IDEA

The structure of a plant-pollinator food web

Jane Memmott
*School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK.
E-mail:
Jane.Memmott@bris.ac.uk*

Abstract

The pollination biology literature is dominated by examples of specialization between plants and their pollinators. However, a recent review shows that it is generalization that prevails in the field, with most plants having a number of pollinators and most pollinators visiting a number of plants. Consequently, the vast majority of plant–pollinator interactions are embedded in a complex web of plant–pollinator interactions. These plant-pollinator webs can be studied in the manner of conventional food webs and the aim of this paper is to illustrate how contemporary methods of web construction and analysis can be applied to plant-pollinator communities.

Insects and other animals visit flowers to obtain food, usually in the form of pollen or nectar. This is one side of a mutually beneficial relationship, the plants obtaining in return the services of the pollinators in carrying pollen from one flower to another (Proctor *et al.* 1996). To date, pollination biologists have typically focused their attention on interactions between one or a few plant species and taxonomically constrained groups of pollinator species such as hoverflies, solitary bees, bumble bees, bats or birds. Consequently, there is a paucity of studies that study entire pollinator communities.

While we know a great deal about specific plant–pollinator interactions, the shortage of information at the community level is unfortunate as characterizing entire pollinator complexes is crucial to a number of research areas. For example, when quantifying the probability of engineered crop genes escaping into natural plant populations (e.g. Klinger *et al.* 1992) the entire suite of potential pollinators must be considered. Similarly, community wide approaches are essential when analysing the evolution of mutualisms in a community context (Jordano 1987), when attempting to restore damaged ecosystems (Montalvo *et al.* 1997) and when choosing and managing pollinators in crop situations (Allen-Wardell *et al.* 1998). Moreover, if the aim of a study is to understand the processes underlying the patterns in the structure of a pollinator community, surveying just a few plant and animal species is likely to bias the sample (Waser *et al.* 1996). Given the potential value of characterizing entire pollinator communities, a protocol for doing so is required. Here I suggest that a food web approach could provide such a protocol. Food webs transcend the narrow habitat and taxonomic divisions that are still a powerful, restricting force in the development of ecological theory (Lawton 1995). Consequently, they may prove ideal for studying taxonomically diverse assemblages such as pollinator complexes.

A number of authors have already advocated a food web approach to pollination biology. Jordano (1987) calculated the connectance of 36 pollinator communities and used the data to investigate how interactions were distributed between sets of mutualistic plants and animals. He revealed significant differences in connectance between assemblages involving different types of pollinators. This led to the suggestion that the different kinds of pollinators have particular modes of interactions with plants and that these modes ultimately determine the overall specificity of the mutualism (Jordano 1987). Waser *et al.* (1996) reviewed the levels of generalization in plant–pollinator interactions and concluded that the use of several plant species by a pollinator and of several pollinator species by a plant species was the rule rather than the exception. Thus starting with one or a few species, will lead into a web of interactions, unless plants and pollinators are obligately related. The implications of this web are discussed by Waser *et al.* (1996) for a number of research areas, including ecology, evolution, behaviour and conservation biology. Kearns *et al.* (1998) point out that the job of conserving pollination systems is made more "subtle and complex" by dint of the fact that pollination interaction webs are relatively richly connected. They also raise the concept of resilience in plant–pollinator interaction webs and list this approach as a priority for further research.

Not only has a food web approach already been advocated, but data exists on community level plant–pollinator interactions (e.g. Clements & Long 1923; Moldenke & Lincoln 1979; Petanidou 1993; Struck 1994). While it is apparent that a monumental effort went into gathering the data, these studies unfortunately fall short of providing the exact information needed to construct quantitative food webs. For example, the pollinators may be lumped into taxonomic groupings, the frequency of the interaction may not be quantified or the study area is not precisely delimited.

In the following section, I will describe how a quantitative plant visitation web was constructed for the plants and pollinators in an English meadow community. A quantitative web shows the density of flowers, insect visitors and the frequency of the interactions between them, in common units. The data were gathered over 1 month with the aim of illustrating how a food web approach could further our understanding of plant–pollinator interactions.

A QUANTITATIVE PLANT VISITATION WEB

In July 1997, flower-visiting insects were sampled in a meadow plot, 250 m by 150 m in size. The insects were sampled by walking transects lengthways across the meadow and recording the identity of the species in each observed flower–insect interaction. Interactions were recorded in a swath 2 m wide along each transect and an average of two transects per day were studied. Insects were either identified in the field, or were collected and identified in the laboratory. During this period a total of 2722 interactions were recorded among 26 species of flowering plant and 79 species of pollinator. A further nine species of plant were flowering in the meadow, but were not seen to be visited by insects.

