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Host plant preference of flower visitors in a mosaic landscape

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Abstract

We compared the flower visitors of 22 flowering plants by means of observation techniques. The study was carried out on the slopes of four hills situated in the Lahn-Dill-Bergland (Central Hesse, Germany). *Centaurea jacea* and *Knautia arvensis* had the broadest range of visiting taxa and are thus important for most flower visitors in small-scaled agricultural landscapes. The fact that honeybees deviated from this pattern confirms that this domestic species rapidly shifts between the most profitable nectar sources. In contrast to other European studies, our results indicate that the preference of bumblebees is only loosely related to the life span of plants and rather relies on optimal energy gain.

Eight groups of plants could be established by means of PCA and ANOVAs: wild bee plants, bumblebee plants, bumblebee/honeybee plants, honeybee plants, hover fly plants, Diptera plants, Coleoptera plants and »universal« plants. We identified plant species that are most suited for a taxon-specific approach to the study of flower visitors in small-scaled agricultural landscapes. It is concluded that the criteria for selecting target plants for monitoring flower visitors should include the region-specific preferences of the faunal taxa under consideration. Moreover, our data confirm the suitability of standardised observation techniques for comparative studies on flower visitors.

Zusammenfassung

Blütenbesuchergruppen und die von ihnen besuchten Blütenpflanzen in einer kleinstrukturierten Agrarlandschaft – Die Blütenbesucher an 22 Pflanzenarten wurden mittels Blütenbeobachtung verglichen. Die Studie wurde auf vier Hängen im Lahn-Dill-Bergland (Mittelhessen, Deutschland) durchgeführt. Die Pflanzen *Centaurea jacea* und *Knautia arvensis* wurden von der größten Zahl unterschiedlicher Taxa besucht und haben eine große Bedeutung für die meisten Blütenbesucher in der untersuchten kleinstrukturierten Agrarlandschaft. Dies trifft für die Honigbiene nicht zu. Hierdurch wird bestätigt, dass sich diese domestizierte Art nicht langfristig an die Blütenpflanzen einer Region anpasst, sondern kurzfristig die für sie einträglichsten Nektarquellen nutzt. Im Gegensatz zu anderen europäischen Studien zeigen unsere Ergebnisse, dass Hummeln, wenn perennierende und ein- bis zweijährige Pflanzen gleichermaßen zur Verfügung stehen, ihre Präferenz nicht an der Lebensdauer der Pflanzen, sondern am best möglichen Energiegewinn orientieren.

Mit Hilfe von PCA und ANOVA konnten acht Pflanzengruppen etabliert werden: Wildbienen-, Hummel-, Hummel/Honigbienen-, Honigbienen-, Schwebfliegen-, Diptera-, Coleoptera- und Universal-Pflanzen. Für bestimmte Blütenbesucher-Taxa konnten Pflanzenarten benannt werden, die sich für Blütenbeobachtungen in einer kleinstrukturierten Landschaft besonders eignen. Bei der Auswahl von Zielpflanzen für Blütenbeobachtungen müssen die regionsspezifischen Präferenzen der jeweiligen Tiergruppe berücksichtigt werden. Unsere Daten bestätigen die Eignung von standardisierter Blütenbeobachtung für vergleichenden Untersuchungen an Blütenbesuchern.

1. Introduction

Flower-visiting insects play an important ecological and economic role in agricultural landscapes. For example, about 84 % of the food plants cultivated in the EU depend on insect pollination (WILLIAMS 1996). Most pollinators are not specialised to particular plant species or families. Oligolectic behaviour has been demonstrated for many bees (WESTRICH 1989 and 1990), but not for butterflies (EBERT & RENNWALD 1991), beetles and Diptera (KUGLER 1970). However, due to the morphology of their mouthparts numerous taxa are confined to specific flowering plants (KUGLER 1970). Many flower visitors thus show forage constancy (KUGLER 1970). This and other species-specific characteristics of the collecting behaviour are spatially invariant. Other traits, in contrast, depend on external factors and may differ from site to site. External factors include flowering density (ALLISON 1990, AGREN 1996, KUNIN 1996), plant diversity (GINSBERG 1983), climatic conditions (HAESELER 1972), habitat isolation (STEFFAN-DEWENTER & TSCHARNTKE 1999), the degree of landscape fragmentation (AIZEN & FEINSINGER 1994, BERGE et al. 1998) and landscape complexity (STEFFAN-DEWENTER et al. 2001). Regional differences in the plants preferred by polylectic bee species have been reported (HAESELER 1972). Similarly, the collecting behaviour of bumblebees is assumed to be site-specific (TERÄS 1976, KEVAN & BAKER 1983, BOWERS 1985, KWAK et al. 1991).

