	0.3	0.2	0.6	0.9	0.1	4.5	0.0

strongly represented on *Typha* (cf. Waitzbauer, 1976).

The Brachycera share with the Symphyta a fairly high preference for *Anthriscus* (6.0), but are even better distributed on *Ranunculus* (9.1).

Syrphidae are well represented in the fauna of N.W. Europe; they have an optimum on *Ranunculus* (21.3, to which the $S_p = 8.8$ of the closely related genus *Caltha* might still be added). *Salix* (15.4), *Crataegus* (11.9), and *Heracleum* (10.5) are other genera harbouring many syrphid species.

Hover flies have a preference for Rosaceae, rather than Umbelliferae (cf. also Table V). Plant genera with a visiting fauna dominated by Syrphidae comprise *Caltha* (8.8), *Cicuta* (3.6), *Tussilago* (2.9), and *Alliaria* (2.5). Based on the series of papers by A.D.J. Meeuse and his students (Leereveld et al., 1976; Meeuse, 1984, and papers cited therein), we had expected *Plantago* to score higher than the 1.2 that was obtained; the reason is the wide host spectrum of its visiting syrphids, resulting in a low contribution of each species to the value of *S*.

Table IV. Distribution of S^c, S^t, and Z^t over the plant genera with the highest values of Z^t, arranged in descending order of Z^t. Values of S^c that are relatively high for a plant genus are printed in bold. (The criterion for the latter information was calculated as follows. Each value of S^c_p was standardised to a value S'^c_p by division by the mean value of S^c; the reason to use this way of standardisation was that no negative values could result. Subsequently, each value S'^c_p was expressed as S''^c_p, its percentage of the value $\sum_{c=RHO}^{REM} S'^c_p$. Values of S^c_p, for which the corresponding $S''^c_p > 33.3\%$, are printed in bold.) The z-standardised importance values of the plant genera for eutropous, allotropous, and hemitropous visitors are given as well (z^{EU}, z^{AL}, and z^{HE}, resp.).

Table VI. Distribution of S^c, S^t, and Z^t over the plant species with the highest values of Z^t, arranged in descending order of Z^t. Values of S^c that are relatively high for a plant species are printed in bold. (For a description of the procedure involved, cf. Table III.) Also presented are the values of V_p, the flower colour (bl/ue, gr/een, pi/ink, pu/rple, re/d, ye/llow, wh/ite), the flower type, and the value of HSF.

