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

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chapter 3

Asymmetric specialization and extinction risk in plant–flower visitor webs: a matter of morphology or abundance?

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Abstract

A recently discovered feature of plant–flower visitor webs is the asymmetric specialization of the interaction partners: specialized plants interact mainly with generalized flower visitors and specialized flower visitors mainly with generalized plants. Little is known about the factors leading to asymmetry and their consequences for the extinction risk of species. Existing studies proposed random interactions proportional to species abundance as an explanation. However, the simulation models used in these studies did not include potential biological constraints. In the present study, we tested the potential role of both morphological constraints and species abundance in promoting asymmetric specialization. We compared actual field data of a Mediterranean plant–flower visitor web with predictions of Monte Carlo simulations including different combinations of the potential factors structuring the web. Our simulations showed that both nectar holder depth and abundance were able to produce asymmetry; but that the expected degree of asymmetry was stronger if based on both. Both can predict the number of interaction partners, but only nectar holder depth was able to predict the degree of asymmetry of a certain species. What is more, without the size threshold the influence of abundance would disappear over time. Thus, asymmetric specialization seems to be the result of a size threshold and only among the allowed interactions above this size threshold a result of random interactions proportional to abundance. The simulations also showed that asymmetric specialization could not be the reason that the extinction risk of specialists and generalists is equalized as suggested in the literature. In asymmetric webs specialists had clearly higher short-term extinction risks. In fact, primarily generalist visitors seem to profit from asymmetric specialization. In our web specialists were less abundant than generalists. Therefore, including abundance in the simulation models increased the difference between specialists and generalists even more.

Introduction

The study of plant–flower visitor interaction webs can give important answers to fundamental ecological questions, such as the factors that determine the structure and stability of communities. The structure of an interaction web can be described in terms of the number of interaction partners. This number varies in plant–flower visitor webs from one up to more than several dozens (Waser *et al.*, 1996). A species with a low number of interaction partners in a local web is called an ecological specialist and a species with a high number of interactions partners an ecological generalist (Ferry-Graham *et al.*, 2002). A recently discovered structural feature of mutualistic interaction webs is the asymmetric specialization of the interacting partners (Bascompte *et al.*, 2003; Dupont *et al.*, 2003; Petanidou & Ellis, 1996; Vázquez & Aizen, 2004; Vázquez & Simberloff, 2002). Flower visitors that visit an ecologically specialized plant species tend to interact with a large number of plant species. Flower visitors that visit an ecologically generalized plant species tend to interact with a small number of plant species. Asymmetric specialization is an intriguing pattern that was found not only in plant–flower visitor webs but also in plant–fruit disperser (Bascompte *et al.*, 2003) and fish–parasite webs (Vázquez *et al.*, 2005). The asymmetric nature of interactions is intriguing because it contradicts the traditional view of symmetric interactions, *i.e.* generalist plants interact with generalist visitors and specialist plants with specialist visitors (Vázquez & Aizen, 2004 and references therein). Surprisingly little is known about the factors that promote asymmetry and the influence of these factors on the extinction risk of the interaction partners. In this paper we want to explore the impact of morphological constraints and species abundance on the degree of asymmetry in a Mediterranean plant–flower visitor interaction web and the influence of both factors on the short-term extinction risks of the species due to chance processes.

Asymmetric specialization in interaction webs seems to be based on a so-called nested structure of the interactions (Bascompte *et al.*, 2003; Dupont *et al.*, 2003; Ollerton *et al.*, 2003). In order to discover nestedness, the species in a plant–flower visitor matrix have to be arranged according to their number of interactions (the visitor species with the highest number of interactions will be found in the first row of the matrix and the plant species with the highest number of interactions in the first column). The interactions in a perfectly nested matrix will occur above a boundary threshold (Atmar & Patterson, 1993), *i.e.* a line from the bottom left corner to the top right corner (FIGURE 3.1a). As a result, generalists interact not just with specialists but also with generalists. A nested pattern of interactions necessarily means asymmetric specialization, the converse is not necessarily true (Vázquez & Aizen, 2004). The nested organization can be thought of as an alternative to a compartmentalized organization with only a small overlap of interacting partners between groups of species, *i.e.* the whole web is divided into a number of smaller webs with few interactions among these sub-webs (Dicks *et al.*, 2002). Compartmentalized webs can be asymmetrically organized, however, in this case without generalist–generalist interactions (FIGURE 3.1b). Both types of asymmetric organization are different from a purely random structure (FIGURE 3.1c).

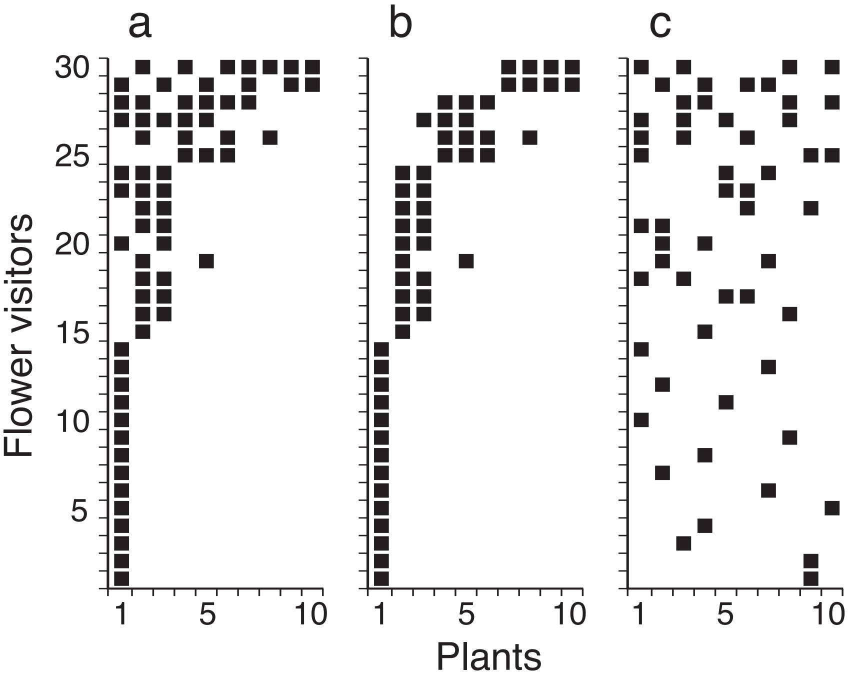

FIGURE 3.1 – Examples of fictitious plant–flower visitor interaction matrices with different types of interaction patterns: (a) nested and asymmetric, (b) compartmentalized and asymmetric, (c) random. Each number labels either a plant or a visitor species. A species–species interaction is indicated with a black square. The species were ordered by the number of interaction partners. For example, in (a) visitor species number 30 visited seven plant species and plant species number 1 was visited by 20 visitor species.