Landscape level monitoring of pollinator diversity critically depends on a thorough examination of regional differences in host plant preference. Thus, the major aim of the study reported here was to analyse the specific associations between plants and flower visitors in a mosaic agricultural landscape of the Lahn-Dill-Bergland – a low mountain range in Hesse (Germany). This region was investigated in the context of a large-scale study on the impact of land-use change on insect communities (WOLTERS et al. 1999). By focusing on 22 flowering plants and their insect visitors we addressed the following questions: (i) are there region-specific patterns in the association between flower visitors and potential host plants, and (ii) are certain plant species particularly suited for monitoring selected groups of flower visitors? Moreover, data were gathered by flower observation to overcome the weaknesses of alternative approaches such as the laborious handling of non-target taxa associated with coloured traps or the site-specific bias associated with dip nets (AIZEN & FEINSINGER 1994, HAESELER 1995, STEFFAN-DEWENTER et al. 2001 and 2002). In addition, unnecessary killing of insects could be avoided. Though flower observation is a well-established technique for collecting qualitative data on flower visitors, standardised approaches allowing qualitative and quantitative comparisons of different observation results are still rare and purely tested (e.g. AIZEN & FEINSINGER 1994, STEFFAN-DEWENTER et al. 2001 and 2002). Therefore an additional question of our study was (iii) are

Tab. 1 Results of the Tukey-HSD-test on the preference of flower visitors for certain host plants. Figures indicate the number of plant species that were significantly less visited by the insect taxon listed in heading of the column than the target plant ($p < 0.05$; bold figures indicate high preference for the target plant). Plant determination follows WISSKIRCHEN & HAEÜPLER (1998). n^a = number of observation units for each plant species (flower, flower heads, umbels)

[illegible]

2. Materials and methods

The study was carried out at five periods of time during 1998 and 1999 on the slope of four hills situated in the rural district of Erda (Lahn-Dill-Bergland, Hesse, Germany). Each slope encompassed an area of app. 35 000 m² and was covered by a region-specific mosaic of grassland, arable land, abandoned land with scrubby vegetation, and forest edges. Soil types varied between sandy loam and loamy sand. 22 plants (or plant groups) were included in the study (Tab. 1).

Monitoring was confined to periods meeting the conditions of »standardised pollinator climate« as defined by WITSACK (1975), POLLARD et al. (1975), TERÄS (1976) and SCHWENINGER (1992). At each of the five observation periods we focused on plants (or plant groups) that were frequent on at least one of the slopes (>10 % of the flowers blooming at that time) (Tab. 2). Within each slope five units of these plants were randomly chosen. Each unit consisted of a defined number of flowers, flower heads or umbels, with the number being adjusted to the morphology of each plant species (Tab. 1). Each unit was observed for 10 minutes (cf. AIZEN & FEINSINGER 1994). In addition to the usual qualitative information this approach allowed a qualitative and quantitative comparison between different observation results. The density of the following insect taxa was determined: Coleoptera, Syrphidae, other Diptera, Lepidoptera, *Apis mellifera*, *Bombus* spp., other Apoidea, other Hymenoptera, and »other taxa«.

