Chapter 9

Community-Wide Patterns of Specialization in Plant–Pollinator Interactions Revealed by Null Models

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Introduction

Understanding the causes and consequences of specialization in species interactions is central to ecology and evolutionary biology. This knowledge is important because specialization may have profound ecological and evolutionary consequences (Brown 1984; Thompson 1994; Waser et al. 1996; Vázquez and Simberloff 2002). A primary question is how common specialization (or generalization) is in nature. Plant-pollinator interactions have been frequently regarded as tightly coevolved and highly specialized, with a general evolutionary trend towards increased specialization (Waser, Chapter 1, this Volume). But the extent to which such specialization actually occurs in most, or even some, of the species in a given community has been recently questioned (Ollerton 1996; Waser et al. 1996).

A limitation of recent discussions about the specialized/generalized nature of plant-pollinator interactions (e.g., Ollerton 1996; Waser et al. 1996; Johnson and Steiner 2000; Gómez 2002) is the lack of null hypotheses with which to contrast the observed patterns of specialization. Without such null hypotheses, it is difficult to ascertain whether either extreme specialization or generalization prevail in nature. For example, Waser et al. (1996) noted that in two early community-wide studies (Clements and Long 1923; Robertson 1928) plants were visited on average by 33.5 and 9.4 pollinator species, respectively. These figures represented a small fraction of all the pollinator species present in those two communities (ca. 220 and 1,150 pollinator species, respectively, assuming 80% of visitors pollinate; Memmott and Waser 2002; Memmott et al. in press), although there is a huge spread around this mean, with several species that interact with only one pollinator and others interacting with more than 50. Just looking at these figures does not tell us much about whether extreme specialization or generalization are unusually common.

Another limitation of recent discussions about specialization in plant-pollinator interactions is that our characterization of specialization is still rudimentary. One particular aspect that has received surprisingly little attention is the degree to which specialization is reciprocal between pairs of interacting species. Biologists have frequently assumed symmetric specialization: either specialists interact with specialists or generalists with generalists (see Thompson 1994; Renner 1998; Vázquez and Simberloff 2002). Under this scenario, reciprocally specialized interactions are more likely to lead to coupled ecological dynamics and coevolutionary change than reciprocally generalized interactions. However, this is not necessarily the case: only a fraction of specialists is likely to interact with specialists, while the rest is expected to interact with moderate to extreme generalists. The existence of asymmetric specialization between interaction partners may have important consequences: rather than reciprocal influences of interacting species on each other's ecological and evolutionary

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processes, it can lead to a situation in which specialists track generalists. However, some degree of asymmetry may be expected from the structural constraints inherent to the assembly of interaction networks, even if species interactions were solely the result of a random process. Thus, as argued above, the existence of a pattern does not mean that the pattern is unusual; we need to compare it with some null expectation.

A possible approach to provide a null hypothesis for patterns of specialization in plant–pollinator interactions is the use of null models—the generation of randomized datasets in the absence of a hypothesized mechanism. Null models have played an important role in many areas of community ecology and biogeography (Gotelli and Graves 1996; Gotelli 2001). This approach may allow us to answer not only whether the occurrence of specialization or generalization is different from some specified null hypothesis, but also whether a particular mechanism may be a likely explanation for such occurrence. Until recently no null model analysis of patterns of specialization in plant-pollinator interactions had been undertaken. Below we describe recent work we have conducted using this approach, present some new results, and identify future avenues of research. Although much remains to be done, our null model approach provides a rigorous way of studying community-wide patterns of specialization in plant-pollinator interactions.

Defining Specialization

When studying specialization, it would be ideal to use a definition that is ecologically and evolutionarily relevant. For a plant, pollinators represent one of many components of their niche, one that has direct consequences in their reproductive performance and, ultimately, in their demography. For a pollinator, flowers usually represent food sources or, in some circumstances, shelter. Therefore, a meaningful definition of specialization would require, for example, measuring the reproductive consequences of each of the interactions between a given plant species and its flower visitors, or the nutritional consequences of each plant species visited by a given pollinator. This type of study is feasible, and there are many examples in the literature, at least for plants (e.g., Schemske and Horwitz 1984; Herrera 1989; Fishbein and Venable 1996; Olsen 1997; Gómez and Zamora 1999); however, conducting such studies for large assemblages of plants and pollinators may be prohibitive, and to date none of the community-wide datasets available in the literature include such information. Most available studies include information only about the occurrence of pairwise interspecific interactions (i.e., which plant species interact with which flower visitor species), although some studies also include information about the frequency of interaction between pairs of species (i.e., how many times a given plant species was visited by a given pollinator species during the course of the study; examples in this Volume are Armbruster, Chapter 12 and Kwak and Bekker, Chapter 16). Thus, our definition of specialization will necessarily ignore most biological details of the interactions, focusing only on their occurrence.

Another important point when talking about specialization is the distinction between what we call "fundamental" vs. "realized" specialization, in direct reference to the niche concept proposed by G. E. Hutchinson (1957). Fundamental specialization refers to the potential interactions that would lead to positive fitness for a given species, under any possible ecological circumstances. Thus, fundamental specialization will ultimately depend on the genetic background of a species. Conversely, realized specialization refers to the actual specialization attained under a particular ecological context. For example, most fig species are fundamentally specialized on one or a few species of pollinating wasps, and they fail to reproduce if they are moved to different environments, unless their specialized pollinators are introduced as well. Conversely, many other plant species that are pollinated by a single pollinator in a particular habitat are often pollinated by a different species in other habitats where they are introduced (Richardson et al. 2000). In the context of our study, we will be restricted to the realized niche, because in most cases we know little about what happens with the interactions outside the arbitrary boundaries of the study.