Asymmetric specialization has been found to be related to the abundance of the species involved (Dupont *et al.*, 2003). Locally rare plants tend to interact with generalized, locally abundant visitors, and locally rare visitors appear to utilize generalized, locally abundant plants. Random interactions proportional to species abundance seemed to be sufficient to explain the observed asymmetric specialization in a null model analysis based on Monte Carlo simulations (Vázquez, 2005; Vázquez & Aizen, 2004). The idea behind this is that visitor individuals rather than visitor species distribute themselves randomly and proportional to the available resources over the plant species (following an ideal free distribution). Thus, abundant visitor species visit many plant individuals and, because they choose plant individuals randomly, many plant species. As a result, rare plant species are visited by few individuals and thus by few visitor species that are most likely ecologically generalized.

The biologically neutral mechanism of random interactions proportional to abundance is based on the assumption that no constraints exist that restrict this process. However, in a previous paper we have shown that nectar holder depth and width set limits to the morphology of nectar- gathering flower visitors (Stang *et al.*, 2006). Visitors rarely try to visit a flower for nectar if their proboscis is shorter and/or thicker than the flower structures hiding the nectar. The observed flower visitors in this study were a random selection out of the potential visitors, *i.e.* those species that have a proboscis as long as or longer than the depth of the nectar holder (Stang *et al.*, 2006). Other studies proposed that morphological mismatching could lead to forbidden interaction which would explain gaps in an otherwise perfectly nested matrix caused by abundance patterns (Dupont *et al.*, 2003; Jordano *et al.*, 2003). In the present study, we want to test the role of size constraints as a biological mechanism responsible for the overall pattern of asymmetric specialization and nestedness. We include both morphological constraints and species abundance in a null model approach to contrast the observed patterns with those obtained from simulation models including different combinations of the potential factors (Gotelli & Graves, 1996).

Asymmetric specialization might have important consequences for biodiversity conservation. The extinction risk of a plant or flower visitor species may not only depend on the number of interaction partners but also on the extinction risk of these interaction partners, which will be influenced by their level of specialization (Ashworth *et al.*, 2004; Memmott *et al.*, 2004; Vázquez & Simberloff, 2002). A specialized species that interacts with a generalist will be less prone to extinction then a specialized species that depends on a specialized interaction partner. The extinction risk of single species and the stability of the whole web in the long term will also be influenced by whether asymmetric specialization is based on a nested or a compartmentalized organization (Melian & Bascompte, 2002; Memmott *et al.*, 2004).

There are indications that generalist and specialist plant species do not differ in reproductive susceptibility due to disturbance (Aizen *et al.*, 2002). It is argued that generalist visitors will be less affected by habitat fragmentation than specialist visitors as they can change their food plants easily. If a flower visitation web is asymmetrically organized and only generalist pollinators will be left over after fragmentation, generalists and specialist plants might depend both on these generalists which would place them in similar conditions (Ashworth *et al.*, 2004). This idea depends on three prerequisites, which will be tested in this study. Firstly, species-specific traits determine the degree of ecological specialization. Secondly, asymmetry is based on nestedness which will provide the necessary redundancy to allow generalists to substitute for specialists (in addition to the possibility that specialists can substitute for other specialists). Thirdly, specialist and generalist plants will have the same chance of becoming extinct in the short term. The knowledge about species-specific short-term extinction risks will also provide the basis to model extinction cascades for plant–flower visitor webs (Memmott *et al.*, 2004).

Overall, we will answer the following questions:

- Is the flower visitation web asymmetrically organized and is this asymmetry a result of a nested structure of the interaction matrix?
- Are morphological thresholds (nectar holder depth and width), random interactions proportional to species abundance, or both responsible for this asymmetric specialization?
- Does asymmetry lead to similar short-term extinction risks due to chance processes for generalists and specialists and how do size thresholds and abundance influence the short-term extinction risk of ecological and morphological specialists and generalists?

Methods

Study system, sampling procedure and size parameter estimation

The data used in this paper come from a previously published study of a Mediterranean flower visitation web. A full description of field methods is given in Stang *et al.* (2006). This flower visitation web consisted of 25 nectar-producing plant species and 111 nectar-collecting flower visitor species spread over five insect orders. We measured size parameters of flowers (nectar holder depth and width) and insects (proboscis length and proboscis diameter), which were found to constrain the potential interactions between the mutualistic partners (Stang *et al.*, 2006). We estimated plant species abundance using two direct measurements: total number of individuals and total number of open flowers. We determined the number of insect individuals and species visiting a plant species during four 15 minutes intervals for each plant species. The intervals were randomly spread over a period of two weeks during the period when the plant was in full bloom. The total observation period of all plant species was 6 weeks during March and April 2003. We observed 1,206 visitor individuals of which 887 fed on nectar or nectar and pollen. The restriction to nectar-producing plant species and nectar-feeding visitors is essential given the morphological constraints we want to investigate.

Interaction asymmetry and nestedness

Interaction asymmetry was estimated by the correlation coefficient between the number of interactions of a species n and the mean number of interactions of its interaction partners m (Vázquez & Aizen, 2004; Vázquez & Simberloff, 2002): a negative correlation between the two shows that interactions are asymmetric, a positive that interactions are symmetric.

We used the following definitions of n and m:

n_{vis} = number of visitor species of a plant species,
n_{pla} = number of plant species visited by a flower visitor species,
m_{vis} = mean number of interactions of the visitor species of a plant species

$$m_{vis} = \frac{\sum n_{pla}}{n_{vis}}$$

m_{pla} = mean number of interactions of the plant species visited by a flower visitor species

$$m_{pla} = \frac{\sum n_{vis}}{n_{pla}}$$

The variables were tested for normality with a Kolmogorov-Smirnov test. Because of the triangular-like distribution of the data, which lead to non-normality, we used a Spearman rank-order correlation coefficient for both plants and visitors. Statistical analysis was performed using SPSS 11.0 (SPSS Inc., Chicago, USA) and Winstat for Microsoft Excel version 2005.1.