Tab. 2 Plant species on which flower visitors were registered during five observation periods that were carried out in 1998/99 on four slopes located in the Lahn-Dill-Bergland (n = number of observation units per plant species)

Period of observation	observed at all slopes (n = 20)	observed at only 1 – 3 slopes
Start of <i>Sarothamnus</i> blooming	<i>S. scoparius</i> , <i>R. acris</i> , <i>S. graminea</i> , <i>T. officinale</i> agg., <i>S. granulata</i>	<i>V. chamaedrys</i> / <i>V. arvensis</i> (n = 5), <i>P. saxifraga</i> (n = 5), <i>Crataegus</i> spec. (n = 5), <i>B. napus</i> (n = 5),
End of <i>Sarothamnus</i> blooming	<i>S. scoparius</i>	<i>A. arvensis</i> / <i>T. perforatum</i> (n = 15), <i>C. leucanthemum</i> (n = 10), <i>T. repens/pratense</i> (n = 5), <i>R. fruticosus</i> (n = 15), <i>S. graminea</i> (n = 5), <i>A. silvestris</i> (n = 10)
blooming of <i>Rubus</i>	<i>C. cyaneus</i> , <i>R. fruticosus</i>	<i>A. arvensis</i> / <i>T. perforatum</i> (n = 5), <i>T. repens/pratense</i> (n = 5), <i>B. napus</i> (n = 10),
blooming of <i>Centaurea</i>	<i>C. jacea</i> , <i>K. arvensis</i> , <i>A. arvensis</i> / <i>T. perforatum</i> , <i>T. repens/pratense</i>	<i>Leontodon</i> spec. (n = 15), <i>H. perforatum</i> (n = 5), <i>T. pulegioides/serpyllum</i> (n = 10), <i>V. sativa angustifolia/cracca</i> (n = 5)
blooming of <i>Campanula</i>	<i>C. rotundifolia/patula</i> , <i>P. saxifraga</i>	

The impact of the factor »plant« on flower visitors (dependent variables) was tested by means of one-way ANOVAs. Dependent variables were: (i) the number of taxa, (ii) the density of the individual taxa, and (iii) density of all taxa. Data sets not fulfilling the criterion of variance homogeneity (Sen and Puri's non-parametric test) were log-transformed. Differences between means were tested with Tukey's HSD test ($p < 0.05$). Plants were classified according to their flower visitors using a principal component analysis (PCA) with individual numbers of Coleoptera, Lepidoptera, Syrphidae, other Diptera, *Apis mellifera*, *Bombus* and other Apoidea as active variables. Plant species were used as supplementary variables, i.e. were not used for classification, but were plotted into the graph with respect to the active variables. All statistical analyses were carried out using STATISTICA for Windows 5.0 (StatSoft, Inc. 1995).

3. Results

A total of 10 218 flower visitors were recorded (see attachment). According to the results of the ANOVAs all dependent variables were significantly affected by the factor »plant« ($p < .0001$; all individuals $F = 9.6$, Lepidoptera $F = 55.0$, Coleoptera $F = 16.2$, Syrphidae $F = 15.4$, other Diptera $F = 17.1$, *Apis mellifera* $F = 26.0$, *Bombus* $F = 18.4$, other Apoidea $F = 5.6$, number of taxa $F = 5.73$). The comparison of means revealed that *C. jacea* and *K. arvensis* were visited by most insect taxa (Tab. 1). These two plant species were significantly preferred by butterflies, hover flies and wild bees (incl. bumblebees).

Host plant selection of the honeybee *Apis mellifera* was very variable (Tab. 1). This species preferred *R. fruticosus*, *C. cyanus*, *B. napus*, *T. pulegioides/serpyllum*, *Crataegus* spec. as well as *T. officinale*. Bumblebees favoured *Vicia* spp., while other wild bees preferred *Campanula* spp. In addition to *C. jacea* and *K. arvensis*, Syrphidae frequently occurred on *A. arvensis* and *T. perforatum* as well as on *Vicia* spp. Other Diptera preferred *Crataegus* spec., *P. saxifraga* and *R. acris*. Coleoptera favoured *B. napus*, *C. leucanthemum*, *Leontodon* spec. and *A. sylvestris*. *C. jacea*, *K. arvensis* and *Leontodon* spec. were the preferred host plants of butterflies (Tab. 1).

