The structure of flower visitation webs: how morphology and abundance affect interaction patterns between flowers and flower visitors

Stang, M.

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chapter 1

General introduction

Pollination, the transfer of pollen grains to the stigma of the plant gynoecium is a crucial step in the sexual reproduction of flowering plants. The majority of flowering plants rely on animals for the transfer of pollen (Nabhan & Buchmann, 1997; Renner, 1988). Because flower visitors gain no direct benefit by pollinating flowers, rewards must lure them. The most common way plants attract animals to visit their flowers is by providing food such as nectar, pollen or oils. While searching for these rewards in the flower, pollen from the flower's anthers may stick to the body of the animal. When the animal visits subsequent flowers in search of more rewards, pollen from its body may adhere to the stigma of these flowers and again, new pollen may stick to the body of the animal.

Flowers differ tremendously in colour, scent, size and shape; and they are visited by an equally diverse morphological and taxonomic array of animals. The most common flower visitors are insects belonging to the orders Hymenoptera, Lepidoptera, Diptera and Coleoptera. But several species of birds, bats, and other mammals also regularly visit and pollinate flowers. A common and longstanding view in pollination biology is that plants should specialize on a small subset of these visitors in order to ensure effective pollination. And indeed, despite the huge morphological and taxonomical diversity of potential interaction partners, flowers show trait combinations that seem to reflect the morphology, behaviour and physiology of certain pollinator types (*e.g.* Faegri & van der Pijl, 1979). For example, red coloured, odourless flowers with deeply hidden and dilute nectar seem to be adapted to hummingbirds or perching birds; blue coloured bilaterally symmetric flowers with moderately hidden and relatively concentrated nectar combined with a pleasant odour are thought to be adapted to bees. These typical trait combinations (termed 'pollination syndromes' in the literature) are found across diverse taxonomic groups of plants and seem to be a result of specialization and convergent evolution.

The prevalence of plants specializing on one taxonomical group of animals has been questioned, however, because community-level studies reveal that most plant species are visited by species belonging to different animal orders or even classes (Herrera, 1996; Waser *et al.*, 1996) and pollination syndromes are not as distinct as they seem to appear (Ollerton & Watts, 2000). Moreover, the concept of pollination syndromes depicts only the taxonomic variation among pollinators. Within a taxonomic group there might be a much greater variation in size and behaviour than among taxonomic groups. For example, flowers that show the typical hawkmoth syndrome (pale coloured flowers with a strong, heavy-sweet perfume which open at night in combination with narrow nectar tubes with ample nectar) differ in the depth at which the nectar is hidden in the flower from a few millimetres up to several centimetres, and hawkmoths differ to the same extent in the length of their mouthparts (Agosta & Janzen, 2005; Haber & Frankie, 1989). But not only field studies question the prevalence of specialization, there are also theoretical doubts that specialization should always be promoted in nature. Because relying on one species or type of pollinator causes variable reproductive success across years, plants might do better to generalize, so long as pollinator population sizes vary independently (Waser *et al.*, 1996). In such cases, a plant may be at an advantage if it attracts several species or types of pollinators, ensuring sufficient pollen transfer every year.

Doubts about the significance of specialization in plant–pollinator interactions and about the existence of discrete pollination syndromes have resulted in a renewed interest in how important and common specialization actually is, and what kind of traits really determine who visits whom (Waser & Ollerton, 2006). The essential first steps for this re-evaluation are an objective quantification of the degree of generalization and specialization and the search for trait combinations that can explain the whole set of interactions in flower visitation webs, rather than explaining only restricted portions of such webs. As an indicator of the degree of generalization a large number of studies follow a pragmatic approach and count the number of species that interact with each other, *i.e.* the number of visitor species observed on a plant species and the number of plant species visited by a flower visitor species (*e.g.* Dupont *et al.*, 2003; Jordano, 1987; Moldenke, 1975; Olesen & Jordano, 2002; Ollerton & Cranmer, 2002; Vázquez & Aizen, 2003). I follow this approach even though it has some drawbacks. Because of the large number of species normally encountered in community-level studies it is often not possible to distinguish whether flower visitors are pollinators or visit flowers without pollen transfer (flower larceny; *e.g.* Irwin *et al.*, 2001), or whether flower visitors are effective or non-effective in their pollen transfer. Yet community studies are a first essential step in the analysis of generalization and specialization.