The insects visiting the flowers came from four orders of insect: Diptera, Lepidoptera, Hymenoptera and Coleoptera. Where possible, the insects were identified to species (34 species), otherwise they were morphotyped (44 morphospecies). While insects ideally would be identified to species, identification to morphotype is sufficient for the purposes of constructing quantitative food webs (Memmott & Godfray 1993). For this pilot study, parasitoids and nonsocial bees were considered as single classes: both groups made up a small proportion of the overall web, 3% and 4%, respectively, of insects sampled. Flower abundance was quantified by counting flower heads, each head being counted as a single flowering unit. Flower heads were counted along three transects at both the beginning and the end of the collecting period. An average of the two counts was then calculated.

The data were used to draw a quantitative plant visitation web (Fig. 1). Although the web appears very
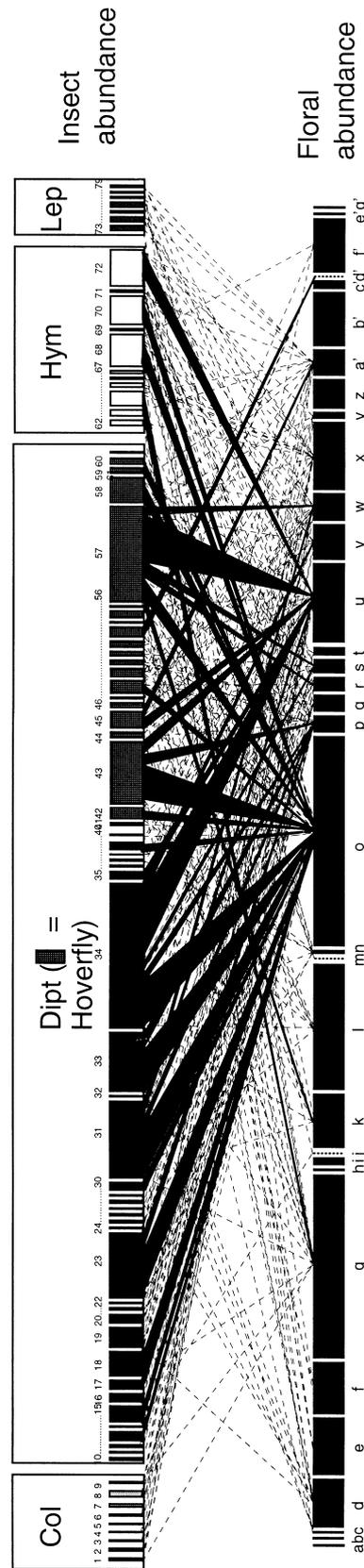
Figure 1 The results of the quantitative sampling for a plant-pollinator community showing the trophic links (pollen and/or nectar feeding) during July 1997. Each species of plant and insect is represented by a rectangle: the lower line represents flower abundance, the upper line represents insect abundance (Col, Coleoptera; Dipt, Diptera; Hym, Hymenoptera; Lep, Lepidoptera). The width of the rectangles and the size of the interaction between them is proportional to their abundance at the field site. Plants shown as a dotted line were present at the field site, but not recorded by the sampling. Interactions shown as a dotted line were observed less than 10 times during the sampling period. The plant and pollinator species are listed in the Appendix.

complicated, as in most published food webs, there are many low frequency interactions and relatively few high frequency interactions in the community. However, the data were gathered over just 1 month and consequently Fig. 1 shows only a small proportion of the expected total flower–insect interactions over a complete flowering season. A number of factors are immediately apparent from the web. Firstly, Diptera are more abundant than all other orders of insect combined. Secondly, plant species are not equally attractive to the pollinator community as a whole. For example, wild carrot, *Daucus carota*, L. attracted 61% of insect species and 42% of insect visitors overall. In contrast, nine plant species were not visited at all. Finally, generalization appears to be the norm for both plants and insects in this community: plants were visited by a median of seven species of insects (range 0–48) and insects visit a median of three species of plant (range 1–18).

There are actually two webs to consider when working on plant-pollinator communities. First, a plant visitation web which identifies the flower choices made by putative pollinators and second, a pollination web which quantifies pollen transfer, thus showing which insect species pollinate which plant species. Obviously the two webs may differ in structure. Flower visitation, as shown in Fig. 1, cannot be assumed to lead to pollination. Moreover, even if non-pollinating visitors are removed from the web, the remaining insects are likely to vary in pollination efficiency. A pollination web would characterize this variation. While characterizing a pollination web for an entire community remains a heady goal, pollination efficiency has been successfully calculated for the insects visiting individual plant species (e.g. Schemske & Horvitz 1984; Fishbein & Venable 1996; Bingham & Ort 1998). If the techniques used on these species could be scaled up and applied to an entire plant community, a pollination web could be constructed.