Given the above limitations, the definition of specialization we use in our analyses is a very simple one: the inverse of the number of interaction partners of a given species (i.e., the fewer interaction partners, the more specialized a species is). Of course, this definition ignores much of the biology and ecology of interactions, since it assumes all interactions are equal, regardless of their relative frequency and quality. However, we believe the use of such a grossly simplified measure of specialization is still useful, for at least two reasons: (i) many previous and current studies have used a similar measure of specialization, and thus we are able to revisit some conclusions with our null model perspective; and (ii) using such simple measures is, at least at present, the only way of studying community patterns of plant–pollinator specialization. Our definition has the additional advantage of allowing us to treat specialization and generalization as two extremes in a continuum, thus getting away from the dichotomy that has pervaded the literature.

Null Models for Patterns of Specialization in Plant–Pollinator Interactions

We have recently developed null models to study patterns of specialization in plant-pollinator interaction networks (Vázquez and Aizen 2003, 2004). The rationale behind the approach is that by randomly generating datasets that share some characteristics with the observed data (such as number of species of plants and pollinators and total number of links among interacting species), it is possible to obtain patterns that can be compared with the observed data (Gotelli and Graves 1996; Gotelli 2001). If the randomized data differ substantially from the real data, and assuming that the null model is "correct," then it is possible to invoke some sort of mechanism responsible for the observed pattern. Conversely, if the randomized data do not differ from the observed data (and, again, assuming that the null model is correct), it is possible to reject the hypothesis that there is a mechanism other than randomness responsible for the observed pattern. It is also possible to compare the explanatory power of different models of increasing complexity that explicitly incorporate particular mechanisms.

We start with an "interaction matrix" compiled from various datasets (see Table 9.1), in which columns represent plant species and rows flower visitor species found in a particular community; a cell with a "1" indicates that a given plant and a pollinator species interact, and one with a "0" indicates no interaction between a pair of species. In addition, some datasets contain information on the frequency of interaction between pairs of species (either total number of pollinator visits recorded per unit time, or number of collected individuals per insect species for each plant species), which we use to construct an "interaction frequency matrix". We use simple measures of specialization, which can be readily calculated from the limited information available in the datasets: s, the total number of species with which a given species interacts, obtained from the binary interaction matrix as the sum of columns or rows for plants and pollinators, respectively; and p, the average value of s of the interaction partners of a given species. We also calculate f, the frequency of interaction of plant and pollinator species, obtained as the row and column sums in the interaction frequency matrix, respectively.

[TABLE 9.1 ABOUT HERE]

The null models we have used are based on randomization procedures. Our simplest null model is one that assumes random interactions among species. Under this model, every species is assigned an interaction by randomly selecting another species from the pool of possible interaction partners. Once every species has been assigned one (and only one) interaction, the remaining interactions are assigned by randomly selecting pairs of plant and pollinator species. Thus, in this model the expected value of *s* (the number of interaction partners) is equal to that probability multiplied by the number of potential interaction partners (*n*) and is the same for all species, independently of their frequency of interaction (Figure 9.1). Thus, this model assumes neutrality at the species level (i.e., all species are equal, regardless of their identity), and allows us to test whether observed patterns of specialization could arise from random interaction among species, independent of their characteristics.

[FIGURE 9.1 ABOUT HERE]

The second null model we have used assumes random interactions among individuals (rather than species), in the spirit of recent neutral models of community structure (Bell 2000; Hubbell 2001). Here, every species is assigned an interaction by randomly selecting a species from the pool of possible interaction partners. Once every species has been assigned one (and only one) interaction, the remaining interactions are assigned proportionally to a species' observed interaction frequency, so that frequently interacting species have a higher probability of being assigned an interaction than rarely interacting species (Figure 9.1). Thus, this model allows us to test a mechanism responsible for the patterns observed in plant-pollinator interactions: that it is individuals (and not species) that interact randomly, which results in species with more individuals (or more frequently interacting individuals) interacting with more other species than rare species.[1]

Patterns of Specialization in Plant–Pollinator Interactions

As discussed above, plant-pollinator interaction networks include species with a broad range of degree of specialization, from very specialized to very generalized. We have recently shown (Vázquez and Aizen 2003) that the number of extreme specialists and extreme generalists is significantly higher than expected under the simplest of our null models, which assumes random interaction among species (Figure 9.2). These results suggest that one or more processes, missing in this simple null model, generate the observed pattern.

[FIGURE 9.2 ABOUT HERE]

The finding that most communities have a high number of extreme specialists and extreme generalists does not mean that such number is equally high in all communities. For example, the percent of plant species interacting with only one partner species among the five plant-pollinator interaction webs analyzed in Vázquez and Aizen (2003) ranged from 0% in Motten's (1982) dataset to 18% in Clements and Long's (1923) dataset, and whereas only 13% of plant species interacted with 20 or more pollinators in Clements and Long's dataset, 23% did in Motten's study. Is it possible to explain such variation in the prevalence of extreme specialization and generalization in communities? One possibility is that such prevalence is determined by community characteristics such as community size (i.e., number of species of plants and pollinators) or number of links (i.e., pairs of interacting species).