| species	col.	type	HSF	RHO	LEP	API	APO	SYM	ACU	PAR	DIP	CAL	BRA	SYR	COL	REM	V_p	S^t	Z^t
Heracleum sphondylium	wh	A	8	0.8	0.3	0.1	3.2	4.3	7.7	30.1	13.2	14.4	3.4	11.8	6.2	0.5	436	95.9	133.3
Anthriscus sylvestris	wh	A	9	0.3	5.5	0.0	2.9	7.6	1.7	2.8	6.1	4.3	6.7	7.0	9.7	2.8	288	57.4	99.4
Daucus carota	wh	A	8	0.4	0.0	0.0	5.4	0.9	17.5	39.3	1.9	1.9	1.8	6.0	7.6	0.5	314	83.3	81.1
Aegopodium podagraria	wh	A	9	0.7	0.2	0.0	2.4	5.5	17.5	7.6	0.8	1.7	3.6	9.8	6.1	1.0	313	56.9	81.0
Taraxacum officinale	ye	B'		1.0	1.7	1.2	14.9	0.3	0.4	1.5	0.5	3.0	1.5	9.6	7.0	0.2	375	42.8	65.6
Calluna vulgaris	pu	B	8	0.9	7.9	0.5	6.1	0.0	1.3	0.0	0.8	2.7	1.2	2.8	1.0	7.0	200	32.1	58.5
Senecio jacobaea	ye	B'	8	0.9	44.8	0.1	5.5	0.0	0.6	2.1	2.9	2.5	1.6	1.3	0.6	0.6	261	63.6	55.2
Angelica sylvestris	wh	A	9	0.5	2.2	0.1	1.8	0.6	2.3	37.8	3.0	3.1	0.3	3.8	0.6	0.8	245	56.8	52.8
Achillea millefolium	wh	B'	9	1.4	3.3	0.0	6.3	0.1	2.4	0.0	1.6	3.2	3.1	0.8	5.4	3.5	247	31.1	51.4
Knautia arvensis	pu	B'	6	3.3	4.4	1.2	5.9	0.0	0.9	0.0	0.3	3.0	1.1	2.3	3.9	0.0	243	26.2	49.5
Cirsium arvense	pu	B'	9	2.0	2.5	0.2	4.3	0.0	5.8	2.4	1.9	3.1	2.0	3.3	6.0	0.0	310	33.5	46.8
Leucanthemum vulgare	wh	B'	9	1.7	1.1	0.0	1.1	1.9	1.6	4.1	0.1	4.2	0.9	1.2	6.5	1.0	208	25.5	39.9
Pimpinella saxifraga	wh	A	6	0.2	0.6	0.0	0.3	1.6	0.1	4.0	3.6	4.2	2.7	1.9	1.6	0.1	123	21.0	34.3
Jasione montana	bl	B'	8	0.4	1.8	0.1	8.6	0.0	7.4	0.0	1.8	2.7	0.4	1.2	2.5	0.0	229	27.0	33.7
Salix repens	gr	AB	8	0.0	1.0	0.1	0.7	1.8	0.1	0.0	2.4	1.9	0.9	4.9	1.2	2.0	92	17.1	31.1
Sorbus aucuparia	wh	AB	8	0.1	1.0	0.0	0.4	0.0	0.9	0.0	0.3	0.2	1.9	5.9	17.6	0.0	126	28.3	29.7
Chamerion angustifolium	pu	B	9	0.5	11.6	0.3	2.1	1.0	3.0	0.0	0.1	0.2	2.2	0.8	2.0	0.5	137	24.3	29.3
Carum carvi	wh	A	6	0.0	0.3	0.0	0.2	2.9	1.9	0.0	1.6	2.7	0.9	0.3	5.0	0.5	92	16.2	27.8
Euphorbia cyparissias	gr	A	5	0.3	1.0	0.0	1.6	0.8	3.5	0.0	0.0	0.0	0.0	4.9	6.1	2.3	112	20.4	26.9
Myrrhis odorata	wh	A	3	0.0	0.0	0.0	0.0	2.0	1.0	0.0	3.9	2.3	2.5	1.0	1.4	0.0	35	14.1	26.2
Centaurea jacea	pu	B'	3	3.1	1.4	0.6	3.5	0.0	0.1	0.0	0.5	0.3	0.6	0.8	0.3	0.5	211	11.7	25.9
Ranunculus acris	ye	AB	9	0.6	0.1	0.0	1.9	0.1	0.1	0.0	0.2	1.2	2.4	4.2	3.1	1.0	190	15.8	25.5
Thymus serpyllum	pi	B	6	0.7	3.5	0.6	4.3	0.0	1.1	0.2	0.4	2.9	0.9	0.5	0.0	0.0	161	15.1	25.4
Rubus fruticosus	wh	B	6	1.5	0.2	0.4	4.0	0.0	1.1	0.1	0.6	1.3	0.9	2.9	2.2	0.0	238	15.2	25.3
Rhamnus frangula	gr	A	8	0.5	0.3	0.2	2.9	0.0	14.5	0.0	0.5	0.0	0.0	1.5	1.5	0.0	104	21.9	24.5
Arum maculatum	pu		5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	17	16.7	24.3
Lotus corniculatus	ye	B	8	3.5	2.1	0.3	6.6	0.0	0.2	0.0	0.1	0.1	0.0	0.0	1.6	0.0	174	14.5	23.8
Caltha palustris	ye	AB	8	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.8	2.4	9.5	3.3	0.0	145	17.3	23.5
Centaurea scabiosa	pu	B'	3	1.6	23.3	0.2	2.1	0.0	0.0	0.0	1.0	0.0	0.0	0.1	1.0	0.0	168	29.3	23.4
Echium vulgare	bl	B	6	1.0	3.8	0.7	5.8	0.0	0.6	0.0	0.4	0.0	0.0	1.6	2.6	0.0	200	16.6	23.2
Potentilla erecta	ye	AB	8	0.3	0.3	0.0	2.5	0.1	0.3	0.0	0.9	0.7	4.2	5.3	0.0	0.0	150	14.4	22.7
Trifolium pratense	pu	B	9	1.6	1.7	1.3	3.1	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.2	0.0	143	8.1	22.5
Veronica chamaedrys	bl	B	7	0.1	1.2	0.0	6.0	0.0	0.0	0.0	0.3	2.3	2.4	1.8	1.0	0.0	135	15.2	21.5
Origanum vulgare	pi	B	4	2.5	2.4	0.3	1.4	0.0	0.0	0.0	1.6	1.0	0.2	0.5	0.2	0.2	163	10.3	19.5
Rubus idaeus	wh	B	6	0.1	2.4	0.2	1.4	0.3	0.5	0.3	1.1	1.2	0.0	5.3	4.0	0.0	141	16.8	19.5
Prunus spinosa	wh	AB	7	0.2	0.0	0.0	1.9	0.3	0.0	0.0	0.3	0.0	0.0	5.2	11.1	0.0	121	19.1	18.9
Chaerophyllum temulum	wh	A	7	0.1	1.0	0.0	0.6	1.1	0.4	2.2	1.0	1.9	0.1	5.0	1.9	0.0	139	15.3	18.6
Hieracium pilosella	ye	B'	9	1.1	0.2	0.0	6.1	0.1	0.0	0.0	0.0	0.6	0.5	0.3	2.3	1.0	150	12.1	17.7
Ranunculus repens	ye	AB	9	0.6	0.1	0.0	0.6	0.0	0.0	3.2	0.1	0.9	0.1	10.0	0.6	0.0	175	16.2	17.3
Succisa pratensis	bl	B'	8	0.9	0.6	0.6	1.7	0.0	0.3	0.0	0.0	0.9	0.9	1.4	0.7	0.0	136	8.0	17.1
Crataegus laevigata	wh	AB	4	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.5	0.6	2.1	2.8	6.4	0.0	107	14.3	17.1
Leontodon autumnalis	ye	B'	9	0.5	0.9	0.2	3.0	0.0	0.2	0.0	0.1	0.7	0.1	2.9	1.8	0.7	189	11.2	15.7
Pastinaca sativa	ye	A	7	0.1	0.0	0.0	0.7	0.0	3.7	0.3	1.0	1.6	0.1	5.6	0.3	0.0	111	13.3	15.3
Silene vulgaris	pi	B	5	0.0	26.9	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.0	110	27.7	15.1
Valeriana officinalis	pi	B'	9	0.4	2.1	0.0	0.4	0.0	0.1	1.8	1.3	1.6	1.4	1.4	1.7	0.0	120	12.2	14.8
Hypochaeris radicata	ye	B'	9	0.2	0.1	0.0	2.3	0.0	0.2	0.5	0.0	2.0	1.6	2.4	0.8	0.0	142	10.3	14.8
Cytisus scoparius	ye	Po	9	0.0	0.1	0.0	0.7	0.0	0.1	0.0	2.0	0.2	0.0	0.3	8.4	1.0	62	13.0	14.5
Cirsium palustre	pu	B'	9	2.0	1.3	0.4	0.5	0.0	0.3	0.0	0.6	0.1	0.0	1.2	0.7	0.0	138	7.3	14.2
Galium mollugo	wh	A	8	0.1	0.1	0.0	0.0	0.0	1.0	0.5	0.3	1.1	1.7	1.5	1.8	1.0	59	9.0	13.6
Mentha aquatica	pu	B	9	0.5	1.8	0.1	0.3	0.0	0.0	0.0	2.8	0.7	0.3	1.1	3.2	0.1	119	10.9	12.9
Typha angustifolia	gr	Po	7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.5	2.5	3.0	0.0	17	11.0	12.7
Filipendula ulmaria	wh	Po	8	0.1	0.1	0.0	0.2	0.0	1.3	0.4	0.3	0.4	0.0	3.8	7.0	0.0	121	13.6	12.6
Lythrum salicaria	pu	B	8	2.0	1.1	0.3	2.1	0.0	0.0	0.0	0.0	0.2	0.0	0.6	1.0	0.0	108	7.2	12.2
Chrysosplenium alternifolium	ye	A	4	0.0	0.0	0.0	0.0	0.3	0.3	1.0	1.8	0.0	0.0	0.0	6.3	1.0	17	10.8	11.8
Scabiosa columbaria	pu	B'	4	2.2	0.6	0.2	2.8	0.0	0.0	0.0	0.5	0.0	0.0	0.3	0.0	0.0	91	6.6	11.7
Bellis perennis	wh	B'	9	0.3	0.5	0.0	2.5	0.1	0.2	0.0	0.2	1.6	1.0	0.9	1.4	0.0	132	8.7	11.5
Eupatorium cannabinum	pu	B'	9	1.6	5.4	0.0	0.5	0.0	1.1	0.0	0.1	0.2	0.2	0.4	1.1	0.2	102	10.8	11.4
Sambucus ebulus	wh	Po	4	2.2	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	2.5	0.5	0.0	86	9.0	11.4
Salix caprea	gr	AB	7	0.3	3.8	0.1	3.1	0.0	0.0	0.3	0.0	0.5	0.4	2.4	0.4	0.0	94	11.3	10.7
Erica tetralix	pi	B	8	1.2	0.4	0.4	0.8	0.0	0.1	0.0	0.6	0.0	0.0	0.2	0.0	0.7	68	4.3	10.4
Stellaria media	wh	AB	9	0.0	0.0	0.0	1.1	0.0	0.1	2.0	3.9	0.9	0.3	0.3	0.4	0.0	73	9.0	10.2
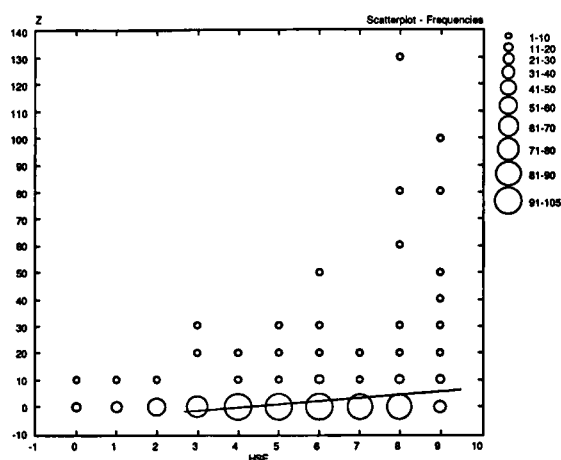
Fig. 1. Frequency scatter plot of HSF against Z for all plant species for which HSF is known.