In order to test if asymmetry was associated with the nestedness of interactions, the species in the plant–flower visitor matrix were arranged according to the number of interactions with their mutualistic partners in descending order. We calculated one commonly used estimate of nestedness: system temperature T (Atmar & Patterson, 1993) by using the Nestedness Calculator software, which was developed by Atmar and Patterson in 1995 (AICS Research, University Park, NM). System temperature T is a measure of the number of deviations of unexpected presences and absences in the observed matrix above and below a calculated boundary threshold of a perfectly nested matrix. For each of these unexpected presences or absences, a normalized measure of global distance to the boundary is calculated, and these values are averaged. T has values ranging from 0° to 100° with T = 0° representing a perfectly nested matrix (no disorder). In a perfectly nested matrix with less than 50% fill the observed interactions will form a concave meniscus in the upper-left corner of the matrix. A matrix is considered significantly nested if the observed T value was smaller than a benchmark value (5%) of 1,000 randomly gathered T values using matrices of similar size and fill.

Species traits and interaction asymmetry

As a first descriptive step of the analysis, we examined the relation between size parameters, abundance estimates and the number of observed interactions of a species (*n*) and the mean number of interactions of its interaction partners (*m*). The smaller *n* or *m*, the more ecologically specialized a species or species group is. For the statistical analysis we used again the non-parametric Spearman rank-order correlation coefficient, because visitor traits could not be transformed to achieve normality.

As a second step of the analysis, we estimated the contribution of size constraints and abundance to asymmetry (measured as the Spearman rank-order correlation coefficient between *n* and *m*) by Monte-Carlos simulation tests based on four different null models. In the first fully random model (*a*) all interactions were possible with the same probability for each species. In the second model (*b*) the possible interactions were constrained by the morphology of the interaction partners, *i.e.* the proboscis of a visitor had to be as long or longer than the depth of the nectar holder of a plant. Within these limits the probability of an interaction was equal for all species. In the third model (*c*) the probability was proportional to the abundance of the species. Each interaction was allowed. The fourth model (*d*) combined morphological constraints with the probability of the interactions being proportional to the abundances of the species.

For the species based simulation models (*a* and *b*) we held the total number of species–species interactions (231) constant. For the individual based simulation models (*c* and *d*) we conserved the number of individual–individual interactions (887). To be able to compare our results with those of Vázquez and Aizen (2004), we used the number of observed insect individuals on a plant species and the number of individuals of a visitor species as the abundance estimates in the random models. In fact, the total number of open flowers of a plant species in the observation plots during peak flowering and the number of visitor individuals per plant species were significantly positive correlated ($r_s = 0.58$, $p = 0.002$, $n = 25$). Because we wanted to estimate the extinction risk of the species, we allowed in our simulations that by chance species might get no interaction. We tested nectar holder depth and nectar holder width as size constraints in the models b and d. However, even if nectar holder width contributed significantly to the variation of the number of visitor species (Stang *et al.*, 2006), our analysis revealed that it did not contribute significantly to asymmetry in the random models *b* and *d*. In order to simplify the discussion we only present the results of the null models including nectar holder depth in this paper.

To test if the observed asymmetry is different from the asymmetry of the random models, we used a difference statistic that compares the observed value of the correlation coefficient between n and m with the distribution of 1,000 randomly generated values. The observed correlation was treated as significantly different from the random ones if the observed value was larger than the 25th largest random value or smaller than the 25th smallest random value. The programme Poptools (Hood, 2005) provided the shuffle algorithm and the difference statistic for the Monte Carlo simulation tests. If the asymmetry of the model was as strong as or stronger than the observed one, we considered the factors that were used to construct the model as a potential cause for the observed asymmetry.

With the correlation coefficient between n and m of the random models we tested the ability of the factors to produce the overall pattern of asymmetry. In order to test which of the random models was able to predict the species-specific components of asymmetry, *i.e.* the observed n and m of each single species, we correlated each n_{random} with $n_{observed}$ and each m_{random} with $m_{observed}$. We indicated the ability of the models to predict the observed n and m of a plant or visitor species with the mean r_s and p values of each of the 1,000 Spearman rank-order correlation coefficients. The higher the mean correlation coefficient is, the better is the match between the random and the observed generalization level of a certain species (n) and the match between the random and observed mean generalization level of its interaction partners (m).

Extinction risk

To obtain an indication of the extinction risk of plant and flower visitor species in relation to their abundance and morphology, we counted for each species the number of zero interactions that were produced during the randomizations, which is an estimate of the short-term susceptibility to extinction by chance processes. Our definition makes the simplification that a plant can only survive if it sets seeds because of the pollination by a flower visitor and that a flower visitor species can only survive and reproduce if it can feed on nectar. We correlated nectar holder depth (plants) and proboscis length (animals) as estimators of the level of morphological specialization with the probability of observing a zero interaction for each of the four random models.

Results

Interaction asymmetry and nestedness

The interactions in our flower visitation web were significantly asymmetrical (FIGURE 3.2). Plant species that were visited by many visitor species were visited, on average, by ecologically specialized species; and plant species that were visited by few visitor species were visited, on average, by ecologically generalized species ($r_s = -0.441$, $p = 0.027$, $n = 25$). The same asymmetric relationship can be observed for the flower visitors ($r_s = -0.233$, $p = 0.014$, $n = 111$). The correlation coefficient was lower for the visitors, caused by a greater variation for visitor species that were visiting a low number of plant species (a stronger triangular relationship).

