

Compartmentalization in plant–insect flower visitor webs

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Summary

1. Interactions between entomophilous flowering plants and their insect visitors were recorded at two mesotrophic grassland communities in Norfolk, and a diagrammatic quantitative web produced for each community.

2. The systems were analysed for compartmentalization using the method of Raffaelli & Hall (1992), based on trophic similarity between pairs of species. Good evidence was found for compartmentalization at both sites.

3. Ordination of the data was used to suggest how the species fall into compartments. The likelihood that groups of plants and insects implied by this method represent real compartments in the web was assessed quantitatively, using trophic similarity indices, and qualitatively, by consideration of the species involved.

4. The compartments reflected classic pollination syndromes to some extent, dividing the insect fauna into a group of butterflies and bees, and a group of flies, at both sites. The compartmentalization was also affected by phenology.

5. Dominant interactions fell within compartments in the web, as might be expected in mutualistic systems.

Key-words: community, mutualism, pollination syndromes, trophic similarity.

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Introduction

Compartmentalization describes the way a food web can be divided into subsections, or compartments, such that organisms within a compartment interact more strongly with one another than with species in other compartments in the web. It is an aspect of food web structure that has attracted interest because it has been related to the stability of the web by theoretical ecologists: May (1973) suggested that compartments could increase a web's stability, while in Pimm's (1982) models, division into compartments made food webs less stable. The search for compartmentalization in real food webs has so far produced varied results, using a number of different detection methods (Pimm & Lawton 1980; Raffaelli & Hall 1992; Memmott, Godfray & Gauld 1994), and has suffered from a shortage of comprehensive data sets.

Pimm & Lawton (1980) devised a statistical test that compared a compartmentalization statistic with the distribution of that statistic from a set of randomly generated webs of similar parameters. Five out of the 12 real data sets they analysed, all of them aquatic,

showed a high probability of being truly compartmentalized, but the average probability across all webs was less than 0.5. However, their method becomes unmanageable when complete food webs containing 50–100 species are considered. Raffaelli & Hall (1992) suggested a simpler method of looking for compartmentalization, based on the distribution of trophic similarity indices between pairs of species. This method, although not so rigorous, agreed with Pimm & Lawton's (1980) when applied to the same data sets. Raffaelli & Hall (1992) applied it to an extensive and well-studied estuarine food web and found no evidence of compartmentalization. Other authors have looked for compartmentalization visually, without using these formal methods. Memmott *et al.* (1994) found no compartmentalization in their tropical leaf miner parasitoid web, but compartmentalization was implied in the food webs of Thomas (1990) and strongly apparent in the ant–myrmecophyte system of Fonseca & Ganade (1996).

It seems likely that certain types of ecological interaction will produce webs that tend to fall into compartments, while others will not. Paine (1980) proposed that the existence of a strong, dominant, interaction leads to the presence of modules of interacting species that are dependent on the effects of the dominant. For example, the presence of the predatory starfish *Pisaster* facilitates the existence of a network of other

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interacting species of predator and prey, by limiting numbers of the mussel *Mytilus californianus*. The dominant interacting species thus create a compartment, but are themselves outside it. As pointed out by Thomas (1990), this logic only applies when the interactions under consideration are negative. In mutualistic systems, strong interactions might be expected to occur within compartments. It is arguable that mutualistic interactions encourage the organization of webs into modules or compartments, by promoting specialized relationships between pairs or groups of species. The only terrestrial food web in which compartmentalization has so far been identified was indeed a system of mutualists (Fonseca & Ganade 1996).

The interaction between flowering plants and their potential pollinators is somewhere we might expect to find compartmentalization (Corbet 2000b) because of the tendency of zoophilous plants to fall into identifiable types or 'syndromes' associated with types of visitor (Faegri & Pijl 1979). Bee-pollinated plants, for example, have nectar-rich flowers with long corolla tubes, in contrast to plants that are beetle- or fly-pollinated and have small, open, pollen-rich flowers. There has been much speculation about the reality or otherwise of pollination syndromes (Johnson & Steiner 2000) since it was pointed out that pollination systems more often consist of generalized interactions (Waser *et al.* 1996). Here, we quantitatively analysed two plant–insect visitor webs for compartmentalization, using Raffaelli & Hall's (1992) method, and attempted to identify the species involved in the compartments, to see if they do indeed fall into the groups that might be expected from observed pollination syndromes.

The use of complete plant–flower visitor webs to address questions in community ecology has been hampered by a lack of empirical data sets (Waser *et al.* 1996) due to the taxonomic and logistical difficulties of including all flower visitors. There are several published studies that consider total plant–visitor systems (Mosquin & Martin 1967; Hocking 1968; Kevan 1972; Moldenke & Lincoln 1979; Moldenke 1979; Parrish & Bazzaz 1979; Arroyo, Primack & Amnesto 1982; Primack 1983; Herrera 1988; Inouye & Pyke 1988; McCall & Primack 1992; Petanidou & Ellis 1993; Struck 1994; Bosch, Retana & Cerdá 1997; Elberling & Olesen 1999; Memmott 1999; Hingston & McQuillan 2000). Many of these find that the system is dominated by generalized interactions (Moldenke & Lincoln 1979; Primack 1983; Herrera 1988; Elberling & Olesen 1999; Memmott 1999), with plant species often visited by several orders of insect. However, only a small number have actually quantified the frequency of different interactions (Parrish & Bazzaz 1979; Herrera 1988; Bosch *et al.* 1997; Memmott 1999), and only in a single study have interactions been quantified at the species or morphotype level (Memmott 1999) rather than at the level of family or order of visitor.

Herrera (1988), McCall & Primack (1992), Bosch *et al.* (1997) and Hingston & McQuillan (2000) used

the data to look for associations of plant species into pollination syndromes with similar visitor profiles and floral characteristics. All found that pollination syndromes espoused by Faegri & Pijl (1979) did not correlate particularly well with plant visitor profiles, although Hingston & McQuillan (2000) found some evidence of bird and bee syndromes and McCall & Primack (1992) found that flower colour was important in determining visitor identity. In other studies, flowering phenology (Herrera 1988) or the quantity of pollen or nectar reward offered (Bosch *et al.* 1997) were found to have more effect on visitor profiles than visible floral traits.