The top-ranking genera for the Coleoptera are strongly dominated by Rosaceae (cf. also Table V): in descending order *Crataegus* (43.3), *Spiraea* (15.6), *Sorbus* (15.3), *Ranunculus* (14.2), *Cornus* (10.7), *Prunus* (10.6), *Rosa* (9.3), and *Filipendula* (8.7).

Distribution of V_p, S^t, and Z^t

Not surprisingly, the number of visitors (V_p), total importance (S_p^t), and relative importance (Z_p^t) are strongly correlated, mostly S^t and Z^t, less so V_p with the other two values (*V-S*: 0.871; *V-Z*: 0.904; *S-Z*: 0.963; $P < 0.000$).

As is evident from Tables IV and VI, the distribution of S^t and Z^t is extremely skewed. Only 50 of the plant genera (9%) and 60 (5%) of the species have a Z^t that falls in the upper 90% of the range that Z^t does assume (-3.47 to $+73.06$ and -2.65 to $+133.30$, respectively). In other words, a small minority of plant genera and species have a very high importance to the anthophilous fauna.

Rarity and commonness

In order to test the correlation of Z^t with plant rarity, we used the plant species data, rarity of genera being not meaningful. Although Z^t is not random-

ly distributed, it was legitimate to use an anova approach, because of the high number of observations. Fig. 1 offers a frequency scatter plot of HSF against Z.

We computed the correlation between the values of z_p and HSF of all relations, for three representative categories, viz. Apidae ($r = 0.09884$; $N = 1633$), Apoidea ($r = 0.07892$; $N = 4973$), and Syrphidae ($r = 0.07407$; $N = 5606$). In all cases $P < 0.000$. For the 785 plant species of which rarity estimates are available, the values of Z^t and HFS were correlated with $r = 0.24646$, again $P < 0.000$. These results indicate a positive, albeit weak, correlation between a plant's commonness and its importance to the entomofauna.

A two-way, fixed effect anova over flower type and HFS, with Z^t as dependent variable was run. The results, summarised in Table VII, show that the mean values of Z^t both for the floral types and HFS differ significantly. Rarity and floral type significantly interacted in an unexpected way. The correlation between commonness and Z^t is very strong and positive in floral type A, fairly strong and positive in type B', much less strong but still positive in types AB and B, and weakly negative in Po. It must be remembered that we lumped in Po wind pollinated plants (*Quercus*, grasses etc.) and plants like *Hypericum* that have pollen as their only floral reward.

These results again indicate that plant commonness is positively correlated with Z^t; this is in favour of the hypothesis that the anthecological relationships are not preponderantly dominated by specialisation of either plants or insects.

H_i versus V_p

The number of visitor species of a plant species, V_p, ranges from 1 to 436 (for *Heracleum sphondylium* L.); the next highest value is 375 for *Taraxacum officinale* L. (Table VI). The mean value is 19.9 ± 1.08 (SE); the median is 6.

The maximal value of the number of plant species acting as a host, H_i, is 443 (for *Apis mellifera* Linnaeus; next highest scores are 352 and 332, for *Pieris napi* (Linnaeus) and *P. brassicae* (Linnaeus),

Table VII. Results of an anova, testing Z^t of plant species against flower type ("type") and hour square frequency ("HFS"). Significance (top) and mean group values (below) of primary effects and interactions are presented.

effect		P
type		0.0001
group		0.0000
interaction		0.0000

type	HFS	av. Z^t
A	*****	7.0487
AB	*****	0.3299
B	*****	0.4298
B'	*****	3.1820
Po	*****	-1.1284
*****	i	-1.1827
*****	ii	-0.6999
*****	iii	-0.1557
*****	iv	1.5404
*****	v	10.3598
A	i	-0.8812
A	ii	0.2911
A	iii	2.5713
A	iv	4.5733
A	v	28.6888
AB	i	-2.1439
AB	ii	-2.1624
AB	iii	-0.5772
AB	iv	1.3941
AB	v	5.1388
B	i	-1.6934
B	ii	-1.2985
B	iii	-0.8539
B	iv	0.9764
B	v	5.0186
B'	i	-1.8194
B'	ii	1.8232
B'	iii	-0.5485
B'	iv	2.2864
B'	v	14.1682
Po	i	0.6244
Po	ii	-2.1530
Po	iii	-1.3702
Po	iv	-1.5282
Po	v	-1.2153

Fig. 2. Frequency scatter plot of V against H (all plant species).

species only, because H_i is less directly interpretable for genera.

Fig. 2 gives a frequency plot of the combinations of the two values. As is indicated in the figure, the values are negatively correlated: Pearson's $r = -0.25482, P < 0.000, N = 26382$; the slightly more appropriate Spearman rank correlation (neither H nor V are normally distributed, but the number of observations is sufficient to alleviate this) that could only be calculated for up to 8000 value pairs, yielded an $R = -0.335855$ ($P = 0.000000$).

Because this negative correlation might be an artefact of the disproportionately large numbers of low values, we repeated the analysis for those relations with both H_i and $V_p \geq 20$; the possibly anomalous honeybee, with its exceptional high H_i was left out as well. This did diminish the strength of the correlation, but not its significance (Pearson's $r = -0.16943, N = 13065, P < 0.000$; Spearman's $R = -0.194051, N = 8000, P = 0.000000$).

Factor analysis

We made a factor analysis, taking z^c [c = Rhopalocera ... Remaining] as 13 variable values, describing the separate plant genera. The analysis yielded three eigenvalues > 1.0, extracting 40, 15, and 8% of variance. Fig. 3a, b shows a plot of the factor loadings.

These plots, and the study of a 3-D rotating

resp.); the average is 10.9 ± 0.57; the median is 3.

As is obvious from the large difference between average and median in both cases, the distributions of H_i and V_p are strongly skewed, like those of S^t and Z^t; only 342 (25.7%) of the relations are above the average V value; 542 (22.5%) of the insect species have a value of H exceeding the average.

Each relation can be described as a pair of values of H_i and V_p. We investigated our data for correlation between these values; this was done for plant

Fig. 3a. Factor plot of the 13 visitor categories against plant genera. Varimax rotation, factor axes 1 and 2.