We used *d*, a statistic that measures the difference between either observed or each of the randomized distributions and the expected degree of specialization in the null model (see Vázquez and Aizen 2003), as a measure of the prevalence of extreme generalization and specialization. The larger the value of *d*, the higher the prevalence of species in these extremes of the continuum. Thus, if specialization and generalization increase with, say, community size, the value of *d* should also increase. Figure 9.3 presents the results of this test for null model 1, for the 18 datasets listed in Table 9.1 (we used model 1 so as to be able to use all 18 datasets; however similar results are obtained if model 2 is used instead). Because number of species and number of links are highly correlated ($r = 0.96$; $P < 0.0001$), we present results for number of species only. The magnitude of the *d* statistic increases with community size for both the randomized and the observed datasets. However, the slope for the observed datasets is significantly steeper than for the randomized datasets (see Figure 9.3). This means that the increase in the prevalence of extreme specialization and generalization in these communities is greater than expected under our simple null model, and implies that more diverse communities support an increasingly higher number of specialists and generalists than expected by chance. This result opens the intriguing possibility that high species richness favors the evolution of extreme specialization and generalization in pollination systems.

[FIGURE 9.3 ABOUT HERE]

An interesting feature of most datasets we have examined so far is a positive correlation between observed frequency of interaction of species (*f*) and number of interaction partners they have (*s*) (Vázquez and Aizen 2003; 2004; see also Figure 9.6 below). In other words, plant species that are visited by many individual pollinators, and pollinators that visit many flowers, tend to interact with more species than rarely interacting species. We hypothesized that this correlation could be partly responsible for the pattern of specialization observed in the datasets. To examine this hypothesis, we conducted two different tests (Vázquez and Aizen 2003). In the first one, we removed the correlation between *f* and *s*, and used the residuals as a corrected estimate of specialization. In the second test, we incorporated the correlation into a null model by assigning interactions proportionally to the frequency of interaction (i.e., null model 2 described above). In both cases, the pattern generated by the null model was closer, and not significantly different from, the observed pattern (Figure 9.2). The important message here is that simple random interaction among individuals (which does not assume any difference among species besides differences in frequency of interaction) does an extremely good job at explaining observed patterns of specialization in plant-pollinator networks.

Patterns of Asymmetric Specialization in Plant–Pollinator Interactions

As we argued above, degree of specialization between pairs of interacting species should not necessarily be symmetric: specialists could, and often do, interact with generalists, and the opposite (generalists interacting with specialists) is also possible and often observed (Petanidou and Ellis 1996; Renner 1998; Vázquez and Simberloff 2002; Minckley and Roulston, Chapter 4, this Volume; Petanidou and Potts, Chapter 10, this Volume). A comparison of the distribution of *s* and *p* observed in communities with that generated by our simplest null model shows that the prevalence of asymmetric specialization in real communities is substantially higher than expected (Vázquez and Aizen 2004; Figure 9.4). This asymmetry is a consequence of specialists being specialized on generalists, or of species being extreme generalists themselves (which necessarily means that they interact with many specialists in the community).

[FIGURE 9.4 ABOUT HERE]

As above, we asked whether the contrasting patterns between observed and randomized data could depend partly on community characteristics, such as number of links or number of species. As a measure of the agreement between predicted and observed asymmetry, we used the percent species in the original dataset falling inside confidence intervals generated by the null model. This percent decreases with increasing community size and number of links (Vázquez and Aizen 2004). In other words, prevalence of asymmetric specialization in plant-pollinator interaction webs increases with web size. This result matches our previous result that prevalence of extreme specialization and generalization increases with community size. Thus, larger communities seem to have proportionally more extreme specialists, extreme generalists and asymmetrically specialized species than smaller communities.

As we did in the previous section, we now ask whether the observed correlation between *f* and *s* may partly account for the distribution of asymmetric specialization observed in the datasets. Incorporating such correlation into the null model (i.e., null model 2) results in a pattern that is, in most cases, strikingly similar to that observed in the data, providing in general a much better fit to the data than model 1 (Vázquez and Aizen 2004; Figure 9.4). Thus, the asymmetry observed in most datasets can be partly accounted for by the relationship between species' frequency of interaction and their estimated degree of specialization.

It is important to mention that two recent studies have independently reached similar conclusions to those reached in our analysis of asymmetric specialization. Jordano et al. (2003; see also Jordano et al., Chapter 8, this Volume) studied the distribution of the number of interactions per species using a large database with datasets on plant–pollinator and plant–seed disperser interactions (which substantially overlaps with the one used by us, listed in Table 9.1). They found that the cumulative frequency of the number of links per species (called "degree" in the network literature) decays as a power law as the number of links increases, although in most cases the power law is "truncated" at large values of links per species, rapidly approaching zero. These kinds of degree distributions in networks are expected when a few nodes (i.e., species) have many links and many nodes have a few links, which necessarily implies that highly connected nodes will be connected to many nodes with a low number of links (Albert and Barabási 2002; Jordano et al. 2003). In a subsequent paper, Bascompte et al. (2003; see also Jordano et al., Chapter 8, this Volume) have elegantly shown that in most cases these plant–animal mutualistic networks have a nested structure, whereby specialized species always interact with a subset of interaction partners of those that interact with the most generalized species. A nested pattern of interactions necessarily means high asymmetry in the degree of specialization of interaction partners.

A Conceptual Framework for Understanding Community Patterns of Plant–Pollinator Specialization

Our null model analyses of plant-pollinator interaction networks from around the world show that both extreme specialization and extreme generalization are common. They also show that asymmetric specialization between pairs of interacting species is not uncommon. Furthermore, our results suggest that these patterns are largely explained by the characteristics of the community (particularly number of interacting species), and by a correlation between the number of interaction partners of species (*s*) and their frequency of interaction (*f*). Therefore, a critical question to understand patterns of specialization in plant-pollinator interactions networks is what factors are behind the *f*-*s* correlation.