CONCLUSION

While the use of a food web approach to study patterns of flower visitation data has been previously suggested, the data presented here, is the first time that this has been done in the field. The web is fully quantified, well resolved and spatially delimited. Moreover, the approach used to gather the data is eminently practical for field use and could be applied to any habitat or ecosystem.

Even though just one months data were gathered, a number of novel patterns have already emerged. In addition to using webs to describe pollinator communities, they can also be used to frame and test hypotheses concerning the processes underlying the patterns. For example, my study might lead to the hypothesis that wild carrot is important in determining pollinator abundance

and diversity. This hypothesis could be tested by removing wild carrot from replicated plots and comparing the resulting web structure with webs from control plots. If its removal led to significant changes (extinction or large changes in abundance) spreading throughout the whole web this species could perhaps be considered a keystone species. The term keystone species was originally used to describe predators (Paine 1966), but the concept has since been applied to species at other trophic levels (Power *et al.* 1996). To date, the concept of keystone species has not been widely applied to pollinator communities.

Visitation and pollination webs could further the research areas mentioned in the introduction. For example, it is frequently assumed in habitat restoration, that once a plant community is restored, then community processes such as pollination will be automatically reinstated. Visitation and pollination webs would allow the pollination systems of pristine and restored habitats to be compared and this assumption to be tested. In crop plant situations, the farmer is often dependant upon wild pollinators whose identity remains unknown. Pollination webs for commercial crops and the plants growing in field margins would identify which insects to manipulate in order to drive the web in a desirable (i.e. high seed set) direction. Finally, if pollination biologists really want to understand how pollinator communities are structured, all flower visitors should be included in their studies. Otherwise, the biologist is in a situation analogous to a person watching a stage play and trying to understand the plot, but only being allowed to hear 10% of the lines spoken by the cast.

Waser *et al.* (1996) state that surveying the pollination interactions of entire local assemblages of plants and pollinators remains "a daunting task". However, my study has shown it to be a feasible task, for the visitation data at least. Food webs are a fundamental component of any attempt to describe how natural communities are structured and how complexes of species interact. They have not been widely applied to pollinator communities–doing so is likely to lead to new patterns that need new theories and perhaps new theories to explain the existing patterns.

ACKNOWLEDGEMENTS

REFERENCES

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., MedellinMorales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biol.*, 12, 8–17.

Bingham, R.A. & Ort, A.R. (1998). Efficient pollination of alpine plants. *Nature*, 391, 238–239.

Clements, R.E. & Long, F.L. (1923). *Experimental Pollination. An Outline of the Ecology of Flowers and Insects.* Carnegie Institute of Washington, Publication No 336, Washington.

Fishbein, M. & Venable, D.L. (1996). Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology*, 77, 1061–1073.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal–connectance, dependence asymmetries, and coevolution. *Am. Naturalist*, 129, 657–677.

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998). Endangered mutualisms: The conservation of plant–pollinator interactions. *Annu. Rev. Ecol. Syst*, 29, 83–112.

Klinger, T., Arriola, P.E. & Ellstrand, N.C. (1992). Crop-weed hybridization in radish (raphanus sativus)–effects of distance and population-size. *Am. J. Botany*, 79, 1431–1435.

Lawton, J.H. (1995). Webbing and wiwacs. *Oikos*, 72, 305–306.

Memmott, J. & Godfray, H.C.J. (1993). Parasitoid webs. In *Hymenoptera and Biodiversity*, eds J. Lasalle & I.D. Gould, Wallingford, CAB International, pp. 217–234.

Moldenke, A.R. & Lincoln, P.G. (1979). Pollination Ecology in montane Colorado: a community analysis. *Phytologia*, 42, 349–379.

Montalvo, A.M., Williams, S.L., Rice, K.J., Buchmann, S.L., Cory, C., Handel, S.N., Nabhan, G.P., Primack, R. & Robichaux, R.H. (1997). Restoration biology: a population biology perspective. *Restoration Ecol.*, 5, 277–290.

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Naturalist*, 100, 65–75.

Petanidou, T. (1993). Pollinating fauna of a phyganic ecosystem: composition and diversity. *Biodiversity Lett*, 1, 9–22.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996). Challenges in the quest for keystones. *Bioscience*, 46, 609–620.