The results of the PCA with flower visitors as active and plants as supplementary variables are summarised in Fig. 1. The cumulative variance explanation is 40 % and the cumulative eigenvalue is 2.8. The exceptional position of *A. mellifera* is clearly shown. Some very loose similarities of this species to other taxa are confined to bumblebees and wild bees. Taxa exclusively including pollinating species are plotted on the right of the PCA diagram; less clearly defined taxa are plotted on the left. The taxa with the closest association to *C. jacea* and *K. arvensis* are plotted in the upper right. Based on these results and on the comparison of means (Tukey test; Tab. 1) eight partly overlapping plant groups can be established according to the host preference of flower visitors (Fig. 2): (A) »universal« plants (*C. jacea*, *K. arvensis*), (B) wild bee plants (*Campanula* spp.), (C) bumblebee plants (*Vicia* spp., *Trifolium* spp., *H. perforatum*), (D) bumblebee/honeybee plants (*C. cyanus*, *R. fruticosus*), (E) honeybee plants (*T. officinale*, *Crataegus* spec., *T. pulegioides/serpyllum*, *B. napus*), (F) hover fly plants (*Vicia* spp., *A. arvensis*, *T. perforatum*), (G) Diptera plants (*Crataegus* spec., *P. saxifraga*, *R. acris*, *C. leucanthemum*), and (H) Coleoptera plants (*C. leucanthemum*, *B. napus*, *Leontodon* spec., *A. sylvestris*).

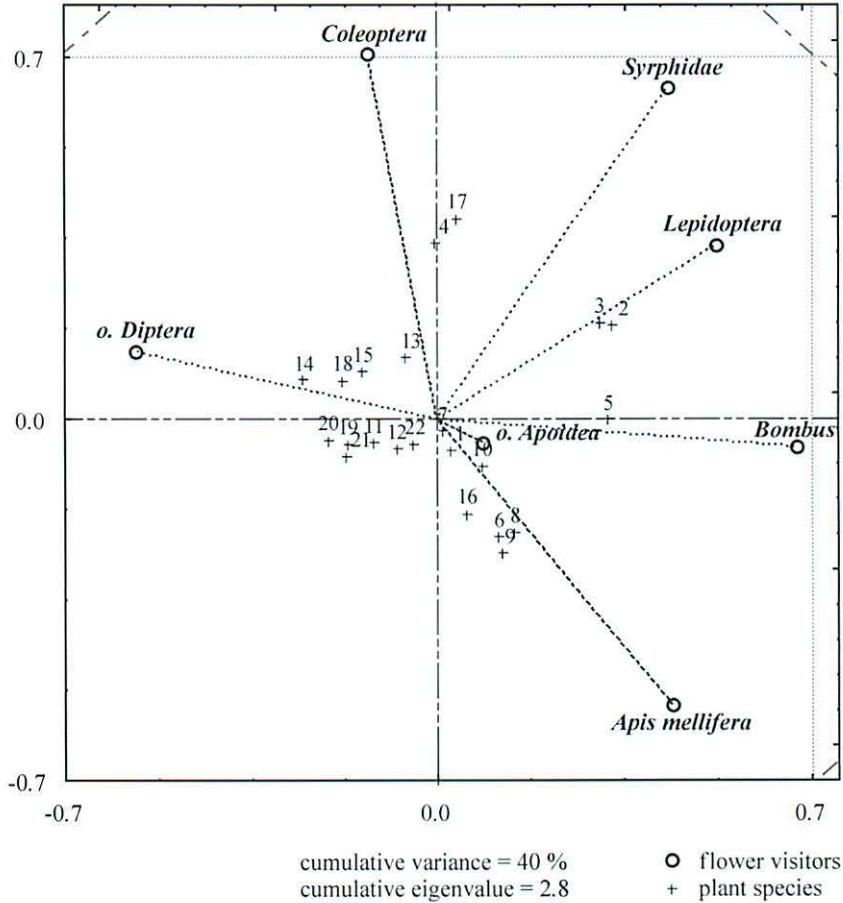


Fig. 1 Diagram of the PCA with flower visitors as active and plants as supplementary variables.