Since the publication of the two influential papers that questioning the importance of specialization (Herrera, 1996; Waser *et al.*, 1996) a growing number of studies during the last 10 years has studied interaction patterns between flowers and flower visitors or reanalyzed existing community-level studies, with new mathematical and statistical approaches with exciting results (Waser & Ollerton, 2006). For example, not so long ago it was considered common sense (at least implicitly) that plant–pollinator interactions are symmetric (Vázquez & Aizen, 2004, and references therein), *i.e.* generalists interact mainly with generalists and specialists with specialists (FIGURE 1.1, top). However, community-level studies revealed that the interactions between plants and flower visitors are mainly asymmetric (Bascompte *et al.*, 2003; Lewinsohn *et al.*, 2006; Memmott *et al.*, 2004a; Vázquez & Aizen, 2004), thus specialists interact primarily with generalists, whereas generalists interact with specialists and generalists (FIGURE 1.1, bottom).

Fairly little is still known about the factors leading to patterns of specialization and generalization at the community level (Jordano *et al.*, 2006; Vázquez & Aizen, 2004, 2006) or the potential consequences of these patterns for species extinctions and the stability of whole plant–flower visitor interaction webs (Ashworth *et al.*, 2004; Memmott *et al.*, 2004a). There is also a lack of knowledge how the degree of generalization affects the degree of morphological matching which should influence the per-visit pollination efficiency of the visitors (Campbell *et al.*, 1996; Johnson &

Steiner, 1997; Nilsson, 1988; although see Wilson, 1995). In particular, the impact of plant and visitor traits that may constrain the kind and number of potential interaction partners, and the frequency of these traits across species and individuals in a local community, have rarely been investigated (Jordano *et al.*, 2006; Vázquez, 2005).

This thesis is an effort to evaluate the reasons for, and the importance and consequences of community-wide patterns of specialization and generalization. My intent is to assess the potential influence of morphology and abundance on the degree of ecological specialization and generalization (*i.e.* the number of plant species visited or the number of visitor species on a plant species), the asymmetry of interactions, the extinction risk of species, and the degree of morphological matching between plants and visitors. To do this I will compare the observed patterns with expected patterns based on the result of simulation models incorporating different combinations of the potential factors. The study system is a species-rich Mediterranean plant–flower visitor community in the southeast of Spain.

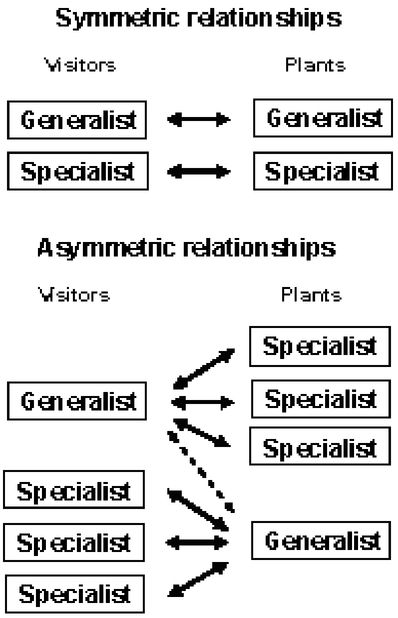

FIGURE 1.1 – Reciprocity of relationships between generalized and specialized plants and visitors. An earlier view assuming ‘symmetric’ relationships (top) has been shown by recent community-level studies to be incorrect; instead interactions are ‘asymmetric’ (bottom), with specialist plants and animals tending usually to associate with generalist partners, although generalist plants and animals do also interact frequently.

I concentrate on the role of morphological traits that potentially constrain the interactions between nectar-producing flowers and nectar-foraging visitors: the depth at which the nectar is concealed inside the flower (which I refer to as 'nectar holder depth'), the width of the nectar hiding tube (which I refer to as 'nectar holder width'), and the size of the place where insects might alight on the flower as they feed (the 'alighting place'). The stronger the morphological restrictions a flower puts on the morphology of its potential visitors, the smaller the range of flower visitor traits that should be observed on a plant species and the more morphologically specialized this species is. This is shown in FIGURE 1.2 for nectar depth and proboscis length. I hypothesize that the smaller the expected morphological range of visitor traits, the fewer visitor species will be observed on a plant species and the closer the morphological fit. The same should be true for the visitor's point of view, thus the smaller the expected morphological range of plant traits, the fewer plant species a flower visitor should visit, and the closer the morphological fit with these plants. As estimates of abundance I chose the number of individuals (visitors) and the number of open flowers during peak flowering (plants). I hypothesize that the higher the abundance of species or