Fig. 3b. As Fig. 3a, factor axes 3 and 2.

model, suggest that the factors fall into three fairly distinct groups. One consists of the Apidae, Apoidea, Rhopalocera, and Lepidoptera; the most isolated member of this group are the Lepidoptera. A second group, almost orthogonal to the first one, is formed by the Symphyta, Aculeata, Parasitica, Diptera, and Calyptrata. The last group is formed by the Brachycera and Syrphidae (that are particularly close to each other), Coleoptera, and Remaining insects. This division of the categories into three groups closely coincides with that in eutropous, allotropous, and hemitropous flower visitors that was proposed long ago by Loew (1884, 1886).

In the tables the categories belonging to the eu-, allo- and hemitropous groups are separated by dotted lines. In Table IV also the standardised importance of the plant genera to these three category groups is summarised in the columns labelled z^{EU}, z^{AL}, and z^{HE}.

As is evident from Table VIII, there is a close correlation between z^{AL}, z^{EU}, and z^{HE}, respectively, and the factor axes 1, 2, and 3.

The proportion of these three groups of the total fauna of 2587 species is 874 (33.8%) eutropous, 747 (28.9%) hemitropous, and 966 (37.3%) allotropous.

Table VIII. Correlation matrix between the values z^{EU}, z^{AL}, and z^{HE} for genera (cf. Table IV) and their loadings on the three factor axes. $N = 569$.

	z^{EU}	P	z^{AL}	P	z^{HE}	P
Factor 1	0.11433	<0.006	0.93172	<0.000	0.26077	<0.000
Factor 2	0.73770	<0.000	0.09867	<0.019	0.17756	<0.000
Factor 3	0.40474	<0.000	0.02392	<0.000	0.83484	<0.000

Plotting the plant taxa together with the categories on the first two factors (Fig. 4a, b) shows that the large majority of the plant genera fall in a tight cluster near the origin of the graph. No structure is apparent in this dense cloud, not even after "zooming in". The relatively few genera outside of this central swarm fall into three, incompletely separated, groups.

One elongated group, parallel to the first, most informative, axis, consists of all Umbelliferae. This group is closely associated with the allotropous insects (cf. also Table V).

A second group, orthogonal to the first axis, is composed of Compositae (in particular *Centaurea, Cirsium, Taraxacum, Senecio, Hieracium*), Leguminosae (*Trifolium, Medicago*), *Knautia, Echium*, with, closer to the central cloud, many Labiatae
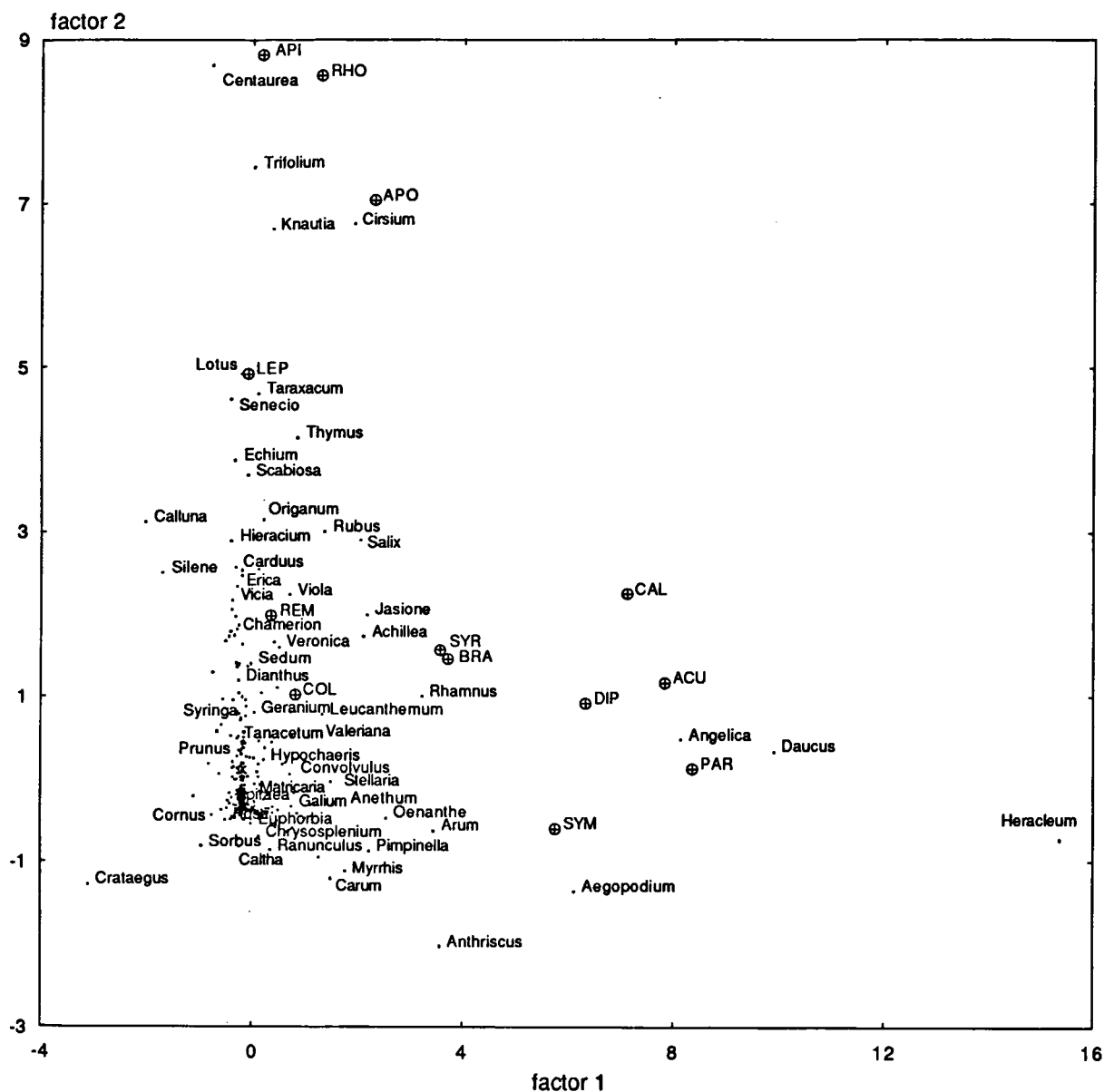
Fig. 4a. Distribution of the plant genera over the factor plot. Only the genera outside of the central "cloud" are labelled. Some names have been slightly shifted respective to their data point for readibility. Loadings of factors are multiplied by 10. Factor axes 1 and 2, varimax rotation.

(*Ajuga, Thymus, Origanum*) and Caryophyllaceae (*Silene*). This group of plants correlates with the eutropous insects delineated above.

The third, least clearly separated group consists of some Rosaceae (*Prunus, Potentilla, Crataegus, Spiraea, Sorbus, Rubus*), some Compositae (*Achillea, Leucanthemum*), *Salix, Galium, Veronica,*

Jasione, Calluna, and *Ranunculus.* This group correlates with the hemitropous visitors. Note that *Anthriscus,* and to a less extent *Aegopodium,* are intermediate between the first and the third group.