1 = *Campanula* spp. (*C. rotundifolia* and *C. patula*), 2 = *Centaurea jacea*, 3 = *Knautia arvensis*, 4 = *Anthemis arvensis*/*Tripleurospermum perforatum*, 5 = *Vicia* spp. (*V. sativa angustifolia* and *V. cracca*), 6 = *Trifolium* spp. (*T. repens* and *T. pratense*), 7 = *Hypericum perforatum*, 8 = *Rubus fruticosus*, 9 = *Centaurea cyanus*, 10 = *Thymus* spp. (*T. pulegioides* and *T. serpyllum*), 11 = *Taraxacum officinale* agg., 12 = *Crataegus* spec., 13 = *Pimpinella saxifraga*, 14 = *Ranunculus acris*, 15 = *Chrysanthemum leucanthemum*, 16 = *Brassica napus*, 17 = *Leontodon* spec., 18 = *Anthriscus silvestris*, 19 = *Saxifraga granulata*, 20 = *Stellaria graminea*, 21 = *Sarothamnus scoparius*, 22 = *Veronica* spp. (*V. chamaedrys* and *V. arvensis*)

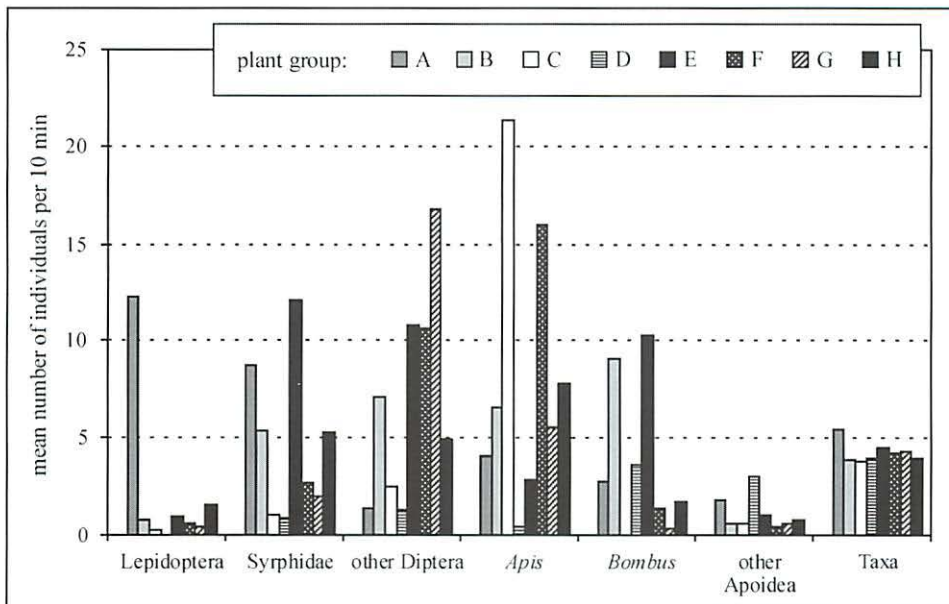


Fig. 2 Comparison of flower visitors per 10 min on the eight groups of flowering plants that are formed with respect to preference of flower visitors to these plants (A: »universal« plants, B: wild bee plants, C: bumblebee plants, D: bumblebee/honeybee plants, E: honeybee plants, F: hover fly plants, G: Diptera plants, H: Coleoptera plants; see text for explanations)

4. Discussion

Centaures jacea and *Knautia arvensis* obviously are important hosts to many flower-visitors in the small-scale landscape mosaic of Erda. The attraction of butterflies by the nectar provided by these two plants was particularly strong. However, even hover flies that are generally known to prefer other plant species were predominantly found on *C. jacea* and *K. arvensis*. The fact that the domestic species *Apis mellifera* does not fit to this pattern is consistent with the observation that honeybees tend to prefer other host plants than native pollinators (GINSBERG 1983, AIZEN & FEINSINGER 1994). This suggests that *A. mellifera* does not develop region-specific associations to certain flowering plants, but rather rapidly shifts between the most profitable nectar sources.