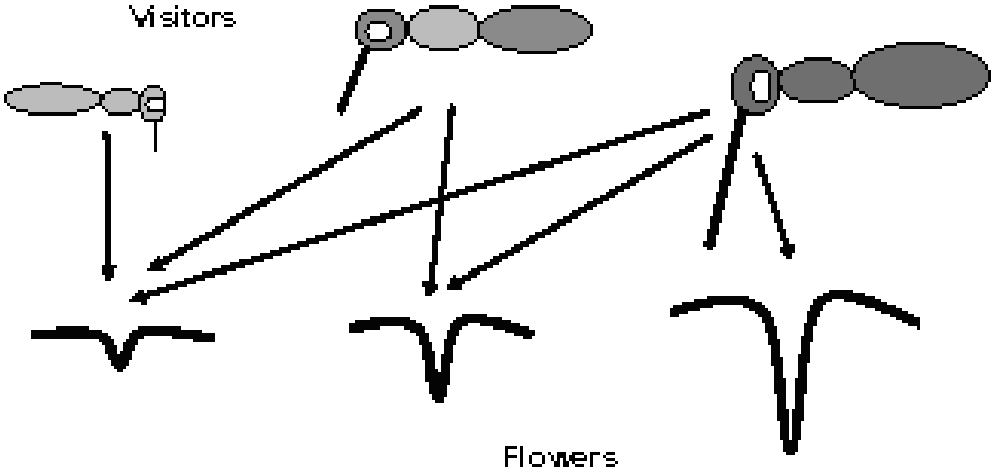

FIGURE 1.2 – A cartoon depicting size constraints (nectar holder depth and proboscis length), which limit interactions between nectar-producing flowers and nectar-searching flower visitors. The insects possess short to long proboscises (top), and the flowers possess shallow to deep tubes (bottom). In principle, short proboscises can reach shallow but not deep nectar; longer proboscises can reach all nectar unless it is more deeply concealed than the proboscis is long.

resources, the larger the number of interaction partners and the higher the impact of an interaction partner on the degree of matching.

The thesis consists of five chapters of which this Introduction is CHAPTER 1 and the Summary is CHAPTER 5. In CHAPTER 2 I show that flower parameters set a size threshold on the morphology of flower visitors. I demonstrate that the number of observed visitor species decreases with increasing nectar holder depth and increases with increasing nectar holder width. Based on nectar holder depth and width the number of flower visitors that can potentially visit a plant species is determined. I demonstrate that the observed number of interaction partners is positively correlated with this potential number and that the observed interaction partners are a random draw out of the whole potential morphological range of visitor species. Within the constraints set by flower morphology, the number of flowers influences the number of interaction partners. The more flowers a plant species produces, the more animal species visit this plant species.

In CHAPTER 3 I ask whether there is a relationship between the degree of generalization of a species and the degree of generalization of its interaction partners and what the potential causes and consequences of this relationship are. In the first part of CHAPTER 3 I demonstrate that the Mediterranean flower visitation web I studied is asymmetrically organized, and that a size threshold in combination with random interactions proportional to species abundance among the potential interactions could be responsible for this asymmetric specialization. In the second part of CHAPTER 3 I study the influence of these factors on the extinction risk of species. The degree of asymmetry may have a profound impact on the extinction risk of a species. The more specialized the interactions, the more prone are the species to extinction by chance processes. If a flower visitation web is asymmetrically organized, this extinction risk might be equalized (Ashworth *et al.*, 2004) and the whole web might be more stable compared to a symmetrically organized one (Memmott *et al.*, 2004a). I show that, even if the web is asymmetrically organized, morphologically specialized species have higher extinction risks than morphologically generalized species. Because specialized species are less abundant in the studied web, the inclusion of species frequencies in the simulations increases the difference between specialists and generalists in extinction risk even more.

Chapter 4 takes up the influence of size thresholds on the degree of morphological matching between proboscis length and nectar holder depth. A close morphological match between flowers and flower visitors can be an important component of high visitation rates (Inouye, 1980; Peat *et al*., 2005; Ranta & Lundberg, 1980) or high per-visit pollination efficiencies (Campbell *et al*., 1996; Johnson & Steiner, 1997; Nilsson, 1988). An analysis of published records of flower visits across north-western Europe (Knuth, 1906) indeed points in the direction of size matching: plants of certain nectar depths are visited mainly by insect groups with corresponding proboscis lengths (Corbet, 2006; Ellis & Ellis-Adam, 1993). This size matching seems at odds with the fact that pollinators with long proboscises will in principle have access to shallow as well as deep flowers. However, the frequency of species and individuals with shallow and deep flowers or with short and long proboscises will influence the average degree of matching. My analysis of the Mediterranean flower visitation web reveals that flower visitors with a short proboscis indeed match on average the nectar depth of flowers more closely than those with a long proboscis. Conversely, plant species with hidden nectar and openly-presented nectar match their interaction partners on average equally closely. I show, under the assumption of random interactions proportional to abundance, that this overall relationship can be the result of the depth threshold and the observed proboscis length and nectar holder depth distributions. Both distributions are right-skewed and resemble seemingly ubiquitous log-normal body size distributions.

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