Proctor, M., Yeo, P. & Lack, A. (1996). *The Natural History of Pollination.* Harper Collins Publishers.

Schemske, D.W. & Horvitz, C.C. (1984). Variation among floral visitors in pollination ability–a precondition for mutualism specialization. *Science*, 225, 519–521.

Struck, M. (1994). Flowers and their insect visitors in the arid winter rainfall region of southern africa–observations on permanent plots–insect visitation behavior. *J. Arid Environments*, 28, 51–74.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996). Generalization in pollination systems and why it matters. *Ecology*, 77, 1043–1060.

APPENDIX

The species shown in Fig. 1 are listed below.

Plants

a, *Ranunculus repens*; b, *R. acris*; c, *Clematis vitalba*; d, *Chamerion angustifolium*; e, *Lotus corniculatus*; f, *Medicago lupulina*; g, *Trifolium pratense*; h, *Trifolium repens*; i, *Vicia cracca*; j, *Lathyrus pratensis*; k, *Linum catharticum*; l, *Agrimonia eupatoria*; m, *Rubus fruticosus*; n, *Angelica sylvertris*; o, *Daucus carota*; p, *Torilis japonica*; q, *Aethusa cynapium*; r, *Hypochaeris radicata*; s, *Leontodon autumnalis*; t, *Leontodon saxatilis*; u, *Leontodon hispidus*; v, *Crepis capillaris*; w, *Eupatorium cannabinum*; x, *Centaurea nigra*; y, *Senecio jacobaea*; z, *Convulvulus arvensis*; a′, *Knautia arvensis*; b′, *Centaurium erythraea*; c′, *Prunella vulgaris*; d′, *Plantago major*; e′, *Galium verum*; f′, *Euphrasia officinalis*; g′, *Odontites verna*; h′, *Rhinanthus minor*.

Pollinators

Coleoptera: 1, Coleoptera sp.1; 2, Coleoptera sp.2; 3, Coleoptera sp.3; 4, Coleoptera sp.4; 5, Coleoptera sp.5; 6, Coleoptera sp.6; 7, Coleoptera sp.7; 8, Cantharidae sp. 1; 9, Curculionidae sp. 1.

Diptera: 10, Diptera sp.1; 11, Diptera sp.2; 12, Diptera sp.3; 13, Diptera sp.4; 14, Conipidae sp. 1; 15, Diptera sp.5; 16, Diptera sp.6; 17, *Scatophaga stercoraria*; 18, Diptera sp.7; 19, Diptera sp.8; 20, Diptera sp.9; 21, Diptera sp.10; 22, Diptera sp.11; 23, Diptera sp.12; 24, Diptera sp.13; 25, Diptera sp.14; 26, Diptera sp.15; 27, Diptera sp.16; 28, Diptera sp.17; 29, Diptera sp.18; 30, Diptera sp.19; 31, Eriothrix rufomaculata; 32, Diptera sp.20; 33, Diptera sp.21; 34, Diptera sp.22; 35, Diptera

sp.23; 36, Diptera sp.24; 37, Diptera sp.25; 38, Tephritidae sp.1; 39, Diptera sp.26; 40, Diptera sp.27; 41, *Chrysotoxum bicinctum;* 42, *Episyrphus arbustorum;* 43, *E. balteatus;* 44, *Eristalis pertinax;* 45, *E. tenax;* 46, *Helophilus pendulus;* 47, *H. trivittatus;* 48, *Melanostoma mellinum;* 49, *M. scalare;* 50, *Meliscaeva auricollis;* 51, *Metasyrphus corollae;* 52, *Platycheirus albimanus;* 53, *P. clypeatus;* 54, *P. scutatus;* 55, *Rhingia campestris;* 56, *Scaeva pyrastri;* 57, *Sphaerophoria scripta;* 58, *Syritta pipiens;* 59, *Syrphus ribesii;* 60, *S. vitripennis.*

Hymenoptera: 61, *Xanthogramma pedissequum;* 62, *Bombus lapidarius;* 63, *B. muscorum;* 64, *B. pascuorum;* 65, *B. terrestris;* 66, *Psithyrus* sp.1; 67, *Apis mellifera;* 68, *Parasitica;* 69, *Formicidae* sp. 1; 70, Symphyta sp. 1; 72, Solitary bees.

Lepidoptera: 73, *Polyommatus icarus;* 74, *Pyonia tithonus;* 75, *Pieris brassicae;* 76, *Incurvariidae* sp. 1 1; 77, *Maniola jurtina;* 78, *Thymelicus sylvestris;* 79, *Aglais urticae.*