Bumblebees, similar to *Apis mellifera*, visited an exceptionally broad spectrum of host plants. This is due to the pronounced polylectic behaviour of this taxon allowing bumblebees to focus on the most profitable food sources available (cf. HEINRICH 1976, PYKE 1979, VISSCHER & SEELEY 1982). Our results also confirm that bumblebees are among the most important pollinators of *Trifolium pratense* (LAGERLÖF et al. 1992, FREE 1993) as well as of *Vicia cracca*, *C. jacea*, *Hypericum* spec. and *Rubus* spec. (DRAMSTAD & FRY 1995). The conclusion that bumblebees prefer perennial plants (FUSSEL & CORBET 1991 and 1992, DRAMSTAD & FRY 1995) seems to be supported by our results, since five of the seven

species categorised as »bumblebee plants« or »bumblebee/honey bee plants« are perennials. However, the most attractive host plants were the annual species *Vicia* spp. and *Centaurea cyanus*. This is consistent with MÄND et al. (2002), who report an increasing attraction of bumblebees to annual and biennial plants in agricultural landscapes. We hypothesise that this apparent contradiction can be explained by a methodological bias. Studies on flower visitors generally focus on areas that are dominated by perennial plants such as edge habitats, meadows, pastures and abandoned land and thus do not allow a comparative analysis of the impact of a plant's life cycle on bumblebees. Our results are not affected by this bias and support the view that the preference of bumblebees for certain food plants is primarily determined by the energy gain (WADDINGTON & HEINRICH 1979). Energy gain depends on factors such as plant morphology (HARDER 1985), productivity or accessibility (RICHARDS 2001) rather than on the duration of the life cycle.

The preference of wild bees for *Campanula* spp. is probably due to the dominance of *Chelostoma* species and *Melitta haemorrhoidalis*, i.e. taxa that are known to be oligolectic on bellflowers (WESTRICH 1990). Bellflowers also are highly attractive to many other oligolectic and polylectic bees (WESTRICH 1989). KEVAN (1999) has demonstrated that *A. arvensis* is the preferred pollen source for Syrphidae. The attraction of hover flies by *Anthemis arvensis*/*Tripleurospermum perforatum* and *C. jacea* found in our study corroborates the important role of Asteraceae for this taxon (LAGERLÖF et al. 1992). The often-reported preference of Syrphidae for yellow flowers (PESCHKEN 1965, SSYMANK 1991, SUTHERLAND et al. 1999) seems to be transient (KEVAN 1978). The high abundance of hover flies on the plant species listed above thus suggests that hover flies are able to adapt to regional differences in the availability of host plants. The marked preference of beetles for *Brassica napus* and *Leontodon* spec. is largely due to the high share of *Meligenethes aeneus* and other *Meligenethes* species (LETHMAYER et al. 1997). This genus responds very positively to the colour »yellow« (NOLTE 1955). Chervil and marguerite attract beetles because pollen and nectar of these plants is easily accessible (KUGLER 1970). The comparison of our results with the literature shows that some of the host plant preferences of flower visitors are common, whereas others seem to be region-specific.

In conclusion, our findings confirm the potential impact of regional conditions on host plant selection by flower visiting insects. The criteria for selecting target plants for monitoring flower visitors should definitely include the region-specific preferences of the faunal taxa under consideration. We suggest that studies aiming at surveying a broad spectrum of flower visitors in mosaic landscapes should focus on *Centaurea jacea* and *Knautia arvensis*. *Campanula* spp. should be included when wild bees that are oligolectic on bellflowers are of major concern. *Vicia* spp. are particularly suited for the simultaneous investigation of bumblebees and hover flies. *Meligenethes*-species (Coleoptera) and many butterflies can be surveyed by observing *Leontodon* spec. *Chrysanthemum leucanthemum* allows to broaden the scope from beetles to Diptera. And finally, we recommend *Pimpinella saxifraga*, *Ranunculus acris* or *Crataegus* spec. as target plants for investigating Diptera. The comparison with data from the literature also shows that the standardised observation technique is a reliable method for comparative studies on flower visitors.

Attachment Mean individual number ($\bar{O}$) and standard deviation (SD) of each flower-visitor group per observation unit of the 22 plant species