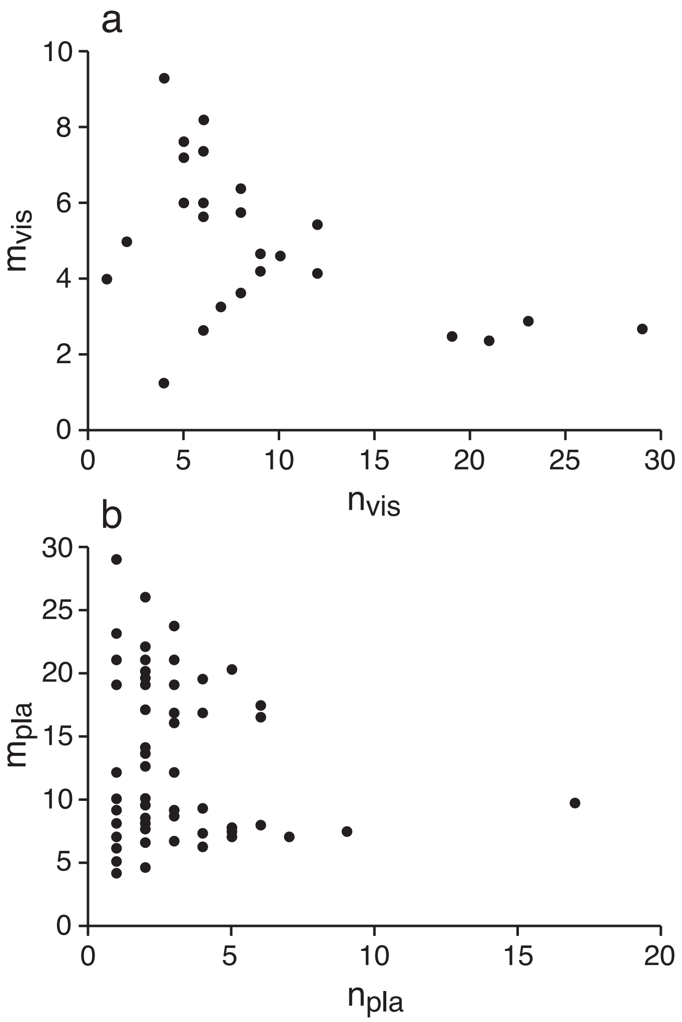

FIGURE 3.2 – The relationship between the number of interaction partners *n* and the mean generalization level of interaction partners *m* of the observed plant–flower visitor interaction web. Each data point represents a plant (a) or flower visitor species (b).

This asymmetry of interactions was a result of a nested structure of the interaction matrix. The plant–flower visitor matrix had a size of 25 x 111 = 2775 potential interactions (without constraints) with an observed fill (connectance) of 8.3%. After ordering the species of the matrix by the number of interactions, the observed interactions (links) occur mainly in the top left corner of the matrix (FIGURE 3.S1). The observed system temperature T was 11.4°. This value was significantly lower than the mean of 1,000 randomizations of the matrix ($T = 25.36°$, standard deviation = 2.07°, $p < 0.001$).

Species traits and interaction asymmetry

A minority of 67 (7.5%) out of the observed 887 nectar-searching insect individuals had a proboscis shorter than the nectar holder of the plants they visited (FIGURE 3.3). A random distribution of interactions throughout the individual based matrix (model *d*) gave an expected value of 272 visitations below the threshold (31%, $\chi^2 = 222.83$, $p < 0.001$).

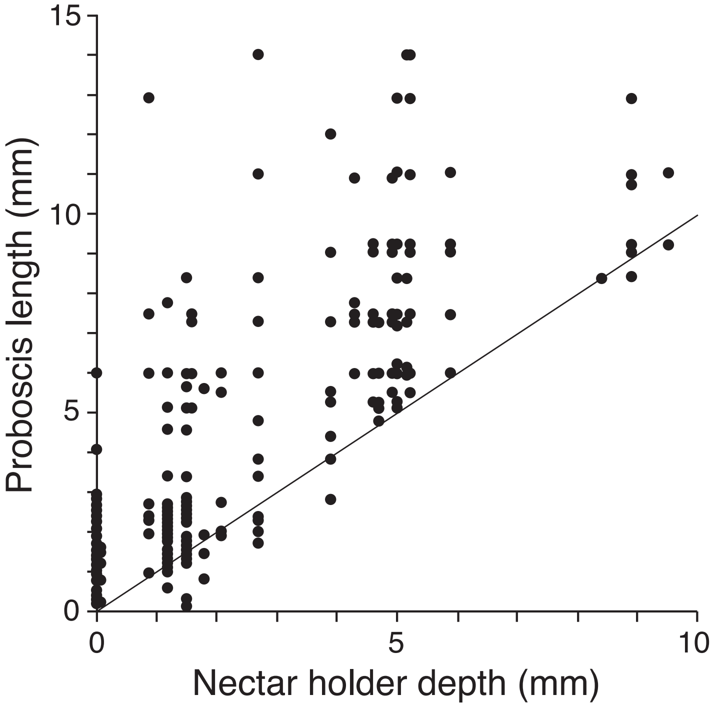

FIGURE 3.3 – The relationship between the proboscis length of the flower visitors and the nectar holder depth of the visited plant species (minimum values (see Stang *et al.*, 2006)). Each data point represents a plant species–flower visitor species interaction. The x = y line represents the expected size threshold. The interactions occur mainly within a triangle above the threshold.

TABLE 3.1 – The relationship between morphological traits, abundance estimates, and the number of interactions partners for the plant (n_{vis}, top of the table) and flower visitor species (n_{pla}, bottom of the table) and the mean number of interactions of these partners (m_{vis} and m_{pla}). Spearman rank-order correlation coefficients and p values (in parentheses) are given.

		Number of interaction partners *n*	Mean number of interactions of these partners *m*
Plants	Nectar holder depth	–0.485 (0.014) *	+0.471 (0.018) *
	Nectar holder width	+0.372 (0.067)	–0.177 (0.387)
	Plant individuals	+0.338 (0.098)	–0.081 (0.700)
	Number of flowers	+0.697 (0.000) **	–0.301 (0.143)
	Number of visits	+0.631 (< 0.001) **	–0.021 (0.921)
Visitors	Proboscis length	+0.326 (< 0.001) **	–0.455 (< 0.001) **
	Proboscis diameter	+0.090 (0.348)	+0.192 (0.043) *
	Visitor individuals	+0.766 (< 0.001) **	–0.336 (< 0.001) **

* = $p < 0.05$, ** = $p < 0.01$

The deeper the nectar holder, the fewer visitor species were observed (decreasing n_{vis}) and the more ecologically generalized they were (increasing m_{vis}, TABLE 3.1, first row). There was no significant relationship between nectar holder width and *n* or *m*. Generalists and specialist animals visited rare plants (with few individuals) and common plants at similar rates. More flowers and more visits resulted in more visitor species (increasing n_{vis}) but not in visitors that were significantly more specialized (decreasing m_{vis}). Flower visitors showed the opposite pattern compared to plants concerning morphology but similar ones concerning abundance. The longer the proboscis, the more plant species were visited (increasing n_{pla}), and the more ecologically specialized the plants that were visited (decreasing m_{pla}). Abundant flower visitor species were found on more plant species (increasing n_{pla}) and visited on average more specialized plant species (decreasing m_{pla}) than rare ones (TABLE 3.1, last row).