Frequency of interaction may be thought of as a function of species abundance. This assumption is particularly appropriate for flower visitors. Abundant pollinators are likely to be observed visiting flowers more often than rare pollinators. However, other factors may also affect *f*, such as pollinator floral preferences, mobility and dependence on flowers as food sources. In the same way, *f* will be a function of plant species abundance and of other factors, including flower attractiveness to pollinators or researchers' choice (i.e., sampling of plant species to estimate pollinator visitation frequencies may be conducted irrespective of plant abundance, so as to obtain similar number of samples for all species). We can define *α* as a parameter that summarizes these different factors that affect *f* independently of abundance. Thus, the frequency of interaction of species *i* may be described as $f_i = \alpha_i A_i$, where A_i is the abundance of species *i*. And since the logarithms of *f* and *s* are linearly related (see Figure 9.6 below), we have $\log s = b \log \alpha A$, where *b* is a constant that determines the strength of the relationship between *s* and *f*. The interesting fact about this simple model is that we can now relate patterns of specialization to well-known patterns of species abundance in communities.

We can now introduce a conceptual model that will help visualize the above findings and hypotheses, and identify what factors should be incorporated in future models aimed at advancing our understanding of patterns of specialization in plant-pollinator interactions (Figure 9.5). We assume that local species richness of plants and pollinators are partly determined by regional species richness (see Ricklefs 1987; Lewinsohn 1991; Cornell 1999). In turn, local species richness will influence the shape of the species abundance relationship (which will usually approximate a log-normal or log-series distribution; Preston 1948; May 1975; Hubbell 2001), so that species-poor communities have steeper rank-abundance curves than their species-rich counterparts. As argued above, local species abundance will partly determine the frequency of interaction among plants and pollinators (*f*). Finally, true degree of specialization (*s*) will be determined by *f* and by other biological factors (see above); however, observed *s* will also be affected by sampling biases. Below we discuss each of these factors and their potential contribution to observed patterns of *s*.

[FIGURE 9.5 ABOUT HERE]

Proximate Determinants of Observed Degree of Specialization

Given the regional and local community contexts in which plant-pollinator interactions occur, it is desirable to understand the role played by each of the three proximate determinants of observed patterns of specialization identified above. These factors are not mutually exclusive, and all are likely contributors to the observed patterns.

Observed *s* could be determined by the random interaction among individual plants and pollinators, so that species that interact more frequently do it with more species than rarely interacting species; this is the basic assumption of our null model 2. The fact that for most datasets null model 2 provides a better fit to the data than model 1 supports this explanation. We are not the first to invoke this kind of mechanism to explain patterns of interaction among species. For example, Southwood (1961) and Janzen (1968) proposed a similar idea to explain the observation that abundant plants tended to host a greater number of species of herbivorous insects than rare plants (i.e., the frequency of encounter hypothesis; see also Strong et al. 1984). Neutrality at the individual level rather than at the species level is also central to recent models of community structure (Bell 2000; Hubbell 2001). Random interaction among individuals would produce a positive correlation between *f* and *s* like the one observed in most datasets we have examined so far.

Other biological factors could also influence the number of interaction partners related to a given species. As we discussed above, pollinator characteristics such as floral preferences, mobility and dependence on flowers as food sources, and plant characteristics such as flower attractiveness to pollinators could be important. These traits could be the result of adaptive processes favoring coadaptation between pairs of interacting species. However, high reciprocal specialization could mean, for most species and under most circumstances, low fitness. For example, Waser et al. (1996), using simple models of plant and pollinator fitness, showed that when the abundance, per-capita visitation rates, or quality of interaction partners vary strongly over time, it should be more beneficial to be a generalist than a specialist. Specialization on a single species should be beneficial only when the abundance and efficiency of the interaction partner are constant in time, which is more likely to occur when the partner is an abundant generalist. On the other hand, high symmetric specialization could mean high risk of extinction (Renner 1998; Vázquez and Simberloff 2002; see also Memmott et al. in press), which could also affect the distribution of degree of specialization in communities.

Finally, observed *s* could be the result of sampling artifacts. First, observed patterns of specialization could be influenced by data aggregation. The information usually available in most datasets typically does not include phenological or spatial patterns in the distribution of abundance (see also Medan et al, Chapter 11, this Volume). For example, consider a pollinator that interacts sequentially with several specialist plants throughout the flowering season; although this pollinator species may interact with many plant species, the number of species with which it interacts at any given time may be much smaller. Likewise, spatial aggregation of data can occur when a widespread species interacts with different species at different locations; if data for such a species are pooled into a single dataset, species may appear more generalized than they actually are at each locality (Fox and Morrow 1981; Thompson 1994).

Second, the observed patterns, particularly the *f*-*s* correlation, could be simply a result of a sampling bias, so that frequently interacting species simply appear more generalized than rare species (Petanidou and Ellis 1996; Vázquez and Aizen 2003, 2004). Ollerton and Cranmer (2002, see also Ollerton et al., Chapter 13, this Volume) have pointed out a similar sampling bias, in which studies that have been conducted for longer periods tend to suggest a higher degree of generalization than those with shorter study periods. Similar sampling artifacts have been invoked to explain other ecological and biogeographic patterns. For example, one explanation of the ubiquitous positive relationship between local abundance and geographical range among species is simply that rare species are less likely to be found at any given site, and thus their geographical range appears smaller than that of locally abundant species (Hanski et al. 1993; Gaston et al. 1997). Similarly, the observation that abundant and widespread plants tend to harbor more species of phytophagous insects (Strong et al. 1984; Leather 1991) has also been attributed to sampling artifacts (Kuris et al. 1980; Stevens 1986; Lewinsohn 1991).