None of these studies tested the plant–flower visitor web for compartmentalization.

Materials and methods

Our field sites were two hay meadows in Norfolk, UK, with similar plant communities (MG5a, *Cynosurus cristatus*–*Centaurea nigra*: *Lathyrus pratensis* subcommunity; Rodwell 1992) and management regimes (mid-July cut and aftermath grazing). Site 1 is an ancient hay meadow, with site of special scientific interest (SSSI) status, at Shelfanger, near Diss. Site 2 is a restoration experiment, seeded in 1994, located at Hickling Broad National Nature Reserve (Pywell *et al.* 1999). Both sites have a relatively uniform plant community.

Insect species composition and abundances were recorded at both sites using a standard 1-m wide belt transect method (Banaszak 1980; Fussell & Corbet 1992). A 100-m transect was walked at a slow pace, and each individual insect seen feeding on a flower within a 1-m strip to one side of the observer was recorded. The first species of flower each insect was seen visiting was recorded. No distinction was made between different types of feeding behaviour. All Hymenoptera, Lepidoptera, Diptera and Coleoptera, longer than 3 mm, were included. The size threshold was imposed to ensure consistency, because smaller insects are easy to miss, can be extremely difficult to identify whilst walking a transect and cannot be comprehensively collected without disturbing insect–flower interactions.

The transect was marked out as 10 parallel, randomly positioned, 10-m sections at the start of the season, and the same route followed each time. Walks were carried out fortnightly between 14 April and 13 May, then weekly until 16 July, on days when conditions conformed to the microclimatic window defined for the national Butterfly Monitoring Scheme (Pollard & Yates 1993). Three walks were carried out each day between the following times: 09:00–10:30, 12:30–14:00, 16:00–17:30.

Insects were recorded to species as far as possible. When an insect was not identifiable immediately, the insect was caught and labelled for later identification. Identifications were carried out using standard keys and the extensive British reference collection at the Cambridge University Museum of Zoology. Specialist

taxonomists provided advice on solitary bees and non-syrphid Diptera, and checked identification of difficult specimens (see the Acknowledgements). Our reference collection of voucher specimens is held in the Department of Zoology, Cambridge University, Cambridge, UK.

Some common insects that cannot be distinguished to species in the field were grouped into morphotypes, an approach that is considered acceptable in the study of food webs (Memmott & Godfray 1993). For common morphotypes, 10 specimens were taken and identified to species. This information is not included here because there are no data on the frequency of interactions of each species within a morphotype. Full species lists are available from the corresponding author. For simplicity, the word species is used to mean species or morphotype in the remainder of this paper.

Abundance of flowering plants was recorded fortnightly between 14 April and 16 July, along the same 100-m transect. Five quadrats were randomly positioned in each of the 10-m sections, and the number of blossom units (Saville 1993) of each flowering species, excluding grasses, was recorded. A blossom unit is defined as the floral unit that a medium-sized bee has to fly, rather than walk, between.

Compartmentalization was tested for using the method of Raffaelli & Hall (1992), which is based on the shape of the frequency distribution of trophic similarity indices. Trophic similarity, represented by the Jaccard coefficient, was calculated between all pairs of species in the web as follows:

$$S_{ij} = \frac{a}{a+b+c}$$

where a is the number of species involved in interactions with both species i and species j ; b is the number of species involved in interactions with i only; and c is the number of species involved in interactions with j only. If the web has compartments, we expect the frequency distribution of S_{ij} values to be bimodal or polymodal, because pairs of species within compartments will have high S_{ij} values, while pairs of species not in the same compartment will have low S_{ij} values. If the web has no compartments, we expect a unimodal distribution. The modality of the distribution is calculated as the number of peaks above the average frequency for that distribution.

This method is not a rigorous statistical test for compartmentalization, because it does not use comparison with randomly generated webs to calculate the probability that the given arrangement of interactions has arisen by chance. However, it provides a strong quantitative indication of whether a web is compartmentalized.

Trophic similarity indices were calculated between all pairs of plant species and all pairs of insect species, but not between pairs containing one plant and one insect, because in a two-tier web such as this there

are no shared interactions between species in different trophic levels. Plants recorded in quadrats but not visited by insects were not included, because they were not strictly part of the interaction web. Raffaelli & Hall (1992) point out that the number of peaks depends on the number of size classes used in the distribution, and in small webs with few matrix elements the distribution of S_{ij} values may be discontinuous, causing polymodality to emerge if a large number of size classes is used. They counter this effect when comparing webs of different sizes by devising a standardizing scale in which small webs are viewed with a smaller number of similarity classes than large webs. Because our webs were both larger than any of the webs used by Raffaelli & Hall (1992) (750 and 1966 possible pairwise interactions at Shelfanger and Hickling, respectively) this problem should not affect our conclusions. We used one more than the maximum number of classes used in their scale, which is for webs with up to 500 possible interacting pairs. We also checked the shape of the distributions with 10 size classes, to ensure that any polymodality is retained if fewer size classes are used.

A polymodal distribution of trophic similarity indices strongly implies compartmentalization, but tells us nothing about the identities of the species in different compartments. We carried out a correspondence analysis (ter Braak 1988) on the quantitative interaction data, to investigate how the insect and plant species fall into groups, based on the species they interact with (Raffaelli & Hall 1992). In the ordination, units were insect species and variables were the proportional abundance of visits to each plant species. Proportional values were used to avoid bias due to the large differences in abundance of different plant species. Inputs were the proportion of all visits by each insect species that were to each particular plant species. To remove noise from the data and simplify presentation, species represented by < 5 observations were not included in the analysis. This left 10 plant species and 16 insect species in the analysis at Shelfanger, and 12 plant species and 37 insect species at Hickling.

The results of the correspondence analyses were presented on a two-axis plot, and groups of plant and insect species that fell close together were defined. Analyses of variance were carried out on the scores within each group, to test whether the groups were significantly different from one another.