The number of plant individuals was not related to nectar holder depth ($r_s = 0.074$, $p = 0.742$, $n = 25$). However, plant species with deeply hidden nectar produced fewer flowers ($r_s = –0.539$, $p = 0.005$, $n = 25$) and were visited by fewer individuals ($r_s = –0.403$, $p = 0.046$, $n = 25$) than plant species with freely accessible nectar. Abundant visitor species had longer proboscises than rare visitor species ($r_s = 0.293$, $p = 0.002$, $n = 111$).

TABLE 3.2 – Comparison of observed interaction asymmetry of plants and their visitors with those based on Monte Carlo simulations. A negative Spearman rank-order correlation coefficient between *n* (number of interaction partners) and *m* (mean generalization level of interaction partners) means asymmetry. The mean rank-order correlation coefficients of 1,000 random runs are given. The values in parentheses are the fractions of random runs with a weaker negative correlation than the observed ones. A significantly different random *r* is indicated with an asterisk (two-sided). The observed correlation coefficients between *n* and *m* were –0.441 for the plants and –0.233 for the flower visitors (see text for further explanations).

Model	Explanation	Plants	Flower visitors
a	Equal probability, no size threshold	–0.043 (0.983) * weaker	–0.016 (0.979) * weaker
b	Nectar holder depth threshold	–0.657 (0.087) equal	–0.412 (0.026) equal
c	Proportional visitor abundance	–0.736 (0.033) equal	–0.145 (0.796) equal
d	Visitor abundance, nectar holder depth threshold	–0.847 (0.001) ** stronger	–0.393 (0.061) equal

* = $p < 0.025$, ** = $p < 0.005$

Null model analysis of interaction asymmetry

The observed negative correlations between *n* and *m* for both plants and visitors were significantly stronger than those obtained from the fully random model (*a*), which were close to zero. The fraction of random runs with a weaker correlation than the observed ones were 0.983 and 0.979 (TABLE 3.2). Thus, random interactions without including size constraints and abundance did not result in a relationship between the level of specialization of plants and visitors. Including nectar holder depth and/or abundance in the null models (model *b*, *c* or *d*) always lead to a negative correlation between *n* and *m*, *i.e.* to asymmetric specialization. These randomly produced negative correlations were as strong (model *b* and *c*) as the observed ones, so that both size constraints and abundance seem to promote asymmetric specialization. The expected asymmetry for the plants was even stronger if based on both factors.

In order to assess if constraints and abundance are able to produce asymmetry on a species-specific level, we tested if they can predict which species are generalists and specialists and with which kind of species they interact. We correlated the random with the observed number of interaction partners (*n*) and the random with the observed mean

TABLE 3.3 – Relationship between observed and random *n* (number of interaction partners) and observed and random *m* values (mean generalization level of interaction partners) for plants and flower visitors. The mean value of 1,000 Spearman rank-order correlation coefficients is given. The significance of the relationship is indicated as the mean *p* value (one-sided, in parentheses).

Model	Explanation	Plants		Flower visitors	
		n_{vis}	m_{vis}	n_{pla}	m_{pla}
a	Equal probability, no size threshold	–0.009 (0.260)	0.008 (0.254)	–0.002 (0.242)	–0.007 (0.259)
b	Nectar holder depth threshold	0.402 * (0.038)	0.399 (0.051)	0.199 (0.073)	0.295 ** (0.003)
c	Proportional visitor abundance	0.584 ** (0.003)	–0.027 (0.314)	0.657 ** (<0.001)	0.051 (0.234)
d	Visitor abundance, nectar holder depth threshold	0.551 ** (0.004)	0.479 * (0.018)	0.632 ** (<0.001)	0.352 ** (0.009)

* = $p < 0.05$, ** = $p < 0.01$

level of generalization of the interaction partners (*m*), see TABLE 3.3. The number of visitor species on a plant (n_{vis}) as well as the number of plant species visited by an insect (n_{pla}) was best predicted by abundance (model *c*) or a combination of the size threshold and abundance (model *d*). However, the mean level of generalization of the interaction partners (*m*) could only be predicted if size thresholds were included in the model (model *b* and *d*). Thus, random interactions proportional to species abundance can predict the number of interaction partners (n_{vis} and n_{pla}) but can not predict the mean level of generalization of these interaction partners (m_{vis} and m_{pla}). To predict the latter we have to include the morphological threshold set by nectar holder depth. Thus, a combination of size threshold and abundance (model *d*) will give the best predictions for *n* and *m* for both plants and visitors.

Extinction risk

Without size constraints and with equal probability for each species to interact with another species (model *a*), there is no differences of extinction risk between generalist or specialist species (FIGURE 3.4a and 3.4b). The inclusion of the size threshold (model *b*) gives an increasing extinction risk with increasing nectar holder depth (FIGURE 3.4c) and decreasing proboscis length (FIGURE 3.4d). Compared to model *a* without constraints,