Uncovering the factors determining the observed *s* is thus key to understand patterns of specialization in plant-pollinator interactions. Although teasing apart biological mechanisms from sampling artifacts is difficult, we believe there are several possible ways of tackling this problem. In the next section we illustrate a possible approach that can be used to disentangle these multiple causes of observed degree of specialization.

The *f*-*s* Relationship: Biological Reality or Sampling Artifact?

Although *f* and *s* are linearly related in a log-log scale (see Figure 9.6), in an arithmetic scale the relationship should reach an asymptote at high values of *f* (because of a finite number of species in the community). Thus, if all species were sampled enough, a flattening of the relationship should be observed, provided that the correlation is the result of a sampling bias; this argument would hold if increased sample size were accompanied by a decrease in the proportion of rarely interacting species. Conversely, decreasing sampling effort should increase the slope of the relationship. However, if the *f*-*s* correlation were not a result of a sampling bias, modifying sampling intensity should not affect the slope of the relationship.

We conducted a simulation to answer the question of whether sampling intensity can affect the *f-s* correlation. Because it is difficult to know what would have happened if we had increased sampling, we asked the opposite: what would have happened if we had sampled with a lower intensity. We used an algorithm that sampled interactions from the interaction frequency matrix until a proportion ψ of the data had been sampled. This simulation can be thought of as a reduction in the time spent in the field by an investigator conducting observations of pollinator visits to flowers. So, for example, we can ask what would have been the pattern observed in the data (and, particularly, the *f-s* relationship), had we spent only 50% of the time conducting observations?

The results of this exercise are very clear. First, reducing the sampling effort to 10% of the original effort does not change the *f-s* relationship: the fitted regression lines for the original and subsampled datasets are virtually undistinguishable from each other (Figure 9.6). The interesting point about this result is that we can argue that sampling effort will be unlikely to affect the *f-s* relationship, and even if we increased sampling effort, this relationship is unlikely to change. Thus, this relationship is unlikely to be simply a result of low sampling effort.

[FIGURE 9.6 ABOUT HERE]

Second, decreasing sampling effort results in a decrease of the difference between the observed and predicted values of the *d* statistic (Figure 9.7). Thus, sampling less intensely could have lead to the conclusion that the observed and expected distributions of *s* under null model 1 are not significantly different. However, for this to happen we must decrease sampling effort to a small fraction of the original (i.e., to 8% or less of the original effort for plants, and 25% or less for pollinators). This result suggests that observed patterns in the distribution of specialization should be robust to moderate variations in sampling effort, and that increasing sampling effort would only exacerbate patterns of extreme specialization and generalization.

[FIGURE 9.7 ABOUT HERE]

An important caveat about the above results is that our simulation makes several simplifying assumptions. First, it assumes that pollinator visits are independent from each other, which is arguably unrealistic: if we observe an individual of a pollinator species A visiting a flower of a plant species B, there is a high chance that the next visit we observe is also of pollinator species A to plant species B, because of temporal and spatial autocorrelation in the distribution of plants and pollinators. Second, the above analysis also assumes that the expected decrease in sampling effort is proportionally the same for all plant and pollinator species. However, this need not be the case: for example, an investigator could choose to increase the proportional sampling on rarely interacting plant species when reducing overall sampling effort, so as to observe at least one visit in every plant species in the community. Future studies should explore how robust the above results are to these simplifying assumptions.

Concluding Remarks

Null models reveal the existence of non-random structure in plant-pollinator interaction networks. Our simplest model, one assuming random interactions among species, shows that extreme specialization and generalization and a high degree of asymmetry characterize this type of network. These results suggest that despite the fact that species are distributed along a continuum of specialization/generalization, the extremes of the specialization gradient could represent two alternative strategies favored by natural selection. In addition, the fact that specialists tend to interact with generalist partners beyond random expectations could relate to a type of coevolutionary dynamics that generate and maintain asymmetric interactions. In turn, asymmetry could constitute an important feature of natural webs contributing to their robustness, resilience, and persistence over time (Melián and Bascompte 2002; Memmott et al. in press). The results that species-rich webs harbor a larger proportion of extreme specialists and generalists and proportionally more asymmetric interactions than species-poor webs is intriguing, and may help explain apparently contradictory claims of high specialization and generalization in tropical latitudes (Bawa 1990; Renner and Feil 1993; Bawa 1994; Renner 1998; Olesen and Jordano 2002; Ollerton and Cranmer 2002; Vázquez and Stevens 2004; see also Armbruster, Chapter 12, this Volume).

However, the fact that most of the variation of these structural features can be accounted for by simple community properties, such as species richness, and differences among species, particularly frequency of interaction, suggests that these ecological factors could represent more proximate determinants of patterns of specialization/generalization or asymmetry, without the need to invoke coadaptation among interacting species resulting from coevolution. Future efforts to develop null models of increasing complexity may help to elucidate the role of the different factors identified above in shaping the structure plant-pollinator interaction webs.