Plant	Lepidoptera		Coleoptera		Syrphidae		other Diptera		<i>Apis mellifera</i>		<i>Bombus</i> sp.		other Apoidea	
	$\bar{O}$	SD	$\bar{O}$	SD	$\bar{O}$	SD	$\bar{O}$	SD	$\bar{O}$	SD	$\bar{O}$	SD	$\bar{O}$	SD
1	0.00	0.00	1.65	1.31	0.85	0.93	1.30	1.03	0.45	0.83	3.65	3.88	7.15	5.69
2	12.65	8.28	1.00	1.65	9.05	9.85	0.80	0.95	4.45	6.89	2.50	2.42	9.05	8.29
3	11.95	6.40	1.65	2.03	8.45	9.66	2.00	2.03	3.65	5.17	2.95	3.05	8.80	6.89
4	0.33	0.53	5.08	3.44	14.08	13.67	4.70	4.60	2.08	4.03	0.13	0.33	4.68	4.86
5	1.60	1.52	0.20	0.45	10.20	3.35	0.80	0.84	3.60	5.32	20.40	11.30	24.20	13.55
6	0.67	1.09	0.17	0.46	2.67	3.92	0.97	1.71	15.67	10.04	2.93	3.56	19.37	12.54
7	0.00	0.00	0.40	0.55	3.20	4.15	3.40	3.36	0.40	0.55	3.80	1.92	5.00	3.16
8	0.43	1.24	2.71	2.30	1.37	2.61	4.54	12.12	21.71	20.59	3.00	4.24	25.29	21.47
9	0.15	0.49	0.00	0.00	0.70	0.98	0.50	0.83	21.00	11.95	2.80	1.96	24.80	12.50
10	1.40	0.97	0.20	0.63	4.50	3.37	5.70	3.68	15.90	13.50	3.70	4.03	20.40	16.77
11	0.05	0.22	2.85	2.30	0.50	0.83	5.80	6.28	5.25	3.06	0.20	0.52	0.00	0.00
12	0.40	0.89	2.00	0.00	3.00	5.20	29.20	11.56	19.80	18.35	1.40	1.52	24.60	20.37
13	2.20	3.35	9.00	4.53	6.40	7.64	5.00	4.95	0.40	0.89	0.00	0.00	3.80	3.70
14	0.55	0.89	4.05	4.55	1.60	1.73	15.95	15.85	0.00	0.00	0.00	0.00	1.10	1.45
15	0.50	0.85	7.00	6.57	2.10	1.91	11.40	9.14	2.10	5.95	0.00	0.00	3.00	5.91
16	0.40	0.63	0.67	0.90	2.73	3.56	1.80	1.70	23.00	16.21	0.33	0.49	23.47	16.06
17	2.47	2.47	14.67	12.42	10.27	7.23	0.60	0.99	1.13	2.88	1.80	3.32	3.80	3.97
18	0.20	0.41	5.60	4.37	1.13	1.77	10.53	3.66	0.33	0.82	0.00	0.00	1.67	1.99
19	0.10	0.31	1.25	1.77	0.00	0.00	7.30	5.29	0.05	0.22	0.05	0.22	0.00	0.00
20	0.16	0.37	1.40	1.78	0.48	0.65	10.32	7.53	0.60	1.78	0.24	0.44	1.80	2.58
21	0.17	0.53	2.63	2.62	0.93	1.33	3.37	3.98	3.75	5.09	0.25	0.54	1.85	3.95
22	0.00	0.00	0.00	0.00	0.20	0.45	1.60	2.07	0.00	0.00	0.00	0.00	2.40	2.88

1 = *Campanula* spp. (*C. rotundifolia* and *C. patula*), 2 = *Centaurea jacea*, 3 = *Knautia arvensis*, 4 = *Anthemis arvensis* / *Tripleurospermum perforatum*, 5 = *Vicia* spp. (*V. sativa angustifolia* and *V. cracca*), 6 = *Trifolium* spp. (*T. repens* and *T. pratense*), 7 = *Hypericum perforatum*, 8 = *Rubus fruticosus*, 9 = *Centaurea cyanus*, 10 = *Thymus* spp. (*T. pulegioides* and *T. serpyllum*), 11 = *Taraxacum officinale* agg., 12 = *Crataegus* spec., 13 = *Pimpinella saxifraga*, 14 = *Ranunculus acris*, 15 = *Chrysanthemum leucanthemum*, 16 = *Brassica napus*, 17 = *Leontodon* spec., 18 = *Anthriscus silvestris*, 19 = *Saxifraga granulata*, 20 = *Stellaria graminea*, 21 = *Sarothamnus scoparius*, 22 = *Veronica* spp. (*V. chamaedrys* and *V. arvensis*)

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