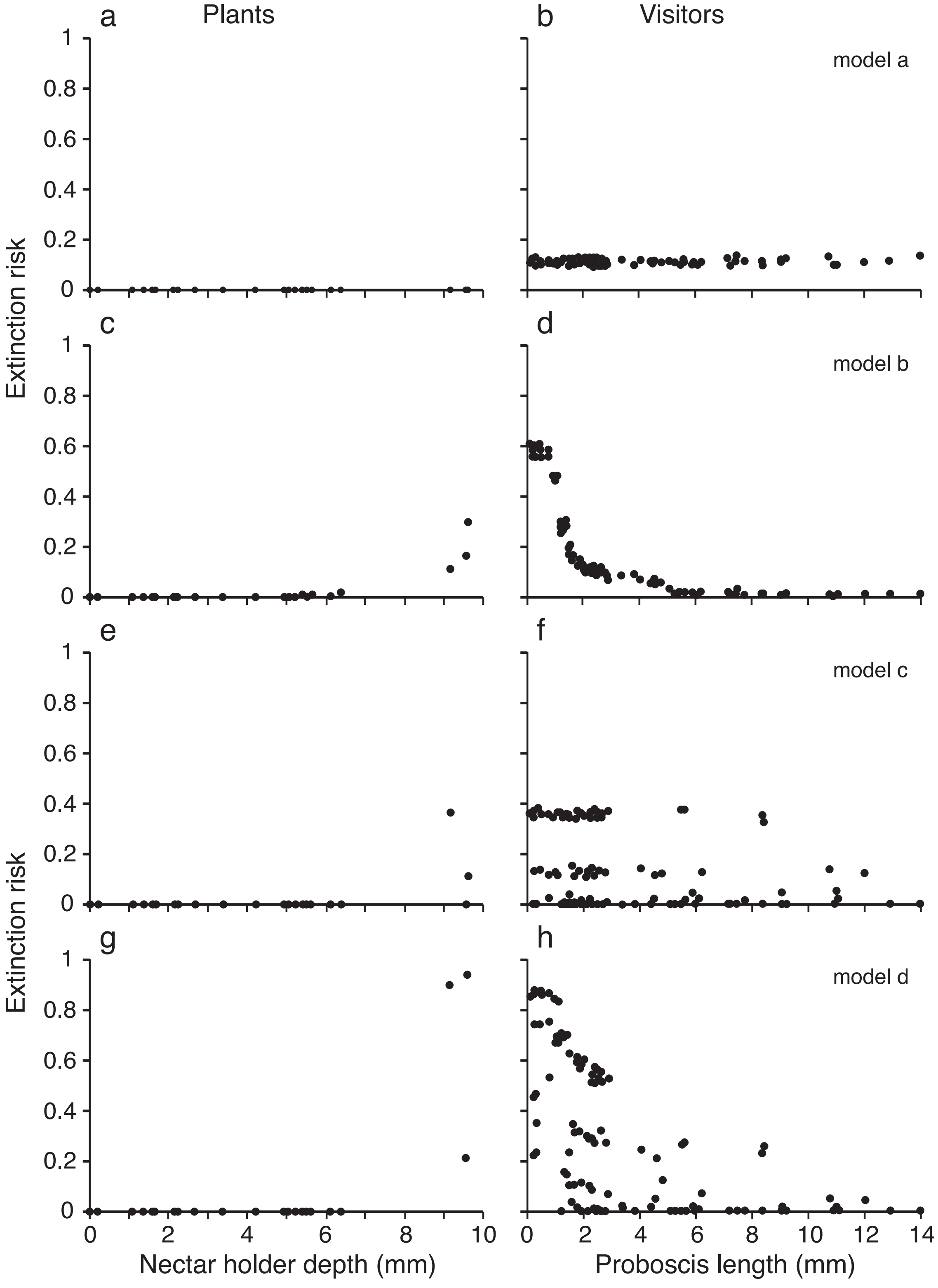

FIGURE 3.4 – Extinction risk of plant and flower visitor species expressed as the probability of having no interaction partners. The probability for each model (*a*, *b*, *c* and *d*) was obtained from the Monte Carlo simulations and plotted against nectar holder depth or proboscis length. Each data point represents a plant or flower visitor species.

species with a long proboscis have now a lower extinction risk while species with deeply hidden nectar or short proboscises have a higher extinction risk. Without size constraints and with the probability to observe an interaction proportional to the abundance of the species (model *c*), the extinction risk shows a similar pattern as for model *b* (FIGURE 3.4e and 3.4f) although with a higher variation. The last model (*d*) shows that, compared to models *b* and *c*, the simultaneous inclusion of constraints and abundance increased the chance of becoming extinct especially for visitors with short proboscises (FIGURE 3.4h) and for plants with deeply hidden nectar (FIGURE 3.4g). Both groups are ecologically specialized. For many ecologically generalized visitor species (visitors with a long proboscis) the extinction risk is lower than when based on equal abundance or abundance alone (model *a*, *b* and *c*).

Discussion

Asymmetric specialization and nestedness

In the Mediterranean plant–flower visitor web we studied, specialists interact mainly with generalists and generalists mainly with specialists. This asymmetric specialization was associated with a nested structure of the interactions. Thus, generalists are not restricted to specialists but also interact with generalists. This result in itself is not new. Up to now almost all of the studied plant–flower visitor webs from all over the world showed an asymmetrical (Petanidou & Ellis, 1996; Vázquez & Aizen, 2004; Vázquez & Simberloff, 2002) and/or nested organization (Bascompte *et al.*, 2003; Dupont *et al.*, 2003; Memmott *et al.*, 2004).

Potential causes of asymmetric specialization

We found that, despite the fact that both species abundance and nectar holder depth can produce asymmetry in the observed web (TABLE 3.2), only nectar holder depth was able to predict which species would be visited by specialists and which by generalists, and thus the level of asymmetry for a particular species (TABLE 3.3). In addition, the asymmetry of the random models that included both size threshold and abundance was higher than compared to those that are based on abundance alone. Vázquez et al. (2005, 2004) questioned the potential role of species traits to explain asymmetric specialization. They argued that neutrality at the individual level alone (visitor individuals distribute themselves randomly among the plant species) can account for the observed pattern. Traits that function as morphological constraints and will lead to 'forbidden interactions' (Jordano *et al*., 2003, 2006) are in their opinion not necessary to explain the level of generalization and thus asymmetry. However, they only included species abundance in their null model analysis and in fact did not test this assertion.

We found that although abundance is able to reproduce the observed level of asymmetry, it certainly did not present the complete picture because it could not made species-specific predictions about the level of generalization of the interaction partners (*m*) (TABLE 3.3). If the probability of an interaction is only proportional to abundance, the identity of the species and thus the traits of the species that interact with each other will change with each change in abundance. However, we found that visitors with a short proboscis hardly ever try to exploit nectar from a flower with deeply hidden nectar (Stang *et al*., 2006). If a plant species with deeply hidden nectar increases in abundance, the maximum number of potential visitor species is constrained by the size threshold. Abundance will only modify how many of the potential visitors will be actually observed. The fact that, in our simulations, abundance alone can produce the asymmetric pattern could be partly an effect of the correlation between size and abundance, *i.e.* with increasing nectar holder depth the number of flowers decreased and with increasing proboscis length the number of individuals per species increased (Stang *et al*., 2006). If interaction asymmetry is the result of a size threshold, it will provide a biological explanation for the boundary threshold in a nested matrix and would allow us to predict were this boundary should be.

The ability of abundance to promote asymmetric specialization could be partly an effect of sampling bias, such as data aggregation, uneven sampling or insufficient sampling (Vázquez & Aizen, 2004). For our web, data aggregation can be excluded because we sampled only within a small area and a short observation period. Additionally, we used equal observation times for each plant species so that a problem of the popular transect method is avoided: common plant species are sampled more intensively than rare ones. Nevertheless, an overall insufficient sampling could have increased the influence of abundance on the degree of asymmetry in our study. Over time, rare species will be observed interacting with more and more species while abundant species are already found to interact with almost all existing potential partners at low sampling intensities. A longer sampling time will thus result in a decreasing degree of asymmetry if the total number of species remains the same. This time effect will not occur in combination with a size threshold because additional interactions will be mainly observed above the size threshold in the top left corner of the matrix. In this case, a longer sampling time will very likely increase asymmetry. This is in agreement with the observation that webs that had the same total number of species are relatively more nested if more interactions were observed (Bascompte *et al.*, 2003). Nevertheless, Vázquez and Aizen (2006) did not find an effect of sampling intensity using a sensitivity analysis. Certainly, more studies are needed to show that the effect of abundance – among the allowed interactions above the size threshold – is mainly based on visitor behaviour and not on sampling intensity or another underlying covarying biological trait.

