

## Multiple meanings and modes: on the many ways to be a generalist flower

Jeff Ollerton<sup>1</sup>, Ant Killick<sup>1</sup>, Ellen Lamborn<sup>2</sup>, Stella Watts<sup>1</sup> & Margaret Whiston<sup>1</sup>

<sup>1</sup> *Landscape and Biodiversity Research Group, School of Applied Sciences, University of Northampton, Park Campus, Northampton, NN2 7AL, U.K. jeff.ollerton@northampton.ac.uk (author for correspondence)*

<sup>2</sup> *University of the Aegean, Department of Geography, University Hill, 81100 Mytilene, Lesvos, Greece*

The concept of a generalist flower appears to mean different things to different people, depending upon their background and training. We assess the different meanings of generalist flowers with respect to the ecological “set and setting” of pollination, and then we discuss notions of ecological, functional and phenotypic generalization. These ideas are explored in more detail using examples from our own published and unpublished studies on the pollination ecology of *Daucus carota*, *Hedera helix*, and *Chamerion angustifolium*, and from the published work of other researchers. Finally we relate these ideas and clarified definitions of “generalist” and “specialist” flowers to the pollination syndrome concept.

**KEYWORDS:** *Asclepias*, Apocynaceae, mutualism, pollination biology, species interactions

### INTRODUCTION

Plant-pollinator interactions span a spectrum from obligate specialists (a single species of pollinator services one plant species) to facultative generalists in which flowers may be adequately serviced by any of a taxonomically broad range of pollinators, which are also visitors to the flowers of many other species. The specialist-specialist portion of this spectrum has received considerable attention from botanists, ecologists and evolutionary biologists because it provides examples of neat, tractable study systems (Faegri & van der Pijl, 1979; Proctor & al., 1996; Waser & al., 1996; Pellmyr, 2002). Generalist systems, on the other hand, are complex, and variable in time and space, and not so easily dissected. This makes them at once less appealing but also, because they represent perhaps the majority of flowering plant interactions (Knuth, 1906; Waser & al., 1996, though see Johnson & Steiner, 2000), an important and representative portion of the spectrum. Debates concerning the ecological and evolutionary importance of generalized plant-pollinator relationships, and their relative frequency in relation to more specialized interactions, have enthused the field of pollination ecology over the past decade (Herrera, 1996; Waser & al., 1996; Johnson & Steiner, 2000; Fenster & al., 2004; Herrera, 2005; Waser & Ollerton, 2006). These debates have, for example, informed our understanding of global biogeographic patterns of plant-pollinator interactions (e.g., Ollerton & Liede, 1997; Olesen & Jordano, 2002; Ollerton & Cranmer, 2002; Johnson & Steiner, 2003; Fleming, 2005; Armbruster, 2006; Ollerton & al., 2006), community-level relationships (e.g., Memmott 1999; Bascompte & al., 2003, 2006; Dupont & al., 2003; Ollerton & al., 2003; Vázquez & Aizen, 2006) and the ways in

which pollination systems evolve (e.g., Waser & al., 1996; Ollerton, 1996; Waser, 1998; Mayfield & al., 2001; Aigner, 2001, 2006; Fenster & al., 2004; Pauw, 2006).

Some disagreements between researchers have arisen because of different definitions of “generalized” and “specialized” interactions. What exactly do we mean by a “generalist flower”? To some, “generalist” seems to mean a “simple” radially symmetrical flower with an easily accessible reward of nectar or pollen. This implies (but does not necessarily mean) that the reward can be utilised by a wide range of flower visitors (e.g., Frame, 2003). However the definition of “generalization” favoured by pollination ecologists (e.g., Waser & al., 1996) relates only to the number of pollinators and says nothing about flower morphology. These two definitions are not mutually exclusive but they do come from very different backgrounds—classical botany on the one hand versus community ecology on the other. In this paper we hope to show that flowers with open access rewards and many pollinators represent simply one aspect of the pollination niche of flowering plants, and one that is not necessarily representative of the majority of “generalist” flowers. As the title of this paper expresses, there are many ways to define a generalist flower, and many ways for a flower to be generalist, some of which, when properly studied, reveal that apparently generalist species are in fact, if not “specialists,” then at least more specialized than they first appear!

It is important that we try to develop a broad conceptual framework for understanding and exploring how plant-pollinator interactions evolve along a continuum of ecological generalization to specialization, the genotypic and phenotypic consequences of such evolution, and the ecological circumstances in which this takes place. Thompson’s Geographic Mosaic Theory has provided one element to this

framework, but is concerned only with spatial variability (Thompson, 2005). Temporal variability, population dynamics of plants and pollinators and the phylogenetic identity of the participants are important too. Linking all of this to changes in gene frequency and the expected phenotypic modification would be the next step.

To the work in progress on development of a unifying framework, our paper is designed to stimulate biologists of all backgrounds to think carefully about exactly what they mean when they describe a flower as “generalist,” and to consider these concepts in relation to our understanding of biotic pollination as an ecological process, and the ways in which this influences floral evolution.

Our paper begins by introducing a scenario that depicts the “pollination set and setting” experienced by a biotically pollinated flowering plant. This scenario relates flower visitors to floral phenotype and the community context in which the plant and pollinator occurs; both of these factors determine which flower visitors are actually effective pollinators. This in turn leads to some refined definitions of pollination generalization and specialization, which are becoming common terms in the pollination ecology literature. In the second section of this paper we illustrate these definitions using examples from our own work, much of it previously unpublished, and from the published literature. Finally we relate this to current debates concerning pollination syndromes.

## BIOTIC POLLINATION AS SET AND SETTING

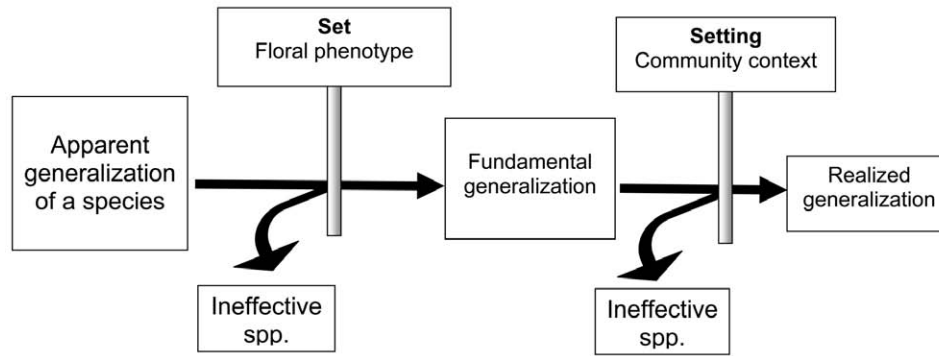
Consider a plant species and its interactions with flower visitors in a community in terms of effective pollinators and ineffective flower visitors (Fig. 1). The “apparent generalization” of the species relates to the number of flower visitors which interact with its flowers, whether pollinators or not. Apparent generalization is moderated by the phenotypic influences of the flower, the set of morphological (size, shape, colour) and biochemical (odour, reward) traits, and the behavioural responses of the flower visitors, which determine the “fit” between the flower and visitors. These considerations distinguish between those flower visitors that do not directly effect pollination in this plant species (ineffective visitors) and actual pollinators. The “fundamental generalization” of the species therefore relates to the number of potentially effective pollinators with which it could interact (Vázquez & Aizen, 2006). The moderating influence between this and the “realized generalization” of this plant species is the setting for the interaction, i.e., the “community context” in which the plant finds itself (Vázquez & Aizen, 2006). For example the presence or absence of potentially effective pollinating species due to habitat disturbance (natural or anthropogenic), small pop-

ulation size of potential pollinators, presence of other plant or animal species which disrupt or modify the interaction between the species and its pollinators, and so forth. All of these can vary between communities and over time in the same community. In addition, certain communities, e.g., those on oceanic islands, are predictably depauperate in pollinator diversity; plants which would be ecological generalists in a different context (e.g., on a mainland) become specialists purely by default of their community setting (Barrett, 1996; Olesen & Jordano, 2002). The realized generalization of our hypothetical plant species is therefore determined by the number of effective pollinator species that can potentially interact with its flowers, i.e., *the set*, within *the setting* of geographical position and temporal variability in a community context (Fig. 1).