Groups of species suggested by ordination were then scrutinized using two different approaches to assess whether they represented real compartments in the web. The first was quantitative. If these groups represent compartments in the web, we expect the mean trophic similarity index (S_{ij}) between species within a group to be greater than the mean S_{ij} between species of that group and species outside the group. A two-sample t -test comparing the within-group S_{ij} values with between-group S_{ij} values for each group was used as a simple statistical test of whether a group fits this criterion for a compartment in the web.

The second approach was to ask the more subjective question: do the groups defined by ordination make ecological sense? Because we predicted compartmentalization in these webs on the basis of functional morphotypes in plants that correspond to the types of insect visitor they supply, we might expect the compartments in the web to reflect such plant morphotypes.

Results

Thirty-six species of insect and 29 species of plant were recorded at Shelfanger; 61 species of insect and 21 species of plant were recorded at Hickling. The insect visitor community was dominated in abundance by social Hymenoptera at Shelfanger, and by Diptera at Hickling. The mean number of plant species–insect species was 2.36 (maximum 10) at Shelfanger, and 2.39 (maximum 10) at Hickling. Plants were more generalized, being visited by a mean of 2.93 (maximum 21) insect species at Shelfanger and 6.95 (maximum 49) species at Hickling. A total of 980 interactions was recorded at Shelfanger, and 3150 interactions at Hickling.

Insect and plant abundances were totalled over the entire season, and used to construct a quantitative interaction web for each site. Webs are presented in Fig. 1, in the style used by Memmott (1999). As well as providing a visual representation of the data, these webs give an indication of the structure of the communities and where we might expect to see compartments. The species or species groups are listed in the Appendix.

Figure 2 shows the distributions of S_{ij} for our two hay meadows. There was clear evidence of compartmentalization in both cases. At Shelfanger the distribution was bimodal. At Hickling there were four peaks above the average frequency for the distribution. In both cases, the bi- or polymodality was preserved when the trophic similarity distribution was viewed at a lower resolution of 10 similarity classes.

Figure 3 shows the results of correspondence analysis at each site, with insects and plants presented on separate graphs for clarity. At each site, species fell

into a number of discrete groups that could represent compartments. Analysis of variance of the two axis values showed that all of these groups were significantly different from one another on at least one axis. The species or morphotypes that fell into each group are listed in Tables 1 and 2. Table 3 compares mean S_{ij} values within and between groups, and suggests ecological features that seem to define the groups.

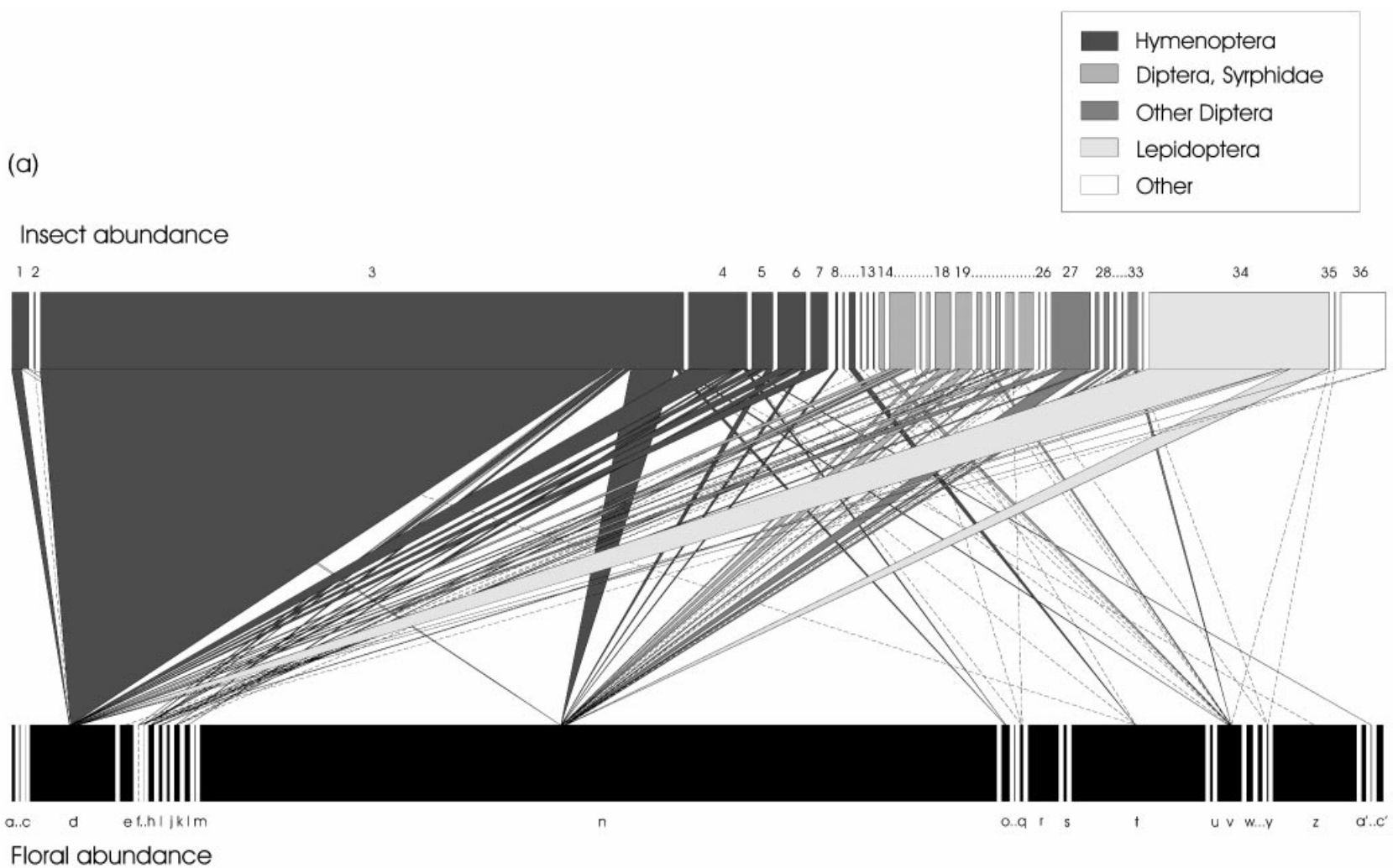
At Shelfanger, the species fell into three groups in the initial analysis. Group 1 comprised mostly bees and butterflies, and the nectar-rich plants that they visited. There were two anomalies in this group, the syrphid fly *Syrphus* sp. and the Hemipteran *Calocoris bipunctatus*. Both species spent the majority of their time visiting *Centaurea nigra*, in common with the bees and butterflies. In the case of *Syrphus* sp. this was a phenological effect, as this species appeared after the peak flowering of *Leucanthemum vulgare*. *Calocoris bipunctatus* was frequently recorded visiting *Centaurea nigra*, although it is not clear whether the species was consuming nectar or pollen, or visiting the flowers for some other reason.