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Footnote

[1] Similar models to the ones developed by us have recently been used by Bascompte et al. (2003) to study nested patterns in plant–animal mutualistic networks (see also Jordano et al., Chapter 8, this Volume). These authors also define two null models, one that makes probability of a species to be assigned an interaction homogenous for all species, and is thus equivalent to our model 1. Their second null model assumes that such probability varies among species, and is proportional to the number of links per species. As the number of links per species changes as the interaction matrix is filled during the randomization process, the species probabilities are changed accordingly. Because frequency of interaction is positively correlated with the number of interaction partners, Bascompte et al.'s null model 2 should be roughly equivalent to our null model 2. Another aspect in which Bascompte et al.'s models differ from ours is in that not all species are required to have at least one interaction. Such a difference can affect the variability of randomized patterns, but should not affect the mean. Thus, in general, our null models are roughly equivalent to those used by Bascompte et al., and conclusions reached with any of the two approaches should be qualitatively similar.

Table 9.1. Datasets describing plant-pollinator interaction webs used to conduct analyses reported in the text.[†]

Dataset	Habitat type	Location	Interaction data[§]	m*	n*	C*
Barrett and Helenurm (1987)	Boreal forest	Central New Brunswick, Canada	individuals caught	12	102	0.14
Clements and Long (1923)	Montane forest and grassland	Pikes Peak, Colorado, U.S.A.	binary	96	276	0.03
Elberling and Olesen (1999)	Alpine subarctic community	Latnjajaure, Sweden	visits	23	118	0.09
Hocking (1968)	Arctic community	Ellesmere Island, N.W.T., Canada	binary	29	86	0.07
Inouye and Pyke (1988)	Montane forest	Kosciusko National Park, New South Wales, Australia	individuals caught	42	91	0.07
McMullen (1993)	Multiple communities	Galápagos Islands	binary	106	54	0.04
Medan et al. (2002)	Xeric scrub	Laguna Diamante, Mendoza, Argentina	binary	21	45	0.09
Medan et al. (2002)	Woody riverine vegetation and xeric scrub	Río Blanco, Mendoza, Argentina	binary	23	72	0.08
Memmott (1999)	Meadow	England	visits	25	79	0.15
Mosquin and Martin (1967)	Arctic community	Melvile Island, N.W.T., Canada	individuals caught	11	18	0.19
Motten (1982)	Deciduous forest	Durham and Orange counties, North Carolina, U.S.A.	visits	13	44	0.25
Olesen et al. (2002)	Coastal forest	Île aux Aigrettes, Mauritius	visits	14	13	0.29
Olesen et al. (2002)	Rocky cliff and open herb community	Flores Island, Azores	visits	10	12	0.25
Ramírez and Brito (1992)	Palm swamp community	Central Plains, Venezuela	binary	33	53	0.06
Schemske et al. (1978)	Maple-oak woodland	Brownfield Woods, Illinois	visits	7	32	0.26
Small (1976)	Peat bog	Mer Bleue, Ottawa, Canada	individuals caught	13	34	0.32

C. Smith-Ramírez et al. (ms.)	Temperate rainforest	Chiloé Island, Chile	binary	24	111	0.11
Vázquez and Simberloff (2002; 2003)	Evergreen montane forest	Nahuel Huapi National Park, Argentina	visits	14	93	0.13

[†] All datasets, with the exception of the unpublished data by C. Smith-Ramírez et al., are available through the Interaction Web Database (Online URL http://www.nceas.ucsb.edu/interactionweb).

[§] Kind of information on plant-pollinator interactions included in each publication: number of individuals caught, number of visits observed, or presence-absence of interaction (binary).

* *m*: number of plant species; *n*: number of flower visitor species; *C*: connectance of the interaction matrix.

Figure legends

Figure 9.1. Schematic representation of null models used by Vázquez and Aizen (2003; 2004) to study patterns of specialization in plant-pollinator interaction networks. In null model 1, the probability of being assigned an interaction in each random draw is equal for all species. The expected value of s (the number of interaction partners) is equal to that probability multiplied by the number of potential interaction partners (n). Thus, if there are 5 plant and 20 pollinator species in the community, the expected value of s for each plant species will be 4. In null model 2, the probability for each species of being assigned an interaction in each random draw is proportional to their observed frequency of interaction (f). Therefore, the expected value of s (the number of interaction partners) is not the same for all species. Thus, for a community with 5 plant and 20 pollinator species, and with the f values shown in the figure, the expected s for each plant species will be 10, 4, 2, 2 and 2.

Figure 9.2. Comparison between observed (black lines) and expected distributions (grey lines with error bars) of s, the number of species of interaction partners (an estimate of degree of specialization). Mean ± 95% confidence intervals are given for expected distribution. Numbers at upper-right corner of plots are the P-values of difference test comparing expected and observed distributions (curves are considered significantly different with $P < 0.05$). Data are from Motten (1982), and results of analyses from Vázquez and Aizen (2003).

Figure 9.3. Difference statistic (d) vs. species richness of plants and pollinators (m+n). The difference statistic measures the difference between the expected and observed number of species in each category of s. Thus, d can be taken as a measure of the occurrence of extreme specialization and extreme generalization (see text). Each dot represents a community (see Table 9.1 for list of datasets). Black circles: d statistic calculated for observed data; white circles: expected valued of d statistic calculated for 1000 randomized communities; randomizations for each community were conducted separately, and thus each dot represents and independent data point. Lines represent the fitted regression line to each set of data; coefficient of multiple determination and probability value associated to each regression are given next to each line. Difference in slopes was tested using Wilks' Lambda statistic in the REG procedure in SAS (SAS Institute 1999): $F_{1,16} = 26.56$; $P < 0.0001$.