## DEFINITIONS OF GENERALIZATION AND SPECIALIZATION

The overview of pollination set and setting suggests that the generalization or specialization exhibited by a flower can refer to one of several aspects of the biology and ecology of that flower and its interactions with pollinators, recently discussed by Fenster & al. (2004), Armbruster, (2006), and Ollerton & al. (2006). For example, *ecological* generalization or specialization refers to the number of effective pollinators with which a plant interacts, i.e., how many species of pollinators are involved in the relationship. At a broader level, *functional* generalization or specialization refers to the diversity of pollinators that service a plant at a higher taxonomic level (typically Family or above) and is usually expressed in relation to that taxon; for example we can describe plants as “bird pollinated” or “fly pollinated.” This tells us nothing about the ecological specialization of that plant: to illustrate, consider two plant species, A and B, which are pollinated by (A) five species of bees from the same genus, and (B) twenty species of bees from seven genera and two families. Both species are equally *functionally* specialized (i.e., they both specialize on bees) but species B is more *ecologically* generalized than species A. Researchers in other areas have constructed meaningful indices of specialization that incorporate phylogenetic information regarding, for example, plants exploited by phytophagous insects or parasite host diversity (Symons & Beccaloni, 1999; Poulin & Mouillot, 2005) and this would be a useful approach for pollination biologists to explore.

Ecological generalization is clearly influenced by the setting in which a plant exists, whilst functional generalization may be seen as the link between set and setting because it is more directly related to our final definition: *phenotypic* generalization or specialization refers to the adaptations exhibited by a flower (e.g., radial or zygomorphic symmetry, specialist rewards, complex scents, specific timing of



**Fig. 1.** The set and setting of biotic pollination. This scenario relates the flower visitors of a plant to the modifying influences (indicated by the shaded “filter” bars) of floral phenotype and community context. The set and setting of biotic pollination act as filters in determining which flower visitors are able to effect pollination, initially due to the fit between plant and flower visitor (set), and ultimately because of the presence or absence of otherwise effective pollinators (setting). The box sizes of Apparent, Fundamental, and Realized generalization reduce in size to illustrate the narrowing spectrum of possible to actual pollinators.

anthesis, etc.), often in relation to functional specialization. We use the term “phenotypic” rather than “morphological” because the latter would exclude scent, nectar characteristics, colour, etc. The concept is perhaps best considered in relation to other taxa within the same clade; for example, in the Apocynaceae we can describe a sequence of increasing phenotypic specialization from basal subfamilies such as Rauvolfioideae with free pollen and separate androecium and gynoecium, to the more derived subfamily Asclepiadoideae with a congenitally fused gynostegium and pollen packaged as pollinia (Endress & Bruyns, 2000). It is important to note that phenotypic specialization does not necessarily always equate with ecological specialization as phenotypic specialists may be ecological generalists and vice versa, as we shall see below.

Notions of floral complexity have been developed by botanists trained in comparative morphology (e.g., Endress 1996; Frame & Durou 2001). Ecologists have been slow to appreciate these ideas of floral organization (bauplan), construction (gestalt), and mode (colour, scent, etc.), who, when they consider floral complexity at all, tend to use their own terminology, relating to phylogenetic constraints, pleiotropy, and local adaptive optima (see, e.g., chapters in Lloyd & Barrett 1996). Complexity as implied by Endress (1996) and later extended by Frame & Durou (2001) is only partly congruous with phenotypic specialization as defined here. To illustrate, the wind pollinated flowers of most grasses (Poaceae) are phenotypically specialized compared to their closest relatives (Rudall & al. 2005); however, under the scheme of Frame & Durou (2001), which distinguishes between phylogenetic and morphological specialization, these flowers would be considered morphologically simple albeit highly derived. Once again we can see that notions of complexity versus specialization (and their reverse, simplicity versus generalization) mean different things to different researchers. This is not neces-

sarily a problem, as long as one defines from the beginning the terminology one is using.

Finally Armbruster (2006) has introduced the term *evolutionary specialization*, which refers to the process of evolving towards specialization. Clearly its converse, *evolutionary generalization* could be defined and there are examples of specialist clades which have evolved derived, generalist species (Armbruster & Baldwin, 1998).

Using these definitions we can begin to consider the different ways in which flowers may be generalists, illustrated with case studies from our own work and culled from the literature.

## CASE STUDIES OF “GENERALIST” FLOWERS

**Example A.** — *Open access flowers in which all visitors provide more or less equally good pollination services (ecological and functional generalization).*

These may be considered “classical” generalist flowers and examples can be found in a wide range of families, e.g., Asteraceae, Ranunculaceae, Rosaceae, and Apiaceae. Flowers or functional floral units are typically radially symmetrical with open access to the reward. An important feature of such flowers is that the identity of the major pollinators is largely determined by their abundance in any one year, and this can fluctuate greatly. From the plant’s perspective however, this is largely of no consequence—pollination occurs whatever happens to the pollinator populations. As an example, consider *Daucus carota* (Apiaceae), a widespread biennial herb, occurring throughout Europe, temperate Asia and North Africa. Each of the many flowers in the compact inflorescence provides a small open access nectar reward for visiting insects, and the inflorescence effectively functions as a

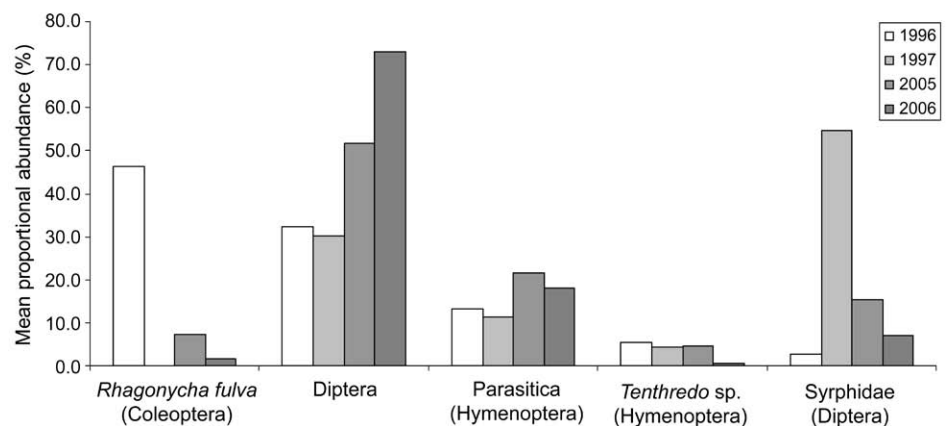
single unit (the “blossom” concept—Faegri & van der Pijl, 1979; Endress, 1996). The range of pollinators is very wide, comprising mainly smaller Hymenoptera, Diptera and Coleoptera (Willis & Burkill, 1895, 1903; Knuth, 1908; Lamborn & Ollerton, 2000). These taxa vary in the amount of pollen which accumulates on their bodies, and this is likely to be an important variable determining their effectiveness as pollinators, given the open flowers and the crawling foraging of the flower visitors (Lamborn & Ollerton, 2000). However all of the insect groups so far investigated carry significant amounts of pollen, with larger insects carrying more than smaller (Lamborn & Ollerton, 2000). These insect taxa vary greatly between flowering seasons in their abundance on *D. carota* flowers (Fig. 2). For example, in our main study population in 1996, *D. carota* was serviced by large numbers of soldier beetles *Rhagonycha fulva* (Coleoptera: Cantharidae) which carry a mean of 15.9 pollen grains per 4 mm<sup>2</sup> (assessed using sellotape sampling—see Lamborn & Ollerton, 2000, for exact methods). These beetles were absent in 1997 when the most frequent flower visitors were hoverflies (Diptera: Syrphidae—carrying 14.3 pollen grains per 4 mm<sup>2</sup>). In 2006 *R. fulva* was virtually absent and the main pollinators were other Diptera (19.1 pollen grains per 4 mm<sup>2</sup>). A large sawfly *Tenthredo* sp. (Hymenoptera: Tenthredinidae) was in relatively low abundance in all years, but carried far more pollen than the other taxa (74.5 pollen grains per 4 mm<sup>2</sup>). The amount of pollen carried by different insects is a crude measure of their potential as pollinators, but pollen removal and deposition may be positively correlated in some systems, e.g., taxa as dissimilar as British *Chamerion angustifolium* (Killick & Ollerton, unpublished data: see below) and South African asclepiads (Ollerton, unpublished data), but not in others (Adler & Irwin 2006). In *D. carota*, the flat umbels of open access flowers and the crawling activities of foraging insects suggest that pollen accumulation probably does correlate with pollinator effectiveness, though this requires further study. Nonetheless, all insects which visit these umbels at least have the potential to be pollinators.