We repeated the factor analysis for plant species (Fig. 5). The distribution of the variables shows a close resemblance with that of the genera. Rather
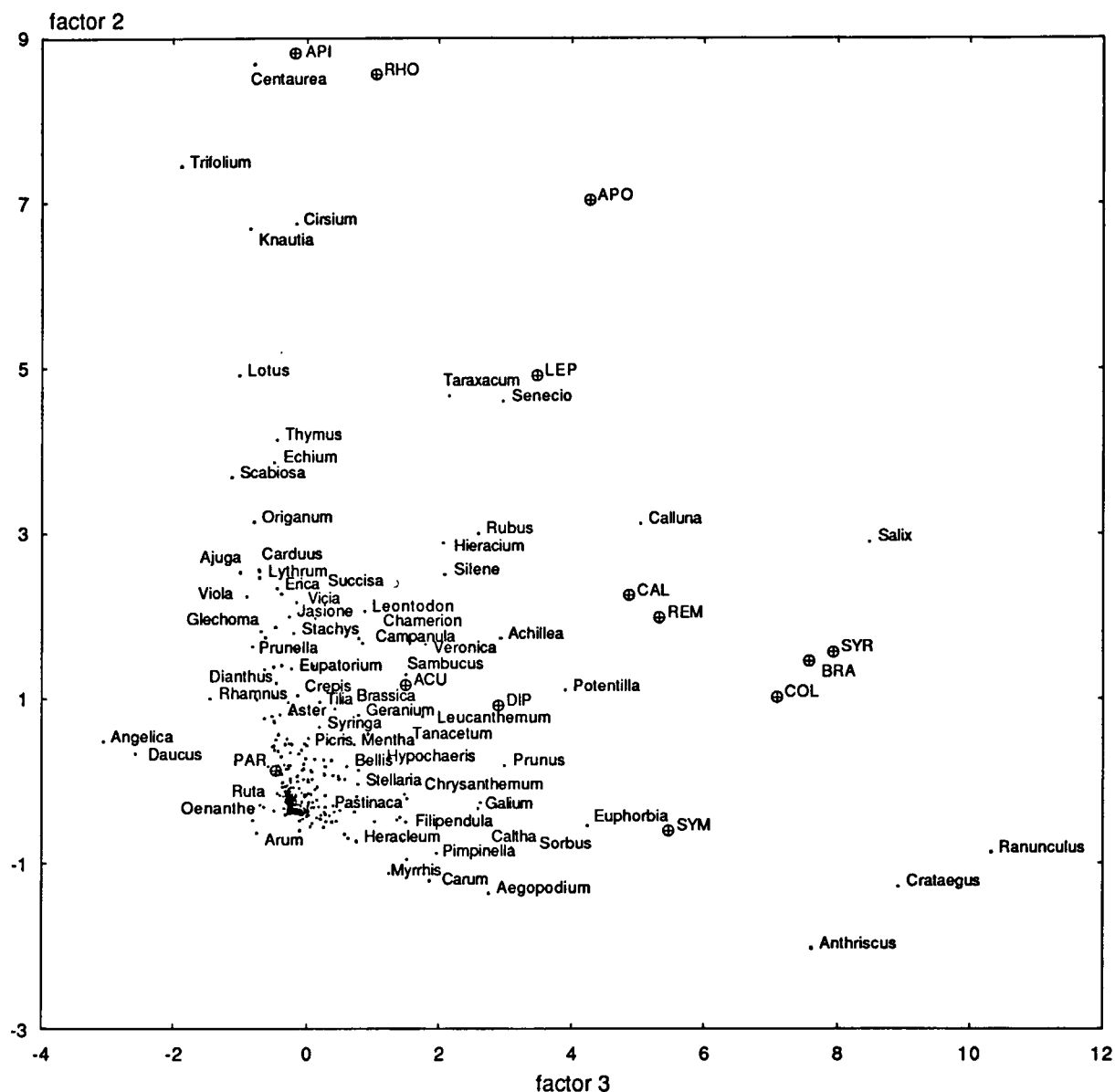
Fig. 4b. As Fig. 4a, factor axes 3 and 2.

than the species names, we added in this graph the flower types. The close association of the first axis with flowers of type A, and the fairly close association of the second axis with flower types B and B' is apparent.

This association was studied in more detail in an anova relating the floral type to the values of z^{EU}, z^{HE}, and z^{AL} (Table IX). The most interesting result of this computation is the significant interac-

tion of these values with the floral type. It shows that not only floral type A is primarily visited by allotropous visitors, but also that type AB is primarily visited by hemitropous insects, while plants of type B, and even more B', are the primary host plants of eutropous insects.

A parallel anova over flower colour confirmed the long standing knowledge that blue, pink, and purple flowers are predominantly visited by eutro-
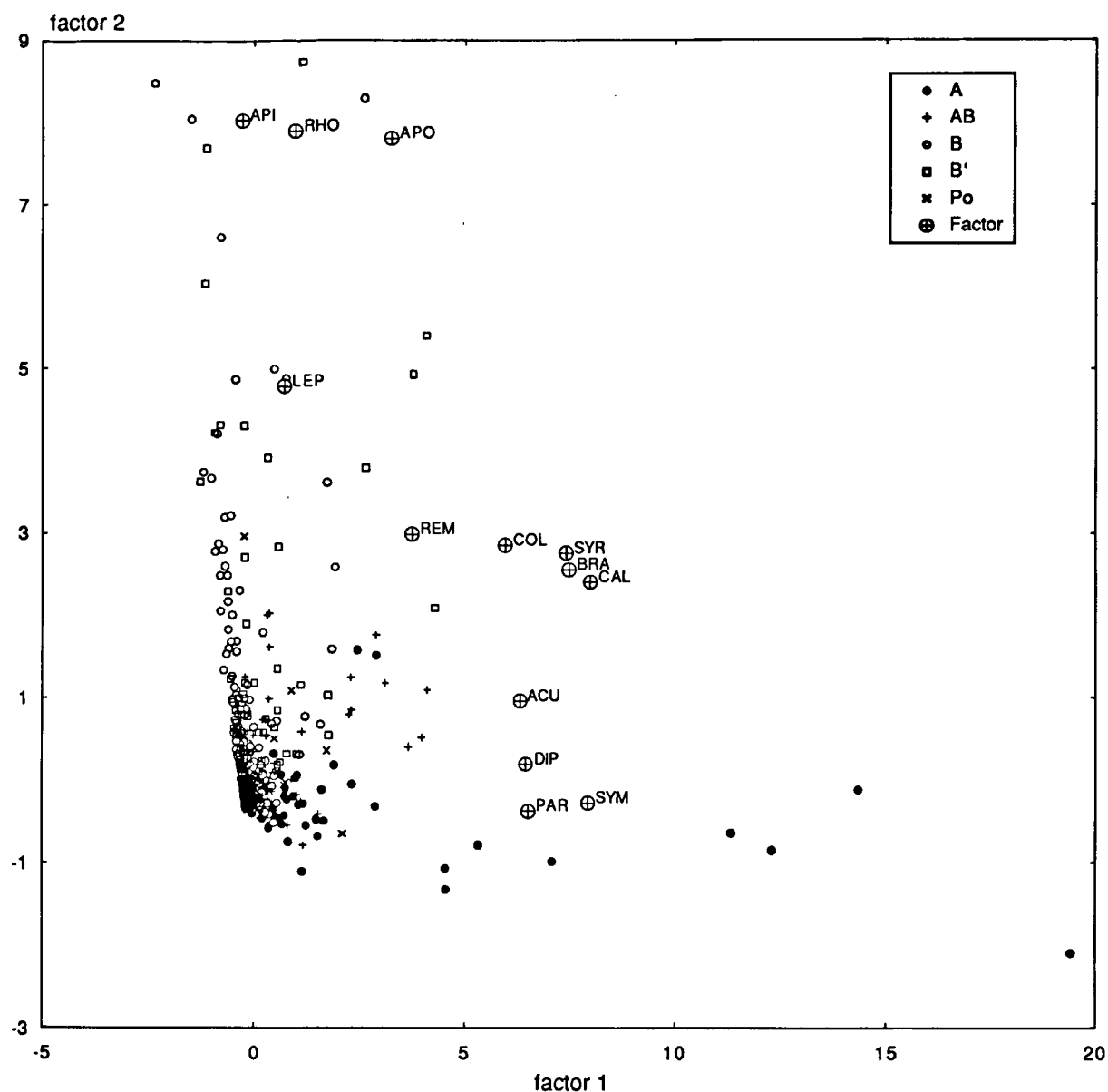
Fig. 5. Factor plot of the plant species, showing the distribution of flower types. Loadings of factors are multiplied by 10. Factor axes 1 and 2, varimax rotation.