Towards a functional definition of generalists and specialists

We found that size thresholds predicted the level of ecological generalization as well as the mean level of ecological generalization of the interaction partners quite well. Thus, morphological traits will provide an essential element to characterize generalists and specialists (FIGURE 3.5). Plants that were ecological specialists had mainly deeply hidden nectar and plants that were ecological generalists mainly openly accessible nectar. Contrary to this, flower visitors that were ecological specialists had mainly a short proboscis and ecological generalists had mainly a long proboscis. Another characteristic of specialists and generalists in our study system was that specialised plants had fewer flowers and received fewer visits whereas generalized plants had many flowers and received many visits (FIGURE 3.5). The same pattern was found for the flower visitors. Ecologically and morphologically specialized flower visitors had few individuals and generalists many. However, there were more specialized visitor species than generalized ones so that all specialized visitor species together had many more individuals than generalized visitors (FIGURE 3.4).

Because of the fact that the ecological level of generalization (the number of interaction partners) is largely determined by the morphological level of generalization (the potential morphological range of interaction partners), the existence of specialist–specialist interactions among nectar producing plant species and nectar consuming visitor species is not very likely. Visitors that can use flowers with deeply hidden nectar are usually able to utilize a wide morphological range of flowers and will do this if necessary (*e.g.* because of a low abundance of flowers with deeply hidden nectar). The depth threshold is a first step towards a functional definition of generalists and specialists. A cost threshold based on energy demands of the visitors or a flight temperature threshold might complete the picture (Corbet, 2006).

Extinction risk of generalists and specialists

Our analysis revealed that nectar holder depth, proboscis length and species abundance influenced the extinction risk of the species. Since asymmetric specialization was promoted by a size threshold, specialists with a small potential morphological range of interaction partners had a higher extinction risk through chance processes than generalists with a potentially broad range (FIGURE 3.5). The high number of individuals of generalist visitor species may reduce the chance of extinctions for a specialist plant species; nevertheless, the low number of flowers of these plants and the low species number of generalized visitors counterbalanced this effect. The suggestion of Ashworth et al. (2004) that asymmetric specialization is the reason that specialist and generalist plant species will show similar reproductive susceptibility to habitat fragmentation seems unlikely. In our simulations only fully randomly determined relationships between plants and flower visitors, *i.e.* relationships without constraints and without considering species abundance, resulted in equal extinction risks of specialists and generalists. Size constraints as well as abundance patterns lead to asymmetry and differences in extinction risks. As a result, it is hard to imagine that asymmetry can equalize the susceptibility to species loss. Nevertheless, asymmetric webs based on a nested organization with generalist–generalist interactions are theoretically more resistant to disturbance and species loss than asymmetric webs with a compartmentalized organization without generalist–generalist interactions (Melian & Bascompte, 2002; Memmott *et al.*, 2004).

The extinction risk of a generalist plant species is mainly lessened by the redundancy of ecologically specialized visitors. In our system these visitors were mostly beetles, flies and wasps. These are often not restricted to flowers as their food so that they may be more or less unaffected by a species loss of flowering plants. Ecologically specialized short-tongued bees, who present another important specialized visitor group of generalized plants, may be relatively more susceptible to disturbance as they depend completely on food provided by flowers. The extinction risk of generalist visitors, which were dominated by bees with long proboscises, is mainly lessened by their morphological flexibility. In fact, especially generalist visitors seem to profit from an asymmetrically structured web (see FIGURE 3.4, extinction risk of generalists of model *b* and *d* compared to model *a*). They can change their interaction partners if necessary. However, for generalized plant species these generalized

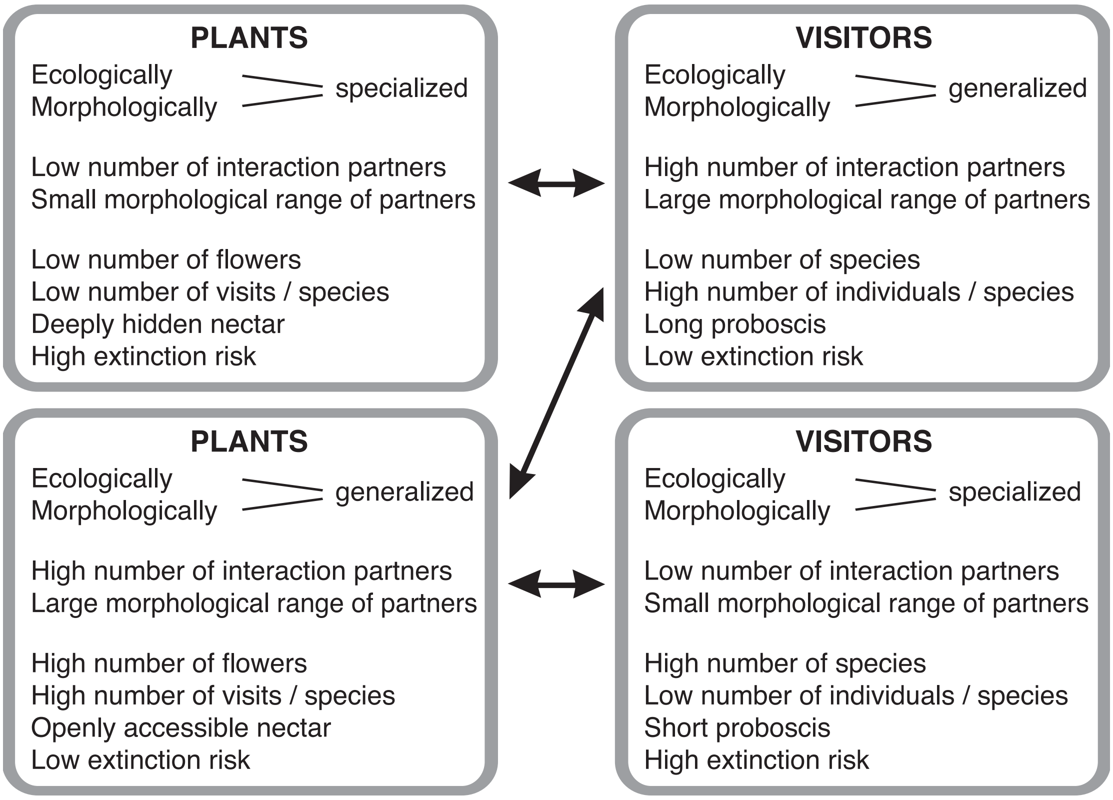

FIGURE 3.5 – Characterization of generalist and specialist plant and visitor species based on the studied interaction web. Species traits and the two different definitions of specialization are given. The potential interactions are indicated with arrows. See text for further explanations.

visitors will have a relatively minor importance because they had, compared to specialist visitors, a small total number of individuals due to a small number of species.