*Daucus carota* has generalist flowers in the sense that they are phenotypically generalized (in relation to other Apiaceae) and attract a taxonomically wide spectrum of pollinators, spanning at least three orders of insects which vary temporally (ecological generalization). However one could argue that *D. carota* shows some degree of functional specialization in that all of its pollinators are relatively small insects with comparatively low energy demands (e.g., Hymenoptera Parasitica) and/or which obtain energy from other sources, e.g., the hunting sawflies (*Tenthredo* sp.). Large pollinators such as bumblebees (*Bombus* spp.), which are abundant at this site, never visit *D. carota*, perhaps because the rewards available per flower are so small in comparison to other flowers in the community. *D. carota* thus filters out some potential pollinators and “specializes” on a broad range of smaller pollinators. In the terminology of Corbet (2006) it is an allophilous species (i.e., it has “flowers with fully exposed nectar and little or no intrafloral temperature elevation”) that attracts mainly insects which are allotropous (small body mass with little or no endothermy) or sometimes hemitropous (larger body mass with some endothermy), excluding the larger eutropous (long-tongued, large, facultatively endothermic) pollinators. Is *Daucus carota* then really a generalist? It exploits a wide range of insects as pollinators, but its nectar presentation schedule of minute amounts per flower serves to exclude large bees from exploiting it. This interaction filter is subtle and in one sense quite specialized, and has moved *Daucus* and comparable Apiaceae into a pollination niche which is rarely exploited in north temperate communities in comparison to, say, large bee pollination.

**Example B.** — *Open access, apparently classical generalist flowers that attract only a very narrow spectrum of pollinators (functional, and possibly ecological, specialization).*

Apparently phenotypically generalized flowers may be more functionally and ecologically specialized than their floral form suggests. There are many such examples in the published literature. The genus *Magnolia* has often been considered to be an archetypal “primitive” angio-

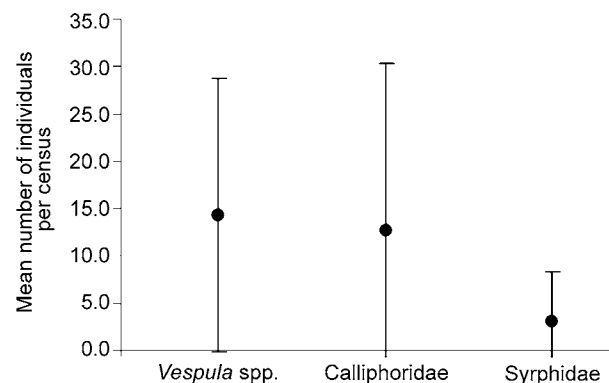
**Fig. 2. Proportional abundances of the main pollinating taxa of *Daucus carota* at the Scrub Field Local Nature Reserve, Northampton, in central England in 1996 and 1997 (data from Lamborn & Ollerton, 2000) and 2005 and 2006 (Ollerton, unpublished data from timed census walks).**



sperm, based on its relatively simple, radially symmetrical flowers and the long fossil history of the Magnoliaceae (e.g., Frumin & Friis, 1999; Thien & al., 2000). However, some species within the genus have quite functionally, and possibly ecologically, specialized interactions with beetles, e.g., *M. tamaulipana* (Dieringer & al., 1999) and *M. schiedeana* (Dieringer & Espinosa, 1994). Similarly, apparently generalist, open-access, bowl shaped flowers in the genera *Papaver*, *Ranunculus*, *Anemone*, and *Tulipa* have been demonstrated to belong to a guild of functionally specialized, predominantly beetle pollinated plants in the Mediterranean (Dafni & al., 1990). In all of these examples the flowers utilise only specific groups of pollinators by the scents or rewards they produce, or by colouration, rather than because they mechanically filter out unwanted visitors, e.g., via flower tube length or complex zygomorphy. Detailed observations of the flower visitors is critical to our accurate understanding of the pollination biology of these “generalist” flowers.

**Example C.** — *Flowers that attract a wide range of visitors, but which are pollinated mainly by a narrow subset of those flower visitors (functional specialization).*

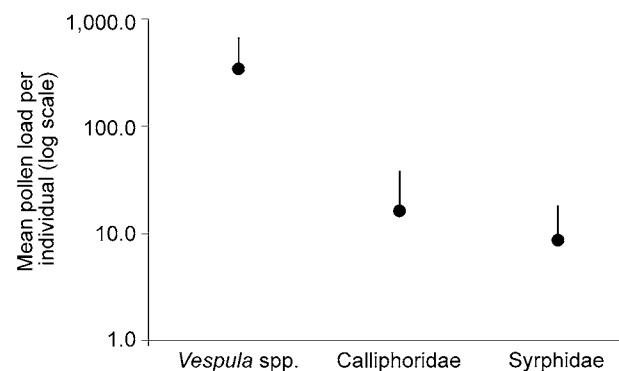
The flowers of common European ivy *Hedera helix* (Araliaceae) are phenotypically generalized, open access flowers that produce large volumes of nectar. Despite, or perhaps because of, the late flowering of this species in northern Europe (typically September to October), it is abundantly visited by a taxonomically wide range of insects, particularly *Vespula* wasps (Hymenoptera: Vespidae), various families of Diptera, and butterflies and moths (Lepidoptera) (Proctor & al., 1996). It therefore appears to be ecologically very generalized. Censuses within a population in Northamptonshire in 1999 showed that the three most abundant flower visiting taxa were *Vespula* spp. and the Diptera families Calliphoridae and



**Fig. 3.** Numbers of individual insects of the three main flower visiting taxa to *Hedera helix* flowers, Northamptonshire 1999. Values are mean ( $\pm$  SD) insects per 30 minute observation period. There is no statistically significant difference in average abundance of the three taxa (Univariate General Linear Model:  $F_{2,26} = 1.52$ ,  $p = 0.24$ ).

Syrphidae (Fig. 3). However the two fly taxa were relatively ineffective pollinators (as judged by pollen loads per insect—see proviso above) with the *Vespula* spp. carrying over twenty times as much pollen on average as Calliphoridae and forty times as much pollen as Syrphidae (Fig. 4). Despite the apparently generalist, open access nature of the flowers, and the broad spectrum of flower visitors, by far the most effective pollinators are *Vespula* wasps. Following Stebbins (1970) and the Most Effective Pollinator Principle (MEPP), *Hedera helix* in this population, and perhaps across northern Europe, can be considered a wasp specialist—most selection on flower colour, scent, and reward, will be driven by the wasps (though see Aigner, 2001, 2006 for a different perspective on this). It is worth noting that *H. helix* shares a number of floral traits in common with other vespidae and pompilid wasp specialized plants; for example, flowers are dull coloured, often pale green or yellow, with distinctive musky scents and with quite concentrated nectar (Proctor & al., 1996; Ollerton, unpublished observations; Ollerton & al., 2003).