pous visitors; white flowers are mainly shared by hemi- and allotropous visitors and yellow flowers by eutropous and hemitropous insects. Yet, apart from the white flowers the numerical differences are not impressive. Yellow, that is often reported as very attractive to Syrphidae (e.g. Kay, 1976; Kugler, 1950; Lunau, 1988; Schneider, 1958), elicits a surprisingly vague result. This agrees with the

preference Barkemeyer (1979) found in hover flies for white over yellow.

Nowhere did the factor analysis reveal discrete groups of plant taxa that would be suggestive of certain flower types, beyond the three groups just described. On the basis of our data we cannot arrive at a detailed flower typology with any predictive power. The position of *Anthriscus* in the factor

Table IX. Results of two fixed effect two-way anova's, having the values z^{EU}, z^{HE}, and z^{AL} as dependent variables (three "repeated measures") and having colour and flower type, resp., as between group variable. Significance (top) and mean group values (below) of primary effects and interactions are presented.

effect	P		effect	P	
colour	0.0021		type	0.0000	
group	0.4767		group	0.0045	
interaction	0.0000		interaction	0.0000	

colour	group	av. Z^t	type	group	av. Z^t
blue	*****	-0.1046	A	*****	0.5065
green	*****	-0.0561	AB	*****	0.0520
pink	*****	-0.0586	B	*****	-0.0368
purple	*****	0.0298	B'	*****	0.0778
red	*****	-0.1700	Po	*****	-0.1223
white	*****	0.1823	*****	eutropous	0.0184
yellow	*****	0.0097	*****	hemitropous	0.1414
*****	eutropous	0.0021	*****	allotropous	0.1265
*****	hemitropous	-0.0436	A	eutropous	-0.0166
*****	allotropous	-0.0303	A	hemitropous	0.6234
blue	eutropous	-0.0076	A	allotropous	0.9125
blue	hemitropous	-0.1992	AB	eutropous	-0.0135
blue	allotropous	-0.1071	AB	hemitropous	0.2119
green	eutropous	-0.1175	AB	allotropous	-0.0424
green	hemitropous	-0.0192	B	eutropous	0.0940
green	allotropous	-0.0316	B	hemitropous	-0.1031
pink	eutropous	0.0505	B	allotropous	-0.1012
pink	hemitropous	-0.1143	B'	eutropous	0.2437
pink	allotropous	-0.1118	B'	hemitropous	0.0118
purple	eutropous	0.2141	B'	allotropous	-0.0222
purple	hemitropous	-0.0868	Po	eutropous	-0.2153
purple	allotropous	-0.0378	Po	hemitropous	-0.0373
red	eutropous	-0.1425	Po	allotropous	-0.1143
red	hemitropous	-0.2243			
red	allotropous	-0.1433			
white	eutropous	-0.0310			
white	hemitropous	0.3050			
white	allotropous	0.2730			
yellow	eutropous	0.0487			
yellow	hemitropous	0.0338			
yellow	allotropous	-0.0534			

analysis illustrates that even in the clearest case, that of the Umbelliferae, typology may lead to erroneous expectations.

Discussion

General; cautions, deficiencies, etc.

Not all anthophilous insects are fully dependent on flowers for their trophic requirements; therefore N and by consequence S and Z, are only approximate measures. This is the more so because the degree in which visitors are bound to a plant species (our value P) can only be roughly quantified.

It is of obvious importance for the validity of our results that no plant or insect group is underrepresented. As to insects, as will be detailed below, some groups have received too little attention indeed; however, because of the outlook of the paper this is less damaging to our conclusion than an unequal treatment of the plants.

Because the majority of our data are derived from the work of anthecologists, whose explicit intention was to gather a comparative picture of the visitor spectrum of all plant species in a local flora (although common plants may have been oversampled), we are reasonably confident in the bal-

ance of the floral part. However, it should be borne in mind that, due to the sampling period of most of our sources, the results are not in all cases applicable to the present situation, viz., regarding those plants that have become more rare or more common. There are, for instance, hardly data available for the now ubiquitous *Heracleum mantegazzianum* Sommier or *Prunus serotina* Ehrhart.

The objection may be made that allegedly anemophilous plants may have attracted less observation hours than notorious entomophiles. Yet open-minded observers like Müller, Mac Leod, and Knuth would certainly have devoted more of their time to anemophilous plants, had these taxa been more ostensibly visited by insects. On the other hand, the surprising behaviour of "Po"-plants in relation to rarity indicates that these data need amplification.

The single most neglected anthophilous taxon are the Thysanoptera (Ananthakrishnan, 1993). They are rarely mentioned and even more rarely identified; however, these tiny insects are common visitors (e.g. in 100 flowers of *Cakile maritima* Scopoli, randomly picked in one population, Mr. G.W. Vierbergen [unpubl.] found 15 thrips specimens belonging to five species).