Group 2 comprised flies, and open flowers providing pollen but not large quantities of nectar. Group 3 represented a single interaction between *Anthophora plumipes* and *Primula veris*. This interaction took place in the early spring, at a time when very few other insects or flowers were in evidence. As neither species interacted five or more times with any other species, it was possible to remove this interaction from the analysis simply by removing the two species involved.

The correspondence analysis of the Shelfanger data excluding the *Primula veris*–*Anthophora plumipes* interaction is shown in Fig. 4. Groups 1 and 2 are now isolated more convincingly, being significantly different in their scores on both axes. However, two insect species and three plant species from the fly group now comprise a separate group, as indicated in Table 3. This group, group 4, contained hoverfly species, and some plants that were pollen rich. The distinction from group 2 seemed to be that these fly species did not spend most of their time visiting *Leucanthemum vulgare*, the most

Table 1. Groups identified by ordination at Shelfanger. Underlined species in group 2 are transferred to a separate group (group 4) when the ordination is repeated without the species in group 3, as shown in Fig. 4

	Group 1	Group 2	Group 3
Insects	<i>Bombus terrestris/lucorum</i> <i>B. lapidarius</i> <i>B. pascuorum</i> <i>B. pratorum</i> <i>Psithyrus vestalis</i> <i>Apis mellifera</i> <i>Syrphus</i> sp. <i>Maniola jurtina</i> <i>Calocoris bipunctatus</i>	<u><i>Episyrphus balteatus</i></u> <i>Eristalis tenax</i> <i>Helophilus</i> sp. <u><i>Sphaerophoria</i> sp.</u> <i>Empis livida</i> <i>Scathophaga stercoraria</i>	<i>Anthophora plumipes</i>
Plants	<i>Centaurea nigra</i> <i>Cirsium arvense</i> <i>C. palustre</i> <i>Lotus corniculatus</i>	<u><i>Filipendula ulmaria</i></u> <u><i>Galium verum</i></u> <u><i>Hypochoeris radicata</i></u> <i>Leucanthemum vulgare</i> <i>Ranunculus acris</i>	<i>Primula veris</i>