Pollinator effectiveness is a function of multiple, interacting traits of flower and flower visitor, including relative sizes, animal behaviour and morphology (e.g., hairiness). In a series of experiments we tried to answer the question: “How easily can plants with generalist flowers evolve strategies to increase the effectiveness of less effective pollinators?” We focused on nectar volume as this is a parameter that is known to vary between individuals and to have an underlying genetic basis (e.g., Leiss & Klinkhamer, 2005), and so could potentially evolve in response to selection if, e.g., increased nectar secretion resulted in increased pollination services. The study system was *Chamerion angustifolium* L. (Onagraceae) a common perennial herb in British grass-

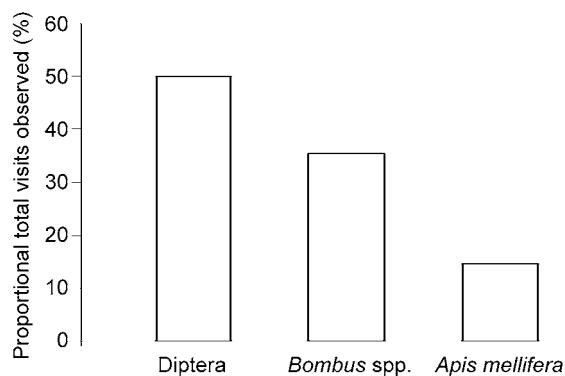


**Fig. 4.** Average pollen loads per individual (mean  $\pm$  SD; note that this is a log scale) for the three most common flower visitors to *Hedera helix* in a Northamptonshire population in 1999. Pollen loads were removed from insects using sellotape. There is a statistically significant difference in mean pollen loads of the three taxa (Univariate General Linear Model:  $F_{2,32} = 7.04$ ,  $p = 0.003$ ) and specifically between that of *Vespula* spp. compared to the other two taxa (Tamhane’s T2 post-hoc test:  $p \leq 0.005$ ).

lands. Its flowers are zygomorphic and held horizontally to the main axis of the stem, but have an open morphology and are visited by bees and flies, and occasionally beetles and butterflies (Knuth, 1908). Following HPLC analysis of the nectar of *C. angustifolium* (Mark Gardener, unpublished data), we constructed an artificial nectar based on the major sugars and their relative proportions (20% weight/volume of sucrose, glucose, and fructose) and added it to flowers in an experimentally controlled format: randomly chosen flowers on individual inflorescences received 0 (i.e., standing crop control), 1, 5, or 10  $\mu\text{L}$  of the artificial nectar. All flowers were virgin. Following single insect visits, stigmas were collected to assess pollen deposition and anthers removed to assess pollen removal using a Coulter Counter.

Surveys of flower visitors in this Northamptonshire population showed that half of the flower visits were by various families of Diptera, including Syrphidae, Phoridae, and Pipunculidae (Fig. 5). The remaining visits were by *Bombus* spp. (ca. 35%) and *Apis mellifera* (ca. 15%). For all of these taxa, increasing the amount of nectar available in the flowers resulted in longer visitation times to those flowers (data not shown). How does an increased time visit affect the reproductive success of individual flowers? For the less frequent flower visitors (*Bombus* spp., *A. mellifera*) increased duration of visit translates as greater amounts of pollen deposited on stigmas (Fig. 6A, C) and larger amounts of pollen removed (Fig. 6B, D). The longer an insect spends on a flower of *C. angustifolium*, the better it functions as a pollinator.

The Diptera visiting *C. angustifolium* flowers were poor pollinators and deposited very little if any pollen (Fig. 6E) and removed similar low amounts of pollen (Fig. 6F). Visitation durations could be 10 times as long for flies as for the two taxa of bees (compare x-axis ranges in Fig. 6) but even flies which remained at flowers for 3 minutes did not necessarily pollinate the flower. In *C. angustifolium*



**Fig. 5. Proportions (as percentages) of all visits to flowers of *Chamerion angustifolium* in a population at Daventry Country Park, Northamptonshire. A total of 146 flowers were observed for 15 minute intervals over three days in August 2002.**

there was no statistically significant relationship between visit duration and pollinating ability for these flies.

The answer to our question: “How easily can plants with generalist flowers evolve strategies to increase the effectiveness of less effective pollinators?” seems to be that they cannot easily do it. Ineffective pollinators such as these flies cannot be recruited into the pool of effective pollinators by a simple increase in nectar rewards. In order to make the flies more effective pollinators would require significant evolutionary changes to, e.g., flower size and morphology. That in turn may have a negative impact on the pollinating effectiveness of the other flower visitors.

**Example D.** — *Flowers that appear to be phenotypically specialized, implying a functionally specialized pollination system, but which in fact are pollinated by whatever flower visitors are a suitable size and shape, and have appropriate behaviour (functional and ecological generalists).*

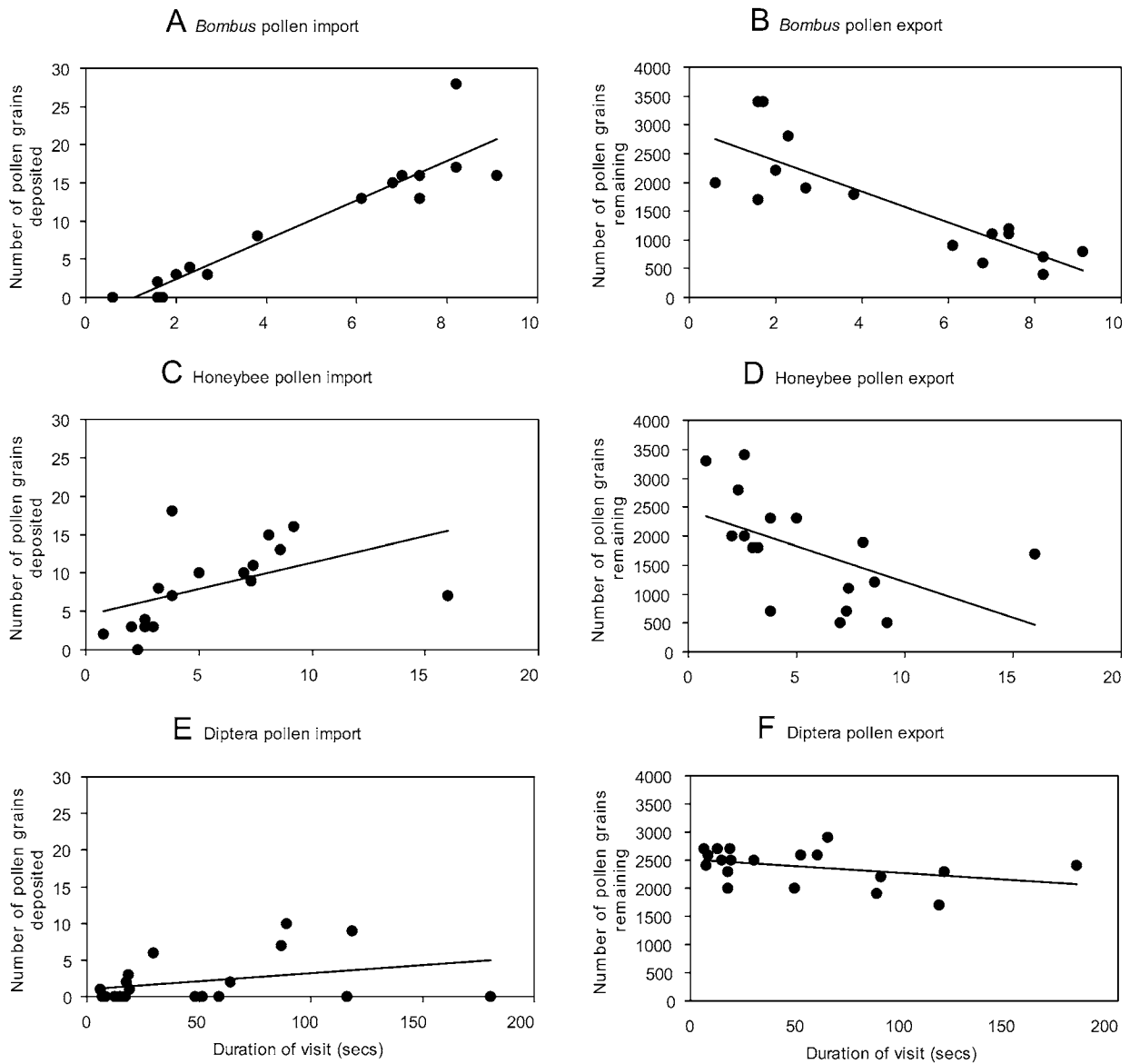
Some of the most phenotypically specialized flowers in the plant kingdom are to be found within the asclepiads (Apocynaceae subfamily Asclepiadoideae). Their fused, synorganized flowers, staminal and corolline outgrowths, and sophisticated pollen packaging are all suggestive of highly ecologically or functionally specialized pollinator relationships. The asclepiads are an ideal model system with which to study questions of generalization and specialization in pollination systems as the pollinaria persistently attach to flower visitors and even when pollinia are deposited in a flower, the translators remain attached to the pollinators. Pollinators can therefore be identified relatively unambiguously, at least in comparison with taxa possessing free pollen (Wyatt & Broyles, 1994; Ollerton & Liede, 1997; Ollerton & al., 2003).