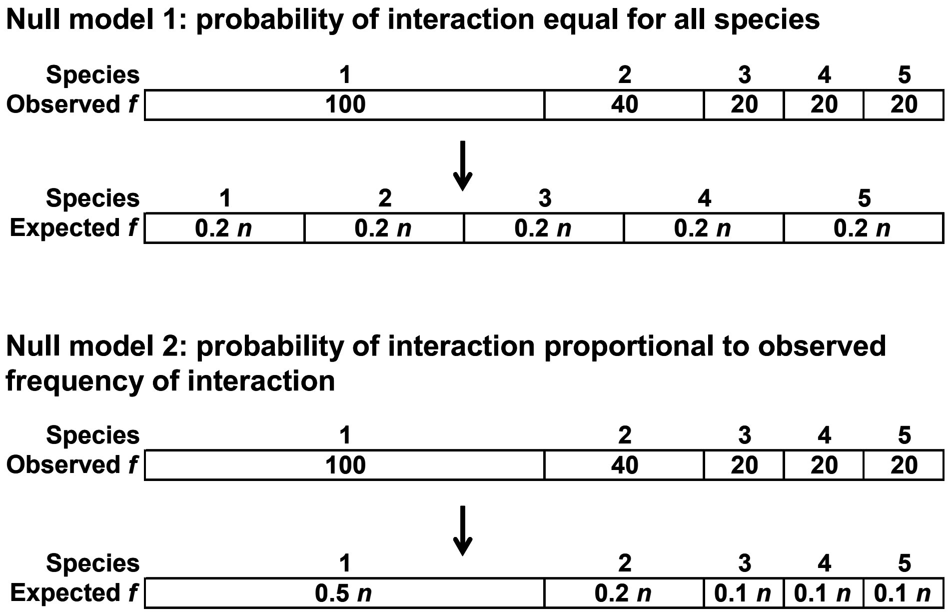
Figure 9.4. Asymmetric specialization in plant-pollinator interactions. Figure shows degree of specialization (s) and average specialization of interaction partners (p). Circles: observed s-p values; black lines: null space for null model 1; grey lines: null space for null model 2. Data are from Inouye and Pyke (1988), and results of analyses from Vázquez and Aizen (2004).

Figure 9.5. A conceptual framework for understanding observed community-wide patterns of specialization in plant-pollinator interactions (see text for explanation).

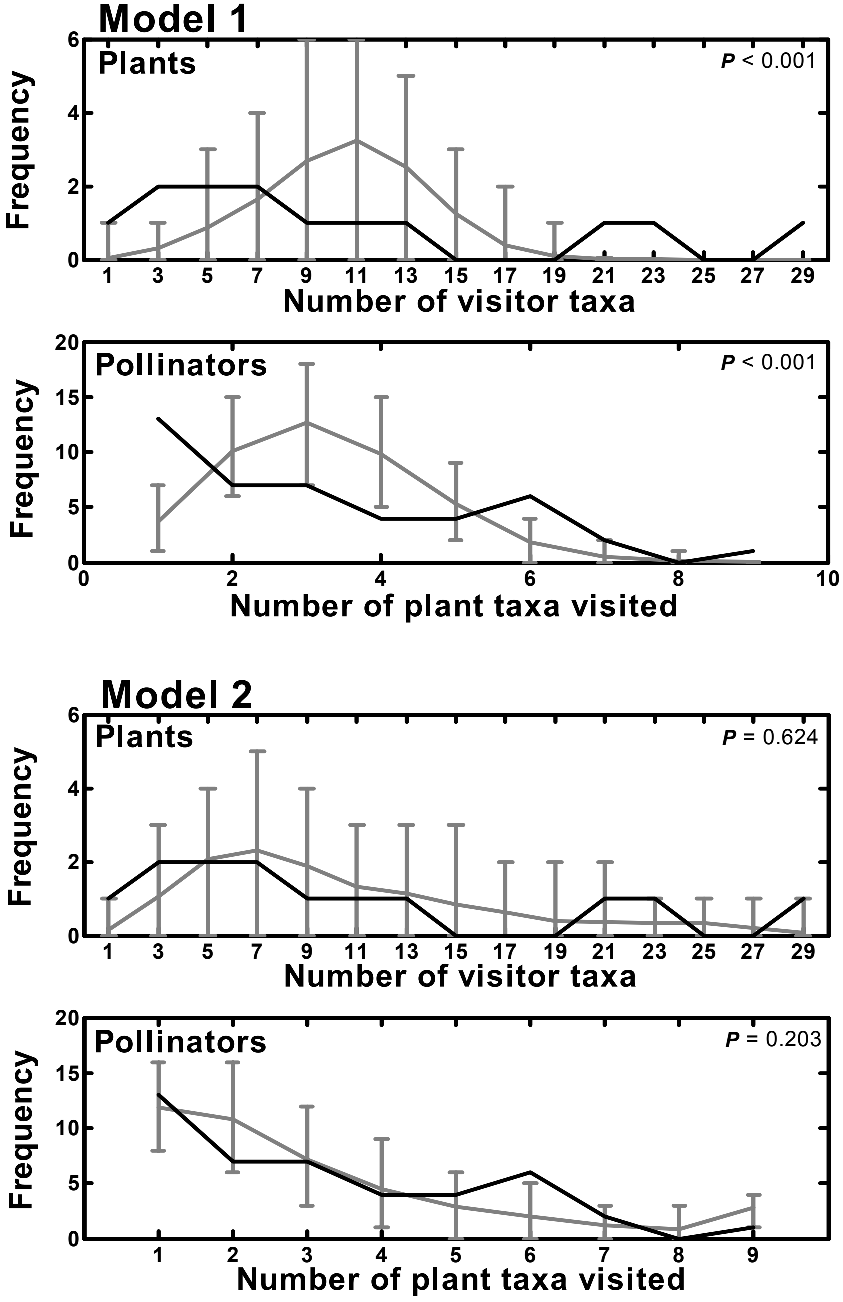
Figure 9.6. Relationship between species' frequency of interaction (f) and the number of interaction partners with which they interact (s) in Memmott's (1999) dataset. Data are shown for two proportional sampling intensities, $\psi = 1$ (crosses), and $\psi = 0.1$ (circles). Lines represent the fitted regression lines of $\ln s$ vs. $\ln f$.