Furthermore, we suspect a serious underrepresentation of night-active Lepidoptera. As a case in point we may refer to Scholten (1949) who described the fortuitous discovery of moths, visiting in large numbers the grasses *Molinia caerulea* (L.) Moench and *Festuca arundinacea* Schreber in the night for the sweet exudate produced by *Claviceps* (ergot) that had infected the inflorescences. He listed 4 species of Arctiidae, 21 Geometridae, 55 Noctuidae and 2 Thyatiridae. Of these, 2 Arctiidae, 7 Geometridae, 9 Noctuidae and both Thyatiridae have to our knowledge never been recorded as flower visitor in the literature. The once universal method of collecting night-active Lepidoptera with "smear" also suggests that the majority of these insects may be attracted by flowers as well (e.g. Lampert, 1907; see also Andrewes, 1936).

Plant genera or plant species

Relations of insects with plant species should not be combined with relations of insects with plant genera. It often is unclear if a plant reference like "*Ranunculus* sp." is to mean either "several or all *Ranunculus* species" or "an unidentified *Ranunculus*". In either case, treating "sp." as a real species would introduce double scoring.

Limiting ourselves then to those plants that are identified down to the species level would have had the advantage of higher precision, but would result in a distorted picture, because some important, but "difficult" plant taxa (like *Hieracium*, *Salix*, *Crataegus*, and *Rubus*) often are not identified to the species level.

Numerical results

Taking the whole flower visiting complex together, we found about 2,600 insect species exploiting some 1,300 plant species; naturally, both values are lower estimates, but this holds more for the insects than for the plants. This is firstly because we included all plants that have been recorded as receiving an insect visit, including genera like *Betula* and *Thuja* that hardly can be called entomophilous. Secondly, many relations concern rare and/or exotic plant species.

In comparison, Müller's (1881) classical study on the anthophilous fauna of the Alps listed 841 insect species, visiting 416 plant species. Mac Leod (1891) found 509 insect species serving 261 plant species in the Pyrenees (Vallée de Luz, Hautes-Pyrénées). Petanidou (1991), working at a very restricted plot in Greece found as many as 666 insect species visiting 133 plant species. Taking these scattered data together, one may conclude that in Europe, where ornithophily and chiropterophily are virtually unknown, the ratio insect : entomophilous plant species is in the order of 2–5 : 1. This is comparable with results reported by Moldenke (1976) from three plots in mid-elevation California having 100, 60, and 187 plant species, and 326, 327, and 316 insect visitors; for four sea-level plots he found 98, 105, 133, and 144 plants, visited by 484, 63, 260,

and 386 insect species.

Kratochwil (1984) found 102 bee species and 56 butterfly species, serving 71 plant species in a plot on the Kaiserstuhl (S.W. Germany). Although these figures concern a partial fauna, they still seem to fit within the limits we suggest. However, in other parts of the world this may be different. Heithaus (1979, cited by Vogel & Westerkamp, 1991) mentions 330 species of bees and wasps visiting 168 plant species in a dry forest in Costa Rica.

The number of anthophilous plant taxa of high importance is surprisingly low; these important genera and species may be equated with the cornucopian plants recognised by Mosquin (1971). Many are members of the Compositae, Umbelliferae, and Rosacae. For the anthophilous insects these are the pivotal plants upon which their existence may depend; hence their importance for the remaining entomophilous plants in an ecosystem may be crucial as well. Many of these cornucopian plants belong to the commonest species in the region, occurring also in disturbed habitats.

Mosquin (l.c.) defined cornucopian species as plants that offer an "unlimited supply" of pollen and/or nectar. He mentions *Taraxacum officinale* and *Salix* sp. as examples, thereby making it clear that "unlimited" must be conceived not so much at the level of individual flowers or inflorescences, but rather of whole plants (*Salix*) or even populations (*Taraxacum*). In other words, a medium-reward plant may obtain the cornucopian badge by the virtue of high local population densities. We expect that this applies to at least several of these most important plant taxa.

Of the 60 highest ranking plant species, 2 are helophytes, 5 chamaephytes, 6 geophytes, 8 phanerophytes, and 39 hemicryptophytes. In terms of life duration, there are 10 biennials, 12 woody species, and 38 perennials. The absence of annuals is striking.

H versus V

The negative correlation between H_i and V_p is not strong, but the data are sufficiently consistent to reject the hypothesis that insects with a small number

of host plants preferably visit those plant species that themselves are visited by a few insect species only. Combined with the strong correlation between Z and commonness, this means that both the anthophilous fauna and the entomophilous flora are strongly dominated by generalists; the few existing specialised relationships do not influence the overall picture. Jordano (1987), who studied the numeric patterns of plant species and their visitors by comparison of many relatively small, well-circumscribed pollination systems from different parts of the world, arrives at the same conclusion.

Typology of flowers and their visitors

The distinction of the visiting fauna in an eutropous, hemitropous, and allotropous segment stands out clearly. A finer subdivision of the three main groups of visitors is not practicable.

Illuminating in this respect is the location of the Rhopalocera, closer to the Apidae than either is to the Apoidea. This may be explained by the common greater average tongue length of Lepidoptera and Apidae, but might also be connected with their larger dependence on nectar as compared to the Apoidea, for which generally pollen is the primary resource. However that may be, it shows that even in those insects maximally adapted to flower visiting, the phylogenetic and ecological positions are not coupled.

As to the plants, we may distinguish an overwhelmingly large group that receives few visitors only, in contrast to a small group that is heavily visited. Only the latter can be subdivided, in three groups that match the eu-, hemi-, and allotropous trichotomy of their visitors. The first group consists mainly of Aggregatae (Compositae, Campanulaceae, Dipsacaceae) plus a number of taxa having likewise many small flowers arranged in dense inflorescences. The second group, that is dominated by Rosaceae, shows a preponderance of fairly large, bowl-shaped flowers, and the third one consists of nearly all Umbelliferae.

The traditional elaborate flower functional typologies have little more use than to describe the few genera with an extreme specialisation (e.g. *Arum*).

The attribution of a plant species to a particular visitor type does no justice to the diversity of the visiting fauna that mostly is available. In this respect our results extend Kugler's (1939, 1950) early dispelling of the labelling of *Veronica chamaedrys* L. and *Circaea lutetiana* L. as syrphid flowers, and his later rejection of the concept of syrphid flowers altogether. The insect-flower relationships of N.W. Europe are strongly dominated by broad, unspecialised relationships that numerically swamp the few cases of specialisation. Likewise, Kevan & Baker (1983) and Kevan et al. (in press) note a limitation in the specialisation of boreal pollination systems.

The principal Umbelliferae: *Heracleum, Anthriscus, Aegopodium, Pimpinella, Daucus, Angelica,* and *Chaerophyllum* are widely spread along the first axis of the ordination. This may be attributed to differences in phenology (the relatively early *Anthriscus* may be set apart on this account), partly also to a different ecology (*Aegopodium*, and to some extent *Anthriscus*, are fairly shade tolerant). This may be a partial explanation of the fact that the fraction of eutropous and hemitropous insects of the total number of visitors (based on *S* values) is 0.91 in *Peucedanum*, 0.57 in *Anthriscus*, 0.47 in *Pastinaca*, 0.40 in *Aegopodium*, and only 0.24 both in *Daucus* and *Heracleum*. Still, one should keep in mind the hypothesis proposed by Bell (1971) that the rigid gross morphological uniformity of this family may hide a multitude of subtle but highly effective floral adaptations.