There are asclepiads that seem to possess only a single species of pollinator, e.g., in the genera *Pachycarpus* and *Miraglossum* in South Africa (Ollerton & al., 2003). However this may have more to do with the higher average levels of ecological specificity in plant-pollinator interactions in Southern Africa overall (driven in part by a relatively depauperate pollinator fauna) rather than the phenotypic specialization of these asclepiads per se (Johnson & Steiner, 2000, 2003; Ollerton & al., 2003, 2006). Overall the asclepiads do not appear to be any more ecologically specialized than other (sub)families of angiosperms, at least in the northern hemisphere (compare Ollerton & Liede, 1997 with Ollerton & al., 2006) and some species can possess extraordinarily ecologically generalized pollination systems. Published surveys of *Asclepias* pollinators in the New World show that despite their phenotypic complexity, these species may attract and may be pollinated by in excess of 100 insect species in a number of instances (Table 1). Some of these studies have sampled more intensively than others, which is one reason why the number of recorded pollinators per species per study varies so widely. Nevertheless there is

also some geographical variation in the pollinators used by particular *Asclepias* species. For example, the extensive sampling of *A. verticillata* by Robertson (1891, 1928) identified 103 pollinating species, but the other studies cited in Table 1 bring the total number of recorded pollen vectors to 126. Fenster & al. (2004) suggested that species in more derived subgenera of *Asclepias*, e.g., *A. syriaca* and *A. solanoana*, were more ecologically specialized than the less derived taxa. Such a conclusion is probably premature: *A. syriaca* in some populations can be very generalized, whereas the pollination biology of *A. solanoana* has been only superficially studied (Table 1). Additionally, a robust

molecular phylogeny for *Asclepias* is not yet available and without it, no conclusions can be drawn as to which taxa are derived (Mark Fishbein, pers. comm., 2007).

Within the asclepiads, available data show that some groups are more specialized than others, with the tribe “Stapelieae” (currently the Ceropegieae) significantly more ecologically specialized than other tribes (Ollerton & Liede, 1997). Most of these species are stem succulent herbs of semi-arid regions, often with foul smelling, leathery flowers which mimic dead and decaying organic material and attract Diptera in search of sites for laying eggs. However the diversity of recorded Diptera



**Fig. 6.** The relationship between pollen import and export, and visit duration to flowers of *Chamerion angustifolium* by bumblebees (A–B, *Bombus* spp.), honeybees (C–D, *Apis mellifera*) and flies (E–F, Diptera). Note that pollen removal is expressed as number of pollen grains remaining in anthers, hence the negative relationships. Data were analysed using linear regression: A,  $r^2 = 0.86$ ,  $p < 0.001$ ; B,  $r^2 = 0.69$ ,  $p < 0.001$ ; C,  $r^2 = 0.19$ ,  $p = 0.045$ ; D,  $r^2 = 0.22$ ,  $p = 0.034$ ; E,  $r^2 = 0.05$ ,  $p = 0.19$ ; F,  $r^2 = 0.09$ ,  $p = 0.11$ .

pollinators of these species is rather low, with most species being pollinated by *Musca domestica* (Muscidae) or Calliphoridae species in the genera *Sarcophaga*, *Lucilia*, and *Calliphora* (Meve & Liede 1994; Ollerton & Liede, 1997). Although these plants are phenotypic specialists, and possess functionally specialized pollination systems, they are ecological generalists in that the flowers may be pollinated by any suitable flies searching for egg laying sites. This may be a common phenomenon amongst other such “sapromyiophilous” taxa, where a broad range of species and genera can act as pollinators, e.g., species of Rafflesiaceae (e.g., Bänziger, 1991, 1996; Bänziger & Pape, 2004) and the genus *Arisaema* (Araceae) investigated by Vogel & Martens (2000).

**Example E.** — *Plant species which are pollinated by different animal species in different parts of their range, and therefore are more ecologically or functionally generalized at a species level than is apparent at a population level.*

The pollination ecology of plant species has often been studied at the population level, which may be inappropriate if one is trying to assess the level of ecological specialization of that species. A number of studies have shown that the pollinators of a plant can vary not only temporally (see Example A above) but also spatially. In fact, *Daucus carota* populations in Greece attract many insects that were not observed in the U.K. study described above, e.g., bees of the genus *Hylaeus* and chafer beetles (Coleoptera) (Lamborn, unpubl. obs.). In species of *Calochortus* (Liliaceae), pollinator identity is strongly dependent on the community and geographical context of the population (Dilley & al., 2000). Similar results have been found for *Lavandula latifolia* (Lamiaceae) by Herrera (1988, 2005) leading him to conclude that the generalized pollination system of this species “was not an invariant, species-level property” but rather a geographically context-dependent trait. This also seems to be true for species of bee-pollinated *Echium*

(Boraginaceae) in the Canary Islands, where the level of ecological generalization of a species is related directly to its geographical range rather than to specific floral traits (Dupont & Skov, 2004).

Perhaps these results are not so surprising in relatively ecologically and phenotypically generalized taxa. However site to site variation in the principle pollinators has also been found in more phenotypically specialized species such as resin-rewarding *Dalechampia* spp. (Euphorbiaceae) in the Neotropics and South Africa, where the identity of pollinators of conspecific taxa seems to be related to the geographical separation of the populations and the presence of congeners (Armbruster, 1985; Armbruster & Steiner, 1992). Further examples are provided by the orchid *Satyrium hallackii* in South Africa (where pollinators may be carpenter bees or hawkmoths and long-tongued flies, depending upon the population; Johnson, 1997) and *Narcissus tazetta* (Amaryllidaceae) in Israel: marshland populations are hawkmoth-pollinated, whereas hillside populations are pollinated by a range of short-tongued insects (Arroyo & Dafni, 1995). Thus species that appear to be very ecologically specialized within a population can be shown to be more generalized when viewed across multiple populations. It has been suggested that populations of such species can in some cases be viewed as ecotypes when floral traits correlate with pollinator size, morphology and behaviour (Armbruster, 1985; Robertson & Wyatt, 1990; Arroyo & Dafni, 1995; Johnson, 1997). Geographical variation in the identities of interacting taxa now holds a central place within some models of coevolution (Thompson, 2005).