Figure 9.7. Difference statistic (*d*) vs. proportional sampling intensity (ψ). Black circles: *d* statistic calculated for observed data; white circles: expected value of *d* statistic calculated for 1000 randomized communities. Randomizations for each community were conducted separately, and thus each dot represents an independent data point. Lines represent the fitted regression line to the equation $\ln d = a + b \ln \psi$. The coefficient of multiple determination and probability value associated to each regression are given next to each line.

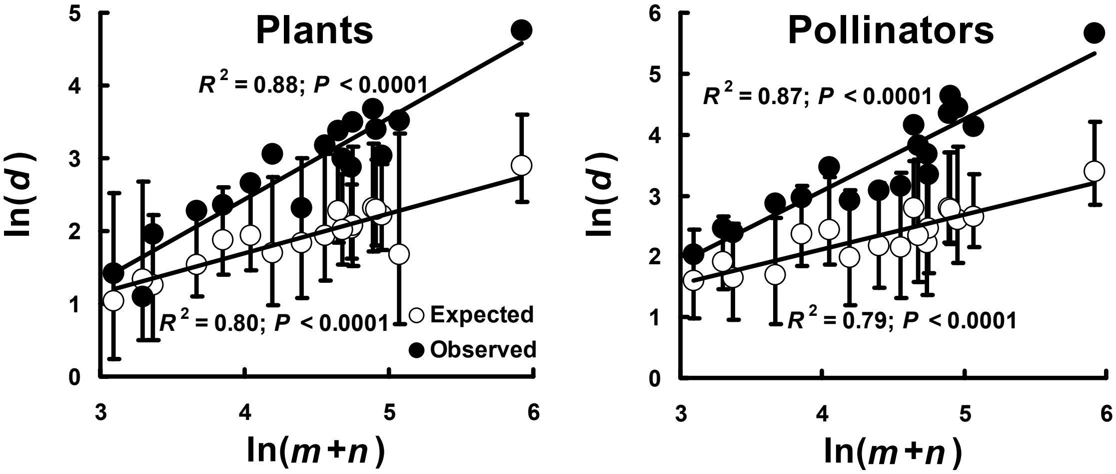
[Figure 9.1]


Null model 1: probability of interaction equal for all species
Species
1
2
3
4
5
Observed *f*
100
40
20
20
20
Species
1
2
3
4
5
Expected *f*
0.2 *n*
0.2 *n*
0.2 *n*
0.2 *n*
0.2 *n*
Null model 2: probability of interaction proportional to observed frequency of interaction
Species
1
2
3
4
5
Observed *f*
100
40
20
20
20
Species
1
2
3
4
5
Expected *f*
0.5 *n*
0.2 *n*
0.1 *n*
0.1 *n*
0.1 *n*

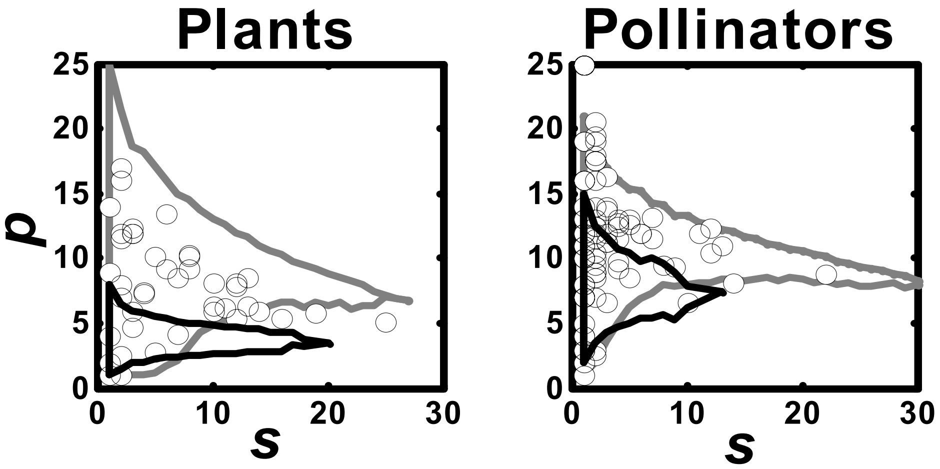
[Figure 9.2]


Model 1
Plants
P < 0.001
Frequency
0
2
4
6
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29
Number of visitor taxa
Pollinators
P < 0.001
Frequency
0
5
10
15
20
0 2 4 6 8 10
Number of plant taxa visited
Model 2
Plants
P = 0.624
Frequency
0
2
4
6
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29
Number of visitor taxa
Pollinators
P = 0.203
Frequency
0
5
10
15
20
1 2 3 4 5 6 7 8 9
Number of plant taxa visited