Given our results, one would expect that mainly generalist–generalist interactions will remain after disturbance. Nevertheless, even generalized visitors could be more susceptible than predicted by our simulations. Generalized visitor species with a long proboscis that depend on nectar provided by flowers can not only use but often depend on a broad range of plant species. Proboscis length and body size are positively related (Stang *et al.*, 2006) and energy demands increase with body size. A combination of high energy demands and an often observed long flight time could make generalists more susceptible to plant species loss than expected. If the generalist flower visitors are threatened because of disturbance, the whole system will be less stable than through the loss of flower visitors that visit only a small number of plant species, are redundant and not obligate flower visitors. As such, generalist visitors are key species in the system (Memmott *et al.*, 2004). Specialized plants have to counterbalance the disadvantage of being specialized by attracting generalized visitors more than expected by chance, *e.g.* by providing more nectar per flower than generalized plants. Specialized visitors have to be mobile and should change the area in order to find suitable nectar plants.

Our discussion has shown that more studies are needed to fully understand the asymmetric structure of the web and the short-term extinction risk of the species in relation to the factors that promote asymmetry. One open question is the potential role of sampling intensity; another open question is the influence of other species traits such as flowering time and nectar amount of the plants, as well as flight time and energy demands of the visitors. Nonetheless, even our relatively simple simulation model (based on one size constraint and, within the allowed interactions, of abundance) was able to reproduce the observed species-specific pattern of asymmetric specialization. It revealed that specialist–specialist interactions among nectar producers and consumers might be rare because of the morphologically based intrinsic flexibility of ecological generalists, and that asymmetry alone will not equalize reproductive susceptibility and extinction risks because asymmetry is caused to a great deal by morphological constraints and abundance patterns.

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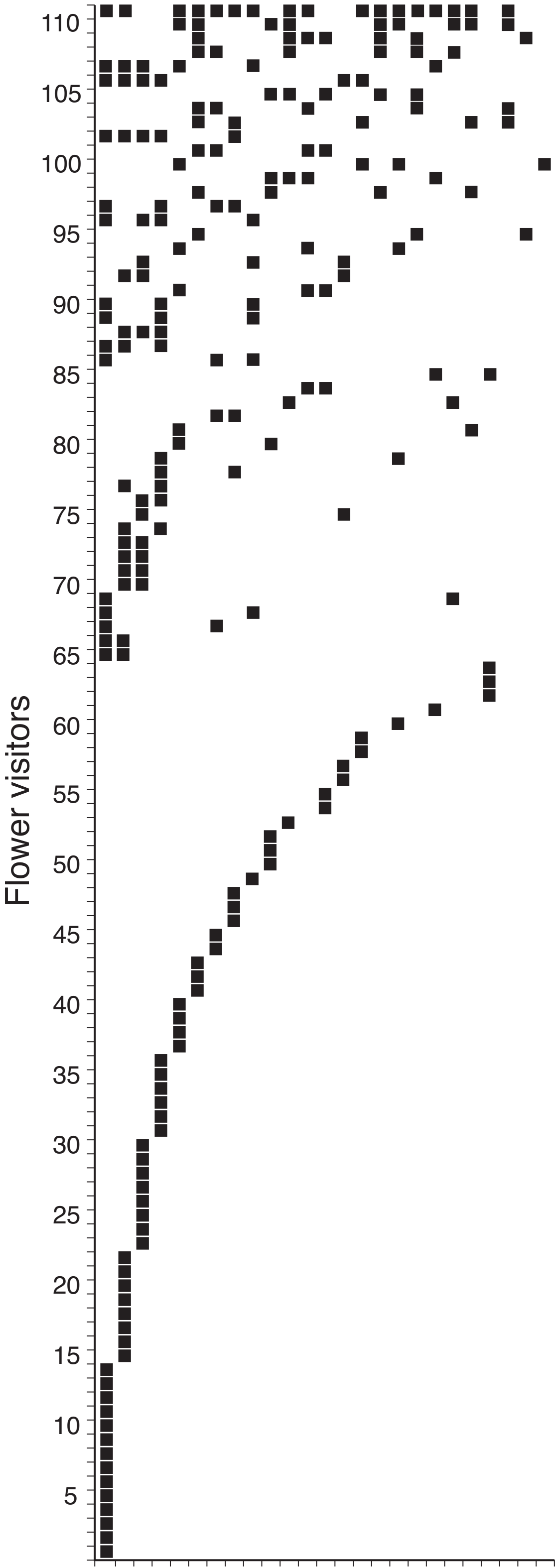
FIGURE 3.S1 – The plant–flower visitor interaction matrix of the studied Mediterranean plant–flower visitor web of nectar producing plant species and nectar searching flower visitor species. Flower visitor species are labelled with numbers, plant species are labelled with their name. A species–species interaction is indicated with a black square. Species in the matrix were ordered by the number of interaction partners.


Flower visitors
110
105
100
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
Helichrysum stoechas
Euphorbia serrata
Euphorbia terracina
Anacyclus valentinus
Teucrium murcicum
Echium creticum
Sonchus tenerrimus
Reichardia tingitana
Phagnalon saxatile
Anthyllis terniflora
Centaurea aspera
Vella lucentina
Moricandia arvensis
Erodium macaloides
Diplotaxis erucoides
Rosmarinus officinalis
Coris monspeliensis
Bituminaria bituminosa
Dorycnium pentaphyllum
Convolvulus althaeoides
Sideritis leucantha
Linum suffruticosum
Asphodelus fistulosus
Vicia pseudocracca
Matthiola fruticulosa