The examples and case studies presented above should give an indication of the complexity of studying the ecology of “generalist” flowers and the importance of accurate observation and experiment in determining effective pollinators in relation to the set and setting of

**Table 1. Pollinators of *Asclepias* spp. in the New World identified by different studies.**

	No. of pollinator species	Sources
<i>A. cornuti</i>	28	Robertson (1891)
<i>A. cryptoceras</i>	1	Payson (1916)
<i>A. curassavica</i>	2, > 3, 9	Ule (1897), Atsatt (1969) cited in Wyatt (1980), Bierzychudek (1981)
<i>A. exaltata</i>	> 3	Queller (1985)
<i>A. incarnata</i>	9, > 13, 122	Robertson (1891, 1928), Macior (1965) Kephart (1979),
<i>A. purpurascens</i>	19	Robertson (1891, 1928)
<i>A. quadrifolia</i>	24	Chaplin & Walker (1982)
<i>A. solanoana</i>	2	Lynch (1977)
<i>A. sullivantii</i>	30	Robertson (1891 & 1928)
<i>A. syriaca</i>	1, > 9, 13, 14, > 23, 62	Robertson (1928), Macior (1965), Willson & Rathcke (1974), Willson & Bertin (1979), Morse (1981); Jennersten & Morse (1991)
<i>A. tuberosa</i>	28, 32, 34	Robertson (1891, 1928); Fishbein & Venable (1996)
<i>A. verticillata</i>	> 15, 16, 19, 103	Robertson (1891, 1928); Macior (1965), Willson & al. (1979); Kephart (1979)
<i>A. viridis</i>	1	Bernhardt (1990)

Source: The studies have been extracted from the online ASCLEPOL database ([http://www.uni-bayreuth.de/departments/planta2/research\\_wgl/pollina/as\\_pol\\_t.html](http://www.uni-bayreuth.de/departments/planta2/research_wgl/pollina/as_pol_t.html)) where the full references can be found.

Note: The data include only those insects known to carry pollinaria, i.e., pollinators rather than simply flower visitors.

pollination. With this in mind, we turn now to an exploration of how generalist flowers fit into the idea of pollination syndromes.

## GENERALIST FLOWERS AND THE POLLINATION SYNDROME CONCEPT

Convergent evolution of phenotypes is common in the natural world, and many unrelated taxa show similar adaptations to comparable lifestyles. “Pollination syndromes” are one such example of convergent evolution, specifically of floral phenotypes which are adapted to attract, reward and be pollinated by particular functional groups of pollinators (they were initially described as “adaptational groups” in the late 19th century by F. Delpino, 1868–1875, cited in Knuth, 1906). In essence pollination syndromes are typological constructs that have subsequently been used to organise angiosperms in relation to their pollinators by categorising flowers according to suites of shared floral traits such as shape, colour, scent, and size (Vogel, 1954; Faegri & van der Pijl, 1979; Proctor & al., 1996). The assumption that biotically pollinated flowers show adaptive traits in relation to their pollinators is broadly true (Waser, 1983), although the relationships between flowers and pollinators are much more ecologically and phylogenetically complex than previously imagined (e.g., Mayfield & al., 2001; Herrera & al., 2002; Aigner, 2001, 2006; Armbruster & al., 1997; Armbruster, 2002; Ollerton & Diaz, 1999; Lamborn & Ollerton, 2000). This at once makes pollination syndromes less useful to pollination ecologists (who are concerned with temporal and spatial variation in pollinator effectiveness) than it is to botanists who wish to functionally classify flowers. However if typological classifications such as pollination syndromes are really intended to reflect the realities of the natural world, they should at least have a high level of predictability across the angiosperms. A recent global

test of pollination syndromes has shown that they do not predict the pollinators of the majority of plants within a community, and are only useful predictors for a narrow, functionally specialized subset of flowering plants, and even then are not fool proof (Ollerton & al., in review)

Where do generalist flowers fit within the pollination syndrome concept? Knuth (1906) cautioned that Delpino’s system “has the defect that all plants are left out of the account which are visited and pollinated by insects of various orders indiscriminately, i.e., the large majority of flowers.” However the applicability of pollination syndromes for generalist flowers to some extent depends upon which definition of “generalist” we use. Ecological generalists may fulfil the criteria for possessing strict pollination syndromes if they are pollinated by a taxonomically narrow range of pollinators, e.g., “bees” or “carriage flies” or “bats.” These ecological generalists may be considered functionally specialized, and this could be reflected in relation to a flower’s pollination syndrome by the degree of phenotypic specialization (Fenster & al., 2004). For example many South American plants which are hummingbird pollinated (functionally specialized) possess long, red or orange tubular flowers and produce copious nectar (phenotypically specialized). However they are often visited, and probably pollinated, by several species of hummingbirds and so in that sense are to some degree ecological generalists (Table 2).

There is currently a great deal of debate about pollination syndromes, centred around their utility for predicting pollinators, the frequency with which plants can be assigned to specific syndromes, and the role of pollinators in shaping floral phenotypes (e.g., Herrera, 1996; Waser & al., 1996; Ollerton, 1998; Ollerton & Watts, 2000; Johnson & Steiner, 2000; Hingston & McQuillan, 2000; Fenster & al., 2004). One conclusion from the recent review by Fenster & al. (2004), was that pollination syndromes are best considered as useful from the perspective of functional specialization, and that consideration of floral evolution in relation to specialization or generalization should focus on

**Table 2. Species of hummingbirds known to visit, and probably pollinate, plants with classical bird syndrome flowers (tubular, red-orange colour, copious nectar) and flowers not fitting this syndrome (*Ananas comosus* and *Passiflora* sp.).**

	<i>Heliconia rostrata</i> (H)	<i>Heliconia hirsuta</i> (H)	<i>Heliconia stricta</i> (H)	<i>Aphelandra</i> sp. (A)	<i>Ananas comosus</i> (B)	<i>Passiflora</i> sp. (P)	<i>Erythrina</i> sp. (F)
<i>Glaucis hirsuta</i>	×			×			
<i>Phaethornis hispidus</i>	×	×					
<i>Phaethornis ruber</i>	×	×		×	×		
<i>Threnetes leucurus</i>	×	×	×				
<i>Campylopterus largipennis</i>	×	×				×	
<i>Florisuga mellivora</i>		×		×		×	×
<i>Anthracothorax nigricollis</i>	×	×	×	×	×		
<i>Thalurina furcata</i>	×	×		×	×		

Source: Data from an unpublished survey by SW at Tambopata Lodge, Tambopata-Candamo Reserved Zone, Peru, Jul–Oct 1997. Observed interactions are marked “×”. Abbreviations: A, Acanthaceae; B, Bromeliaceae; F, Fabaceae; H, Heliconiaceae; P, Passifloraceae.

functional groups of pollinators as well as on the number of species of pollinators. This can potentially be a useful approach. However, it assumes that members of a functional group have similar behaviours and will therefore select for similar floral traits, imposing consistent selection on floral phenotype. At the moment there are few data to assess the validity of this assumption, however instinctually appealing it may be. The assumption is certainly not true for some taxa even within a species. For example, *Bombus terrestris* subspecies and populations vary in their sensitivities to colour and in flower colour preferences, including a more or less pronounced preference for red flowers (Chittka & al., 2004). That such closely related taxa should vary so significantly is surprising. What should we therefore expect from different genera or families that are classed as a functional group?

Assessing plants according to their ecological or functional generalization can lead to quite different conclusions regarding the biology of generalist flowers. Fenster & al., (2004) re-analysed the Robertson (1928) dataset in terms of functional groups of pollinators and concluded that about three quarters of the plants “exhibit specialization onto functional groups, a very different conclusion than that reached by Waser et al. (1996), who used the same data.” In fact we would argue that it is only a different conclusion because a different question was being asked. Waser & al. (1996) were concerned with ecological specialization, not functional specialization, and were asking questions about risk spreading strategies involving the exploitation of multiple species as pollinators rather than just a single species. Whether that risk is spread across functionally similar taxa or across very different taxa does not matter, the conclusion regarding the importance of ecological generalization still holds.