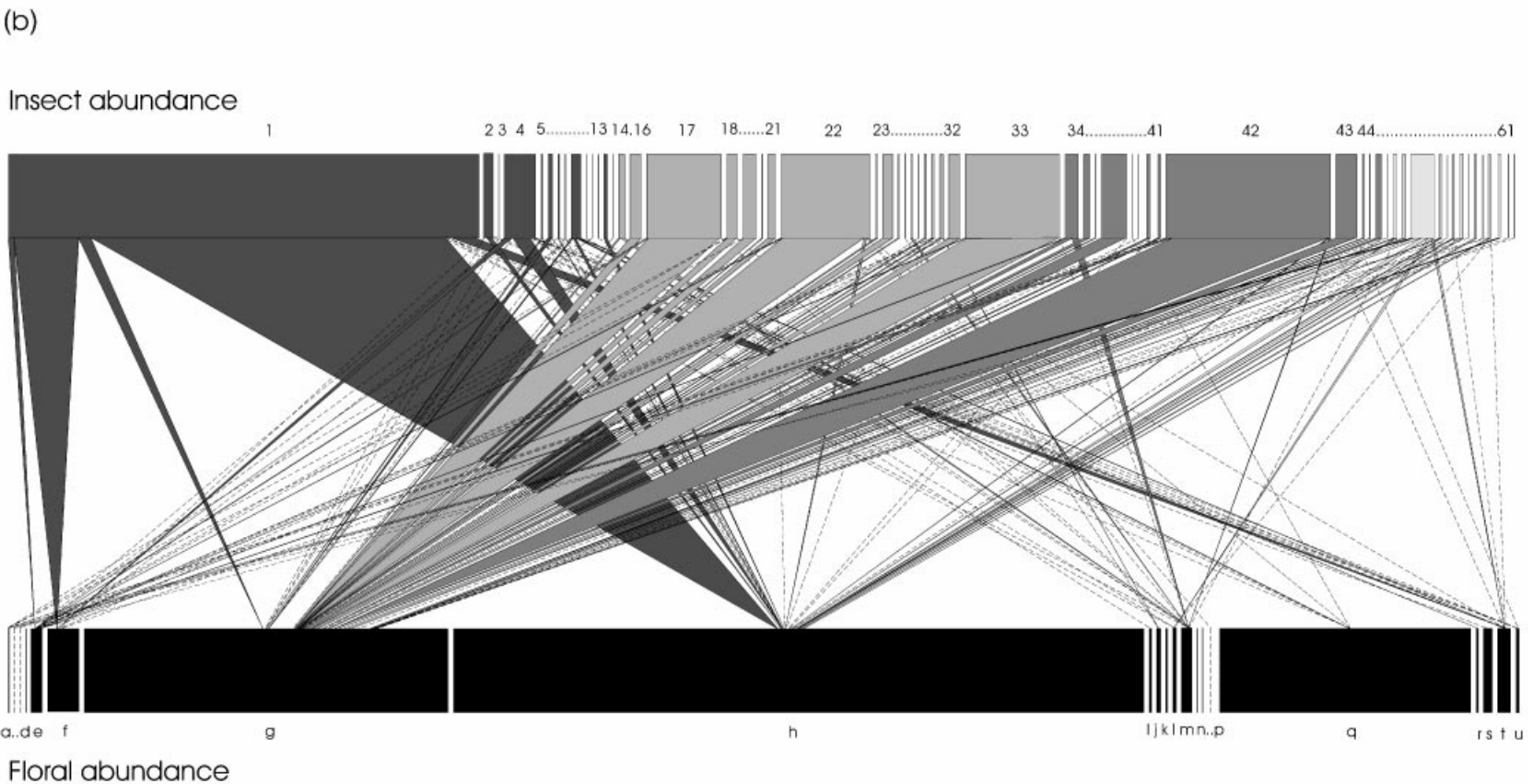


Fig. 1. Quantitative plant–visitor webs for (a) Shelfanger and (b) Hickling. Each species/morphotype of plant and insect is represented by a rectangle. Species identities are listed in the Appendix. The width of the rectangles is proportional to their abundance at the field site. Plants shown with a dotted line were present at the site but not recorded by sampling. Interactions are shown as connecting triangles, the sizes of which reflect the proportion of all recorded visits by that insect that were to that particular plant. Interactions shown as a dotted line were observed only once during the sampling period.

Table 2. Groups identified by ordination at Hickling

	Group 1	Group 2	Group 3
Insects	<i>Bombus. terrestris/lucorum</i> <i>B. hortorum</i> <i>B. pascuorum</i> <i>Andrena wilkella</i> <i>Megachile willughbiella</i> <i>Lasiommata megera</i> <i>Maniola jurtina</i> <i>Polyommatus icarus</i> <i>Thymelicus</i> sp. <i>Zygaena filipendulae</i>	<i>Psithyrus vestalis</i> <i>Chrysogaster</i> sp. <i>Eristalis sepulchralis</i> <i>Eristalis intricarius</i> <i>Eristalis</i> sp. (<i>E. nemorum</i> + similar) <i>Eristalis tenax</i> <i>Helophilus</i> sp. <i>Helophilus trivittatus</i> <i>Lejogaster</i> sp. <i>Platycheirus</i> sp. <i>Sphaerophoria</i> sp. <i>Syrphus</i> sp. <i>Syrphid pipiens</i> <i>Tropidia scita</i> <i>Empis livida</i> <i>Lucilia</i> sp. <i>Odontomyia tigrina</i> <i>O. viridula</i> <i>Phaonia incana</i> <i>Pollenia</i> sp. <i>Rhagio tringarius</i> <i>Scathophaga stercoraria</i> <i>Lycaena phlaeas</i> <i>Microlepidoptera</i> sp. 1	<i>Cheilosia albitarsis</i> <i>Neosasia tenur</i> <i>Anthomyid species 1</i>
Plants	<i>Centaurea nigra</i> <i>Lathyrus pratensis</i> <i>Lotus corniculatus</i> <i>Prunella vulgaris</i> <i>Trifolium dubium</i> <i>T. repens</i> <i>Vicia cracca</i> <i>V. sativa</i>	<i>Achillea millefolium</i> <i>Hypochoeris radicata</i> <i>Leucanthemum vulgare</i>	<i>Ranunculus acris</i>

Table 3. Are the groups identified by ordination real compartments in the web? This table suggests functional definitions for each group, and shows results of quantitative analyses of trophic indices. *P*-values are from a one-tailed two-sample *t*-test of within vs. between group S_{ij} values for each group. S, Shelfanger; H, Hickling

Site	Group	Possible biological definition of the group	Mean S_{ij} within group	Mean S_{ij} with other groups	<i>P</i> -value
S	1	Mostly bees/butterflies and nectar-rich flowers with long corolla tubes.	0.31	0.22	0.004*
S	2	Flies and open, nectar-poor, flowers	0.24	0.21	0.16
S	3	A single early spring interaction	—	0.05	—
S	4	Hoverfly species mainly visiting plants other than <i>Leucanthemum vulgare</i>	0.32	0.13	0.017*
S	2 with group 4 species removed	Flies visiting mainly <i>Leucanthemum vulgare</i> and <i>Ranunculus acris</i>	0.38	0.24	0.035*
H	1	Bees/butterflies and nectar-rich flowers with long corolla tubes	0.30	0.24	0.010*
H	2	Mostly flies and open, nectar-poor, flowers	0.45	0.25	0.000*
H	3	Flies visiting mainly <i>Ranunculus acris</i>	0.50	0.24	0.057

*Significant at $\alpha = 0.05$.

abundant pollen-rich plant in the community, and did not visit *Ranunculus acris* at all. The flies remaining in group 2 all visited *Leucanthemum vulgare* more than any other species and, with the exception of a single visit by *Eristalis tenax*, did not visit *Filipendula ulmaria*, *Galium verum* or *Hypochoeris radicata* at all.

Group 1 and group 4 met the quantitative test for a true compartment, as did group 2 after the extraction of the species in group 4. It was not possible to carry

out the *t*-test on group 3 because there was only a single within-group S_{ij} value.

At Hickling, the species fell into three groups, all of which were significantly different on both axes. Group 1 comprised bees and butterflies visiting nectar-rich flowers. Group 2 comprised mostly flies visiting open, nectar-poor, flowers. The third group in this case was a group of three insects associated with *Ranunculus acris*. One of these, the syrphid *Cheilosia albitarsis*, is known

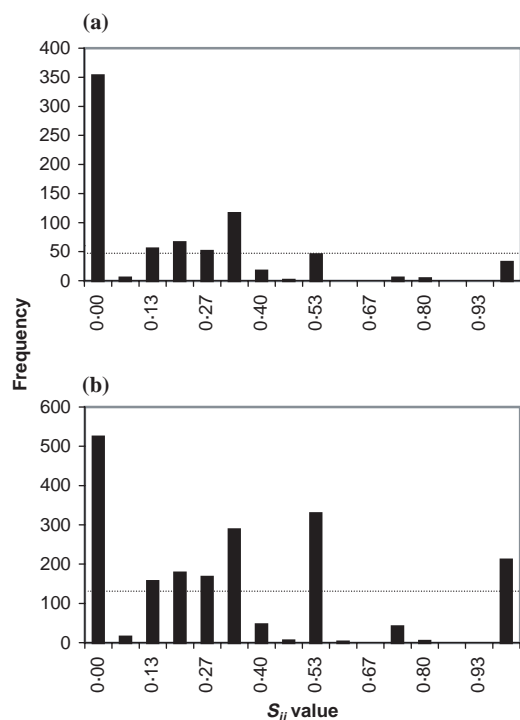


Fig. 2. Frequency distribution of S_{ij} values at (a) Shelfanger and (b) Hickling, showing bi- and polymodality, respectively. The mean frequency for each distribution is represented by a dotted line.

to have an association with *Ranunculus* species (Stubbs & Falk 1996).