In an earlier note (Ellis & Ellis-Adam, 1992) we have drawn attention to the large number of visitor species of *Cirsium arvense* (L.) Scopoli, in comparison to that of the other *Cirsium* species, and even more the superficially similar *Carduus* species. Like in the Umbelliferae, a close taxonomic and morphological, or even ecological, proximity is a bad predictor of the anthophilous relationships of a plant.

To underline the decoupling of plant systematics and pattern of visitors, we may briefly describe the situation in the genus *Veronica*. *V. chamaedrys* L. is the most important species (Z_p = 21.5), visited mainly by bees and hemitropous insects; there is no preponderance of any particular category (not even Syrphidae, as was found already by Kugler, 1939).

Of the remaining species, *V. officinalis* L. and *V. scutellata* L. are visited predominantly by Brachycera; *V. arvensis* L., *V. beccabunga* L., *V. longifolia* L., *V. opaca* Fr. and *V. teucrium* L. are visited in the first place by Apoidea. *V. anagalis-aquatica* L., *V. montana* L. and *V. spicata* L. are primarily visited by Aculeata. Among the few visitors of *V. agrestis* L., *V. incana* L., *V. latifolia* L., and *V. triphyllos* L., Apidae dominate, while Calyptrata dominate in *V. serpyllifolia* L., Diptera in *V. persica* L., and Coleoptera in *V. hederifolia* L.. The only registered visitor of *V. virginica* L. is a butterfly.

Practical implications

Integrated pest management

A strip of spontaneous vegetation along an agricultural field may function as a reservoir of insects that are beneficial either as crop pollinators or as predators or parasitoids of pest insects (Kevan et al., 1990; Molthan & Ruppert, 1988; Ruppert, 1993; Schneider, 1988; Syme, 1975; Weiss & Stettmer, 1991). In a program of integrated pest management the border fauna has often been able to suppress many potential pest outbreaks. Many of these insects are anthophilous (Van Emden, 1962).

Often the protection of the field borders is limited to shielding against the application of herbicides and insecticides; otherwise the strips undergo the normal treatment of harvesting and tillage, which means that the spontaneous flora will remain restricted to annuals and biennials. Our results indicate that the most valuable, viz. cornucopian, plants are predominantly woody or herbaceous perennials. Such plants need more stability. From the standpoint of integrated pest management, we feel that protected field borders will be but a poor alternative of hedgerows.

Cryptobiota conservation

The management of nature reserves is largely centred on vertebrate animals and flowering plants,

and little attention is paid to the cryptobiota. The usual rationale for this attitude is that what is good for the vertebrates + flowering plants, will also be good for the cryptobiota. The present study illustrates that this view is incomplete. Hardly any of the plants recognised above as cornucopian would be considered worth protection. Yet, these plants should be considered protection priorities, for the sake of the host of insect visitors that depend on them (Kevan & Baker, 1983). *Cirsium arvense* is a case in point. This common pest thistle since a long time is the target of eradication programs, even enforced by local legislation (Ellis & Ellis-Adam, 1992). Still, the existence of an equivalent of over 30 anthophilous insect species alone depends on this single plant.

Nature reserves, especially the smaller ones, regularly may pass through periods in which the number of wild flowers is too limited to sustain the local anthophilous fauna. Often it is possible to enable the development of an abundant weed zone in the border area of the reserve. Our results show that there is generally no reason to fear that this assemblage of ubiquitous flower donors will be too unattractive to fulfil its intended function. Of course, this does not hold for the relatively limited number of strictly oligolectic visitors, like the *Campanula*- or *Lysimachia*-visiting bees.

The role of neophytes is altogether limited. Among the top 200 plant species we find no more than five exotic ones, the most important being *Buddleja davidii* Franch. ($Z_p = 7.1$), *Symphoricarpos albus* Blake (4.1), and *Hesperis matronalis* L. (3.8). The three most important neophyte genera are *Syringa* ($Z_p = 1.7$), *Buddleja* (1.0), and *Symphoricarpos* (1.0). The first two are primarily visited by Lepidoptera (and to a lesser extent Rhopalocera), the latter is mainly visited by Aculeata.

Many organisms presently have to survive in the outskirts of urbanised areas; flower-visiting insects are no exception (Jacob-Remacle, 1989a, b; Owen, 1978a, b; Owen & Owen, 1975). At least as far as their food habits are concerned, our data suggest that gardens and roadside vegetations may supply them with the resources on which they can survive. However, the conclusion by Jacob-Remacle (1989b) that even in an urban environment exotic plants are less visited than native plants, which matches well with our results, warns against too much optimism.

One of the most important flowers is *Calluna*, with a Z^t of 32.9. *Calluna* heathlands traditionally are stocked in the flowering season with large numbers of honeybee hives, even when they are maintained as nature reserves. Honeybees are atypical flower visitors, not only by their high numbers and the shifting location of their hives, but also by their extremely wide flower range ($H_i = 443$). A detailed study of the competition pressure that honeybees may exercise on the wild anthophilous fauna is urgently needed, like Morse (1981) has documented the interaction between bumblebees and hover flies. Pending such studies we can only urge that the number of honeybee hives in heaths (and probably in other types of reserves as well) should be kept at a low level (see also Douglas, 1977; Holmes, 1961; Kato, 1992; Percival, 1974; Ricciardelli d'Albore, 1984; Schäffer, 1983; Sugden & Pyke, 1991; Williams et al., 1991).

Anthophilous potential

It seems promising to estimate the potential value of a given plot, site or reserve for either the complete anthophilous fauna or one or more categories, basically by calculating the value $\sum_{p=1}^{n} A_p S_p$ (n: total number of plant species in the plot, A_p: abundance of plant species p in the plot). The availability of this value may be useful in those cases where a complete plant list is available, but where entomological work has still to begin. We hope to bring the results of such an approach in a forthcoming publication.

Rare plant populations

Also, the presence of a sufficient supply of pollinators may be essential for the pollination of rare or threatened plants of which the population size is insufficient to attract pollinators on their own account (Dorn, 1982; Frankie et al., 1990; Kevan, 1975; Senft, 1990). Attractive plants may function

as "magnet species", thereby enhancing the visitation rate of other, less interesting but superficially similar species (Vogel & Westerkamp, 1991). Our results give an indication of the types of vegetation that are most suitable to fulfil that role.

Conversely, the presence of a top attractant close to a threatened population of a less attractive plant may put its remaining pollination options in jeopardy (see e.g. Campbell, 1985; Mosquin, 1971; Petanidou et al., 1991; Rathke, 1983, 1988).

Finally

Reading Knuth's (1893) eulogy of Sprengel, we found that, among other citations from Sprengel's book, he cited the lines we already had chosen as motto for the present paper. Knuth comments, in translation: "In these words we find the origin of the distinction, that has recently been made by E. Loew, in eutropous, hemitropous, and allotropous insects." It seems as if one strand in the tradition of anthecology after two centuries bites its tail.

Acknowledgements

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