## CONCLUSIONS

In this paper we have not attempted an exhaustive review of the literature, but rather have tried to analyse and define generalist flowers in ways which are biologically and ecologically meaningful and which cut across traditional discipline boundaries within the biological and environmental sciences, i.e., classical botany versus pollination ecology. As with so many things in biology, simple dichotomies (“generalized versus specialized”) mask a far more complex and variable reality. Using more exact terms such as ecological, functional and phenotypic generalization enables us to study floral biology with greater precision and ultimately allows for a better understanding of plant-pollinator interactions. To cite an example, recent analyses by Ollerton & Cranmer (2002) and Ollerton & al. (2006) have shown that despite intuition and speculation, pollinator-plant relationships in tropical

communities have similar levels of ecological generalization to those in temperate and subtropical regions. However, tropical communities do tend to have larger numbers of functionally specialized pollination systems per community, on average, and probably also greater phenotypic specialization (see also Armbruster, 2006, for some similar, and also divergent, view points).

Pollination biology, as Charles Darwin recognised, has much to offer to researchers interested in questions regarding plant and animal evolution, behaviour, and ecology, precisely because it requires an understanding of such a wide range of different organisms with very varied biologies. We are at an exciting and particularly fertile period in the development of our knowledge of floral biology, pollinator behaviour, and the ecology of pollination (Waser & Ollerton 2006) and we would urge researchers interested in the biology of generalist flowers to draw on evidence and data from beyond their immediate intellectual tradition. Such a multidisciplinary approach is required if we are ever to successfully realise the hoped for conceptual framework for understanding the ecology and evolution of plant-pollinator interactions.

## ACKNOWLEDGEMENTS

JO would like to thank Professor Gerhard Gottsberger and Dr. Dawn Frame for the invitation to take part in the symposium at the 17th International Botanical Congress, Vienna, 2005. The authors are grateful to The Wildlife Trust for Bedfordshire, Cambridgeshire, Northamptonshire, and Peterborough for permission to work on the Scrub Field Local Nature Reserve, to Dewi Morris for permission to carry out field work in Daventry Country Park, and Dr. Mark Gardener (The Open University) for nectar analysis. SW would particularly like to thank the numerous friends who helped with data collection in Peru and sponsored her field work there in 1997. Finally, sincere thanks to Dawn Frame, Amots Dafni and an anonymous reviewer for their detailed comments and discussions on earlier versions of this paper.

## LITERATURE CITED

- Adler, L.S. & Irwin, R.E. 2006. Comparison of pollen transfer dynamics by multiple floral visitors: experiments with pollen and fluorescent dye. *Ann. Bot. (Oxford)* 97: 141–150.
- Aigner, P.A. 2001. Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos* 95: 177–184.
- Aigner, P.A. 2006. The evolution of specialized floral phenotypes in a fine-grained pollination environment. Pp. 23–46 in: Waser, N.M. & Ollerton, J. (eds.) *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.

- Armbruster, W.S.** 1985. Patterns of character divergence and the evolution of reproductive ecotypes of *Dalechampia scandens* (Euphorbiaceae). *Evolution* 39: 733–752.
- Armbruster, W.S.** 2002. Can indirect selection and genetic context contribute to trait diversification? A transition-probability study of blossom-colour evolution in two genera. *J. Evol. Biol.* 15: 468–486.
- Armbruster, W.S.** 2006. Evolutionary and ecological aspects of specialized pollination: views from the arctic to the tropics. Pp. 260–282 in: Waser, N.M. & Ollerton, J. (eds.), *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.
- Armbruster, W.S. & Baldwin, B.G.** 1998. Switch from specialized to generalized pollination. *Nature* 394: 632–632.
- Armbruster, W.S., Howard, J.J., Clausen, T.P., Debevec, E.M., Loquvam, J.C., Matsuki, M., Cerendolo, B. & Andel, F.** 1997. Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. *Amer. Naturalist* 149: 461–484.
- Armbruster, W.S. & Steiner, K.E.** 1992. Pollination ecology of 4 *Dalechampia* species (Euphorbiaceae) in northern Natal, South Africa. *Amer. J. Bot.* 79: 306–313.
- Arroyo, J. & Dafni, A.** 1995. Variations in habitat, season, flower traits and pollinators in dimorphic *Narcissus tazetta* L. (Amaryllidaceae) in Israel. *New Phytol.* 129: 135–145.
- Bänziger, H.** 1991. Stench and fragrance: unique pollination lure of Thailand's largest flower, *Rafflesia kerrii* Meijer. *Nat. Hist. Bull. Siam. Soc.* 39: 19–52.
- Bänziger, H.** 1996. Pollination of a flowering oddity: *Rhizanthus zippelii* (Blume) Spach (Rafflesiaceae). *Nat. Hist. Bull. Siam. Soc.* 44: 113–142.
- Bänziger, H. & Pape, T.** 2004. Flowers, faeces and cadavers: natural feeding and laying habits of flesh flies in Thailand (Diptera: Sarcophagidae, *Sarcophaga* spp.). *J. Nat. Hist.* 38: 1677–1694.
- Barrett, S.C.H.** 1996. The reproductive biology and genetics of island plants. *Philos. Trans., Ser. B.* 351: 725–733.
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M.** 2003. The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. U.S.A.* 100: 9383–9387.
- Bascompte, J., Jordano, P. & Olesen, J.M.** 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312: 431–433.
- Chittka, L., Ings, T.C. & Raine, N.E.** 2004. Chance and adaptation in the evolution of island bumblebee behaviour. *Populat. Ecol.* 46: 243–251.
- Corbet, S.A.** 2006. A typology of pollination systems: implications for crop management and the conservation of wild plants. Pp. 315–340 in: Waser, N.M. & Ollerton, J. (eds.), *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.
- Dafni, A., Bernhardt, P., Shmida, A., Ivri, Y., Greenbaum, S., O'Toole, C. & Losito, L.** 1990. Red bowl-shaped flowers—convergence for beetle pollination in the Mediterranean region. *Israel J. Bot.* 39: 81–92.
- Dieringer, G., Cabrera, L., Lara, M., Loya, L. & Reyes-Castillo, P.** 1999. Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). *Int. J. Pl. Sci.* 160: 64–71.
- Dieringer, G. & Espinosa, J.E.** 1994. Reproductive ecology of *Magnolia schiedeana* (Magnoliaceae), a threatened cloud forest tree species in Veracruz, Mexico. *Bull. Torrey Bot. Club* 121: 154–159.
- Dilley, J.D., Wilson, P. & Mesler, M.R.** 2000. The radiation of *Calochortus*: generalist flowers moving through a mosaic of potential pollinators. *Oikos* 89: 209–222.
- Dupont, Y.L. & Skov, C.** 2004. Influence of geographical distribution and floral traits on species richness of bees (Hymenoptera: Apoidea) visiting *Echium* species (Borraginaceae) of the Canary Islands. *Int. J. Pl. Sci.* 165: 377–386.
- Dupont, Y.L., Hansen, D.M. & Olesen, J.M.** 2003. Structure of a plant-pollinator network in the high altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* 26: 301–310.
- Endress, P.K.** 1996. *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge Univ. Press, Cambridge.
- Endress, M.E. & Bruyns, P.V.** 2000. A revised classification of the Apocynaceae s. l. *Bot. Rev.* 66: 1–56.
- Faegri, K. & van der Pijl, L.** 1979. *The Principles of Pollination Ecology*, 3rd ed. Pergamon Press, Oxford.
- Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D.** 2004. Pollination syndromes and floral specialization. *Annual Rev. Ecol. Evol. Syst.* 35: 375–403.
- Fleming, T.H.** 2005. The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos* 111: 556–562.
- Frame, D.** 2003. Generalist flowers, biodiversity and florivory: implications for angiosperm origins. *Taxon* 52: 681–685.
- Frame, D. & Durou, S.** 2001. Morphology and biology of *Napoleonaea vogelii* (Lecythidaceae) flowers in relation to the natural history of insect visitors. *Biotropica* 33: 458–471.
- Frumin, S. & Friis, E.M.** 1999. Magnoliid reproductive organs from the Cenomanian-Turonian of north-western Kazakhstan: Magnoliaceae and Illiciaceae. *Pl. Syst. Evol.* 216: 265–288.
- Herrera, C.M.** 1988. Variation in mutualisms—the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* 35: 95–125.
- Herrera, C.M.** 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. Pp. 65–87 in: Lloyd, D.G. & Barrett, S.C.H. (eds.), *Floral Biology*. Chapman and Hall, New York.
- Herrera, C.M.** 2005. Plant generalization on pollinators: species property or local phenomenon? *Amer. J. Bot.* 92: 13–20.
- Herrera, C.M., Medrano, M., Rey, P.J., Sanchez-Lafuente, A.M., Garcia, M.B., Guitian, J. & Manzaneda, A.J.** 2002. Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proc. Natl. Acad. Sci. U.S.A.* 99: 16823–16828.
- Hingston, A.B. & McQuillan, P.B.** 2000. Are pollination syndromes useful predictors of floral visitors in Tasmania? *Austral Ecol.* 25: 600–609.
- Johnson, S.D.** 1997. Pollination ecotypes of *Satyrium hal-lackii* (Orchidaceae) in South Africa. *Bot. J. Linn. Soc.* 123: 225–235.
- Johnson, S.D. & Steiner, K.E.** 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* 15: 190–193.