Groups 1 and 2 convincingly met the quantitative test for a real compartment. The presence of the cuckoo

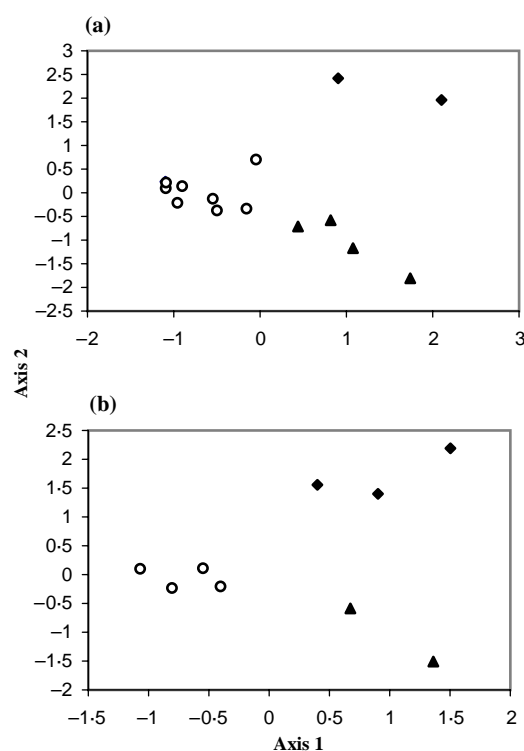


Fig. 4. Results of the correspondence analysis on Shelfanger data with the *Primula veris* and *Anthophora plumipes* excluded: (a) insects; (b) plants. Circles = group 1; triangles = group 2; diamonds = group 4.

bee *Psithyrus vestalis* in group 2 was anomalous and reflected the behaviour of this species. Not foraging for a brood, these bees are often found resting on composite flowers for long periods of time (L. V. Dicks, personal

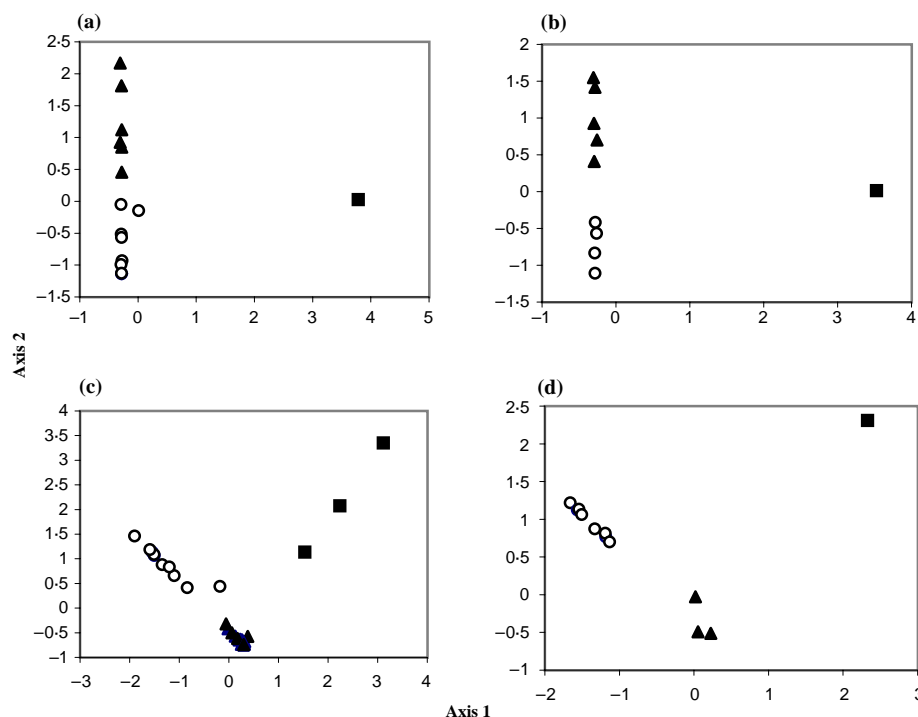


Fig. 3. Results of correspondence analyses on species interaction data, showing how the insects and plants at each site fall into groups: (a) insects and (b) plants at Shelfanger; (c) insects and (d) plants at Hickling. Circles = group 1; triangles = group 2; squares = group 3.

observation). The same species was in group 1 at Shelfanger, where it was associated mostly with *Centaurea nigra*. At Hickling, the most common composite flower was *Leucanthemum vulgare* and so the species was associated with this plant. There were also two species of Lepidoptera in group 2. One was a very small moth species that aggregated on *Leucanthemum vulgare* capitula. The other, *Lycaena phlaeas*, has a shorter tongue than the other butterfly species in this community (Corbet 2000a) and may therefore prefer to feed from flowers with shorter corolla tubes.

Group 3 did not meet the quantitative test for a true compartment, but this may be because the small number of species in the group reduced the power of the test.

The groups defined by ordination all seemed to represent true compartments in the webs, in that they all reflected true foraging relationships and, with one exception, they met our quantitative test. Do the compartments in these two plant–visitor webs meet with ecological expectations based on pollination syndromes? To a large extent they do. At both sites, bees and butterflies, large insects which require large quantities of nectar, were grouped with plants with pink, purple or yellow tubular flowers and long corolla tubes, and flies were grouped with open, yellow or white less nectar-rich flowers.

However, flies and fly flowers were further separated at both sites, into separate compartments that reflected foraging relationships but did not seem to fit any generalized pattern of plant–insect interactions or plant morphology. In common with the findings of Hingston & McQuillan (2000), there was no separate butterfly group, although a butterfly pollination syndrome (Faegri & Pijl 1979) is often alluded to in the literature.

Members of the plant family Asteraceae were split between the bee/butterfly and the fly group at both sites, seemingly on the basis of colour. Those with purple florets were visited by bees and butterflies, while yellow- or white-flowered species were visited by flies. This seems likely to be related to the quantity of nectar available, and the length of the corolla. Petanidou & Smets (1995) measured quantity of sucrose per flower for a range of plant species in the Greek phrygana, and found that members of the thistle and knapweed genera *Centaurea* and *Carlina* had more than an order of magnitude more sugar per floret than members of the genus *Hypochoeris*, and florets at least twice as deep. Unfortunately, because we did not measure floral characteristics directly in this study, it was not possible to be certain that the same was true of our species.

Discussion

The two plant–visitor systems studied here are similar to temperate communities studied by other authors in the generalized nature of many of the interactions, particularly in the case of plants (Moldenke & Lincoln 1979; Primack 1983; Herrera 1988; Elberling & Olesen

1999; Memmott 1999). Most plants are visited by two or more orders of insect.

The number of species in these systems may be underestimated, due to the exclusion of very small insects. Insects in the < 3 mm size category are most likely to be flies, beetles or thrips, so these groups are under-represented in the data. However, in order to gather quantitative data on the interactions themselves, it is necessary to record insects to a taxonomic resolution that can be defined in a field situation with as little need for intrusive capturing as possible. This can either be achieved by identifying to family or higher, or by identifying to morphotype and to species wherever possible and excluding very small insects. We felt the latter approach would provide more information about the true nature of the community.

The use of these quantitative data in the multivariate analysis provides a better assessment of how species fall into groups according to their interactions than if binary data are used, as in other studies (Raffaelli & Hall 1992; Hingston & McQuillan 2000). For example, both *Lathyrus pratensis* and *Trifolium dubium* were visited by six insect species at Hickling. *Lathyrus pratensis* was quite specialized, receiving 89% of its visits from *Bombus terrestris/lucorum*. *Trifolium dubium*, on the other hand, was more generalized, receiving approximately 40% of its visits from each of two different bee species, and 5% of its visits from four other species, two of which were flies.

The observation that plants are more generalized than insects in these systems is not surprising, when the nature of pollinating systems is considered. There are invariably many more insect species than plant species, and most insects show a degree of generality in their foraging choice (Waser *et al.* 1996). As pointed out by Elberling & Olesen (1999), this leads to plant species having far more generalized interactions than the insect species in pollination webs.

It is partly for the same reason that the compartmentalization of our plant–visitor webs does not separate out all of the possible pollination syndromes. Neither butterflies, nor Corbet's proposed long-tongued bee compartment (Corbet 2000b), for example, are apparent. If the plant species richness equalled that of insects, we might expect the separation of compartments to be more complete. But with a limited number of flower types to choose from, many insects make opportunistic use of forage plants that are not ideally suited to them. The long-tongued bee species *Bombus pascuorum*, for example, has many forage plants in common with both shorter tongued bees (*Bombus terrestris/lucorum*) and butterflies at both sites. As these plant communities are not unusual in their species diversity, we suggest this method of defining compartments empirically is more realistic than estimating them on the basis of pollination syndromes.

It could be argued that if our web was a true plant–pollinator web, only including those interactions that provided an effective pollination service, more

compartments may have emerged. Visits of the short-tongued bumblebees to plants with a long corolla tube such as *Lotus corniculatus* and *Lathyrus pratensis*, for example, often involved nectar larceny through a hole chewed in the back of the flower. These interactions would not appear in a plant–pollinator web, because the insect does not collect or deposit pollen. However, given the extensive overlap of forage species, it is not clear that such considerations would change the distribution of the species amongst compartments.

Phenology is another important factor affecting how the web breaks up into compartments. The most obvious example is group 3 at Shelfanger, a pair of species that are isolated purely by phenology. *Anthophora plumipes* is not a species that has a particular specialized relationship with *Primula veris* (Bond & Kirby 1999). It is a long-tongued species that happens to be around early in the spring, when the nectar resource available on Shelfanger meadow consists almost entirely of *Primula veris*. The presence of *Syrphus* sp. in the bee and butterfly group at Shelfanger is a phenological effect and the separation of the syrphids and plants in group 4 at Shelfanger is also partially phenological. *Filipendula ulmaria* and *Galium verum* flower late in the season and so tend to be visited by fly species appearing later on the site, such as *Episyrphus balteatus*.

It is also possible that the fourth group of flies at Shelfanger reflects the type of feeding behaviour. In a study of hoverfly foraging by Gilbert (1981), *Episyrphus balteatus* and *Sphaerophoria scripta*, the two syrphid species transferred to group 4, were classified as pollen feeders, while the two remaining in group 2 were largely nectar feeders. If the plants in group 4 were more pollen-rich than those remaining in group 2, then these two groups may reflect this ecological distinction. Unfortunately, because we did not record feeding behaviour, or measure nectar and pollen rewards, such a proposal requires further study.

One noticeable feature of the webs is that at both sites they are dominated by a small number of abundant plant and insect species. At Shelfanger, *Bombus lapidarius* accounted for 54% of all visits, while at Hickling 41% of all visits were *Bombus terrestris/lucorum*. In the plants, *Centaurea nigra* received 74% of all visits at Shelfanger; *Leucanthemum vulgare* received 15% of all visits at Shelfanger and 50% of all visits at Hickling; and *Lotus corniculatus* received 35% of all visits at Hickling. Such inequality in plant–visitor webs, which is largely based on differences in abundance, has been noted by other authors (Moldenke & Lincoln 1979; Memmott 1999).

The interactions of these abundant species dominate the plant–visitor web (although in the case of plants, not necessarily the community) and could be described as strong within the system. Clearly, to estimate the strength of an interaction on the basis of its frequency may be misleading, for example if an uncommon visitor was the only effective pollinator of a plant species. However, abundance is an important aspect of pol-

linator function (Primack & Silander 1975) and has been used as an estimate of interaction strength by Jordano (1987). In our compartmentalization process, the strong interactions, for example between *Bombus terrestris/lucorum* and *Centaurea nigra* at Shelfanger, are placed within compartments also containing other species, which agrees with the expectation of Thomas (1990). A similar pattern was observed in bird seed disperser–plant systems by Jordano (1987).

To summarize, these pollination systems are compartmentalized, as predicted by Corbet (2000b). Our data suggest that, in hay meadows at least, pollinator communities fall into groups that can be interpreted to some extent on the basis of the classical pollination syndromes, informed by consideration of tongue length, pollen/nectar distinction and phenology.

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Appendix

LISTS OF SPECIES/MORPHOTYPES FOR EACH SITE

Insects are named according to the RES *A Checklist of British Insects* (Kloet & Hincks 1978; Chandler 1998); plants are named according to Stace's *Flora of the British Isles* (Stace 1997).

SHELFANGER INSECTS

1, *Bombus terrestris/lucorum*; 2, *Bombus hortorum*; 3, *Bombus lapidarius*; 4, *Bombus pascuorum*; 5, *Bombus pratorum*; 6, *Psithyrus vestalis*; 7, *Apis mellifera*; 8, *Andrena chrysosceles*; 9, *Andrena pubescens*; 10, *Anthophora plumipes*; 11, *Lasioglossum calceatum*; 12, *Lasioglossum villosulum*; 13, *Cephus pygmaeus*; 14, *Cheilosia bergenstammi*; 15, *Episyrphus balteatus*; 16, *Eristalis intricarius*;

17, *Eristalis* sp.; 18, *Eristalis tenax*; 19, *Helophilus* sp.; 20, *Melanostoma* sp.; 21, *Meliscaeva* sp.; 22, *Platycheirus* sp.; 23, *Sphaerophoria* sp.; 24, *Syrphus* sp.; 25, *Tropida scita*; 26, *Volucella bombylans*; 27, *Empis livida*; 28, *Eriothrix rufomaculata*; 29, *Lucilia* sp.; 30, *Pollenia* sp.; 31, *Sarcophagus* sp.; 32, *Scathophaga stercoraria*; 33, *Lycaena phleas*; 34, *Maniola jurtina*; 35, *Panameria tenebrata*; 36, *Calocoris bipuncta*.

SHELFANGER PLANTS

a, *Ajuga reptans*; b, *Anthriscus sylvestris*; c, *Cardamine pratensis*; d, *Centaurea nigra*; e, *Cerastium fontanum*; f, *Cirsium arvense*; g, *Cirsium palustre*; h, *Filipendula ulmaria*; i, *Galium verum*; j, *Geranium dissectum*; k, *Hypochoeris radicata*; l, *Lathyrus pratensis*; m, *Leontodon hispidus*; n, *Leucanthemum vulgare*; o, *Lotus corniculatus*; p, *Orchis mascula*; q, *Orchis morio*; r, *Plantago lanceolata*; s, *Potentilla erecta*; t, *Primula veris*; u, *Prunella vulgaris*; v, *Ranunculus acris*; w, *Rumex acetosa*; x, *Saxifraga granulata*; y, *Taraxacum officinale* agg.; z, *Trifolium dubium*; a', *Trifolium pratense*; b', *Trifolium repens*; c', *Veronica chamaedrys*.

HICKLING INSECTS

1, *Bombus terrestris*llucorum; 2, *Bombus hortorum*; 3, *Bombus lapidarius*; 4, *Bombus pascuorum*; 5, *Bombus pratorum*; 6, *Psithyrus vestalis*; 7, *Andrena haemorrhoa*; 8, *Andrena pubescens*; 9, *Andrena wilkella*; 10, *Lasioglossum calceatum*; 11, *Lasioglossum leucozonium*; 12, *Lasioglossum villosulum*; 13, *Megachile willughbiella*;

14, *Anasimyia contracta*; 15, *Cheilosia albitarsis*; 16, *Chrysogaster hirtella*; 17, *Eristalinus sepulchralis*; 18, *Eristalis intricarius*; 19, *Eristalis* sp.; 20, *Eristalis pertinax*; 21, *Eristalis tenax*; 22, *Helophilus* sp.; 23, *Helophilus trivittatus*; 24, *Lejogaster* sp.; 25, *Melanostoma mellinum*; 26, *Meliscaeva auricollis*; 27, *Neoascia tenur*; 28, *Parhelophilus versicolor*; 29, *Platycheirus* sp.; 30, *Sphaerophoria scripta*; 31, *Syrphus* sp.; 32, *Syritta pipiens*; 33, *Tropida scita*; 34, Unidentified Anthomyid species; 35, *Empis livida*; 36, *Eriothrix rufomaculata*; 37, *Lucilia* sp.; 38, *Chloromyia formosa*; 39, *Nemotelus pantherinus*; 40, *Odontomyia tigrina*; 41, *Odontomyia viridula*; 42, *Phaonia incana*; 43, *Pollenia* sp.; 44, *Rhagio tringarius*; 45, *Sarcophaga* sp.; 46, *Scathophaga stercoraria*; 47, *Tetanocera ferruginea*; 48, *Lasiommata megera*; 49, *Lycaena phleas*; 50, *Maniola jurtina*; 51, *Polymommatus icarus*; 52, *Pyronia tithonus*; 53, *Ochlodes venata*; 54, *Thymelicus* sp.; 55, *Adela rufimatrella*; 56, *Autographa* sp.; 57, *Oligia* sp.; 58, *Zygaena filipendulae*; 59, microlepidoptera sp. 1; 60, *Malachius viridus*; 61, *Rhagonycha fulva*.

HICKLING PLANTS

a, *Achillea millefolium*; b, *Centaurea nigra*; c, *Cirsium arvense*; d, *Galium verum*; e, *Hypochoeris radicata*; f, *Lathyrus pratensis*; g, *Leucanthemum vulgare*; h, *Lotus corniculatus*; i, *Lychnis flos-cuculi*; j, *Plantago lanceolata*; k, *Primula veris*; l, *Prunella vulgaris*; m, *Ranunculus acris*; n, *Ranunculus repens*; o, *Rumex acetosa*; p, *Taraxacum officinale* agg.; q, *Trifolium dubium*; r, *Trifolium pratense*; s, *Trifolium repens*; t, *Vicia cracca*; u, *Vicia sativa*.