- Johnson, S.D. & Steiner, K.E.** 2003. Specialized pollination systems in southern Africa. *S. African J. Sci.* 99: 345–348.
- Knuth, P.** 1906. *Handbook of Flower Pollination*, vol. 1. Clarendon Press, Oxford.
- Knuth, P.** 1908. *Handbook of Flower Pollination*, vol. 2. Clarendon Press, Oxford.
- Lamborn, E. & Ollerton, J.** 2000. Experimental assessment of the functional morphology of inflorescences of *Daucus carota* (Apiaceae): testing the ‘fly catcher effect’. *Funct. Ecol.* 14: 445–454.
- Leiss, K.A. & Klinkhamer, P.G.L.** 2005. Genotype by environment interactions in the nectar production of *Echium vulgare*. *Funct. Ecol.* 19: 454–459.
- Lloyd, D.G. & Barrett, S.C.H.** 1996. *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*. Chapman & Hall, New York.
- Mayfield, M.M., Waser, N.M. & Price, M.V.** 2001. Exploring the ‘most effective pollinator principle’ with complex flowers: Bumblebees and *Ipomopsis aggregata*. *Ann. Bot. (Oxford)* 88: 591–596.
- Memmott, J.** 1999. The structure of a plant-pollinator food web. *Ecol. Lett.* 2: 276–280.
- Meve, U. & Liede, S.** 1994. Floral biology and pollination in stapeliads—new results and a literature review. *Pl. Syst. Evol.* 192: 99–116.
- Olesen, J.M. & Jordano, P.** 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology* 83: 2416–2424.
- Ollerton, J.** 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems. *J. Ecol.* 84: 767–769.
- Ollerton, J.** 1998. Sunbird surprise for syndromes. *Nature* 394: 726–727.
- Ollerton, J. & Cranmer, L.** 2002. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* 98: 340–350.
- Ollerton, J. & Diaz, A.** 1999. Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. *Oecologia* 119: 340–348.
- Ollerton, J. & Liede, S.** 1997. Pollination systems in the Asclepiadaceae: a survey and preliminary analysis. *Biol. J. Linn. Soc.* 62: 593–610.
- Ollerton J., Johnson S.D., Cranmer, L. & Kellie, S.** 2003. The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Ann. Bot. (Oxford)* 92: 807–834.
- Ollerton, J. Johnson, S.D. & Hingston, A.B.** 2006. Geographical variation in diversity and specificity of pollination systems. Pp. 283–308 in: Waser, N.M. & Ollerton, J. (eds.), *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.
- Ollerton, J. & Watts, S.** 2000. Phenotype space and floral typology: towards an objective assessment of pollination syndromes. *Norske Vidensk.-Akad. I, Mat.-Naturvidensk. Kl., Avh., Ny Ser.* 39: 149–159.
- Pauw, A.** 2006. Floral syndromes accurately predict pollination by a specialized oil-collecting bee (*Rediviva peringueyi*, Melittidae) in a guild of South African orchids (Coryciinae). *Amer. J. Bot.* 93: 917–926.
- Pellmyr, O.** 2002. Pollination by animals. Pp. 157–184 in Herrera, C.M. & Pellmyr, O. (eds.), *Plant-Animal Interactions: An Evolutionary Approach*. Blackwell Science, Oxford.
- Poulin, R. & Mouillot, D.** 2005. Combining phylogenetic and ecological information into a new index of host specificity. *J. Parasitol.* 91: 511–514.
- Proctor, M., Yeo, P. & Lack, A.** 1996. *The Natural History of Pollination*. HarperCollins, London.
- Robertson, C.** 1891. Flowers and insects, Asclepiadaceae to Scrophulariaceae. *Trans. Acad. Sci. St. Louis* 5: 569–598.
- Robertson, C.** 1928. *Flowers and insects: Lists of Visitors of four hundred and fifty-three Flowers*. Privately published, Carlinville.
- Robertson, J.L. & Wyatt, R.** 1990. Evidence for pollination ecotypes in the yellow-fringed orchid, *Platanthera ciliaris*. *Evolution* 44: 121–133.
- Rudall, P.J., Stuppy, W., Cunniff, J. Kellogg, E.A. & Briggs, B.G.** 2005. Evolution of reproductive structures in grasses (Poaceae) inferred by sister-group comparison with their putative closest living relatives, Ectodiocoleaceae. *Amer. J. Bot.* 92: 1432–1443.
- Stebbins, G.L.** 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual Rev. Ecol. Syst.* 1: 307–326.
- Symons, F.B. & Beccaloni, G.W.** 1999. Phylogenetic indices for measuring the diet breadths of phytophagous insects. *Oecologia* 119: 427–434.
- Thien, L.B., Azuma, H. & Kawano, S.** 2000. New perspectives on the pollination biology of basal angiosperms. *Int. J. Pl. Sci.* 161 (Suppl.): S225–S235.
- Thompson, J.N.** 2005. *The Geographic Mosaic of Coevolution*. Univ. Chicago Press, Chicago.
- Vázquez, D.P. & Aizen, M.A.** 2006. Community-wide patterns of specialization in plant-pollinator interactions revealed by null models. Pp. 200–219 in: Waser, N.M. & Ollerton, J. (eds.), *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.
- Vogel, S.** 1954. *Blütenbiologische Typen als Elemente der Sippengliederung*. Fischer, Jena.
- Vogel, S. & Martens, J.** 2000. A survey of the function of the lethal kettle traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal. *Bot. J. Linn. Soc.* 133: 61–100.
- Waser, N.M.** 1983. The adaptive nature of floral traits: ideas and evidence. Pp. 241–285 in: Real, L.A. (ed.), *Pollination Biology*. Academic Press, New York.
- Waser, N.M.** 1998. Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* 82: 198–201.
- 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.
- Waser, N.M. & Ollerton, J. (eds.)** 2006. *Plant-Pollinator Interactions: from Specialization to Generalization*. Univ. Chicago Press, Chicago.
- Willis, J.C. & Burkill, I.H.** 1895. Flowers and insects in Great Britain I. *Ann. Bot. (Oxford)* 9: 227–273.
- Willis, J.C. & Burkill, I.H.** 1903. Flowers and insects in Great Britain II. *Ann. Bot. (Oxford)* 17: 313–349.
- Wyatt, R. & Broyles, S.B.** 1994. Ecology and evolution of reproduction in milkweeds. *Annual Rev. Ecol. Syst.* 25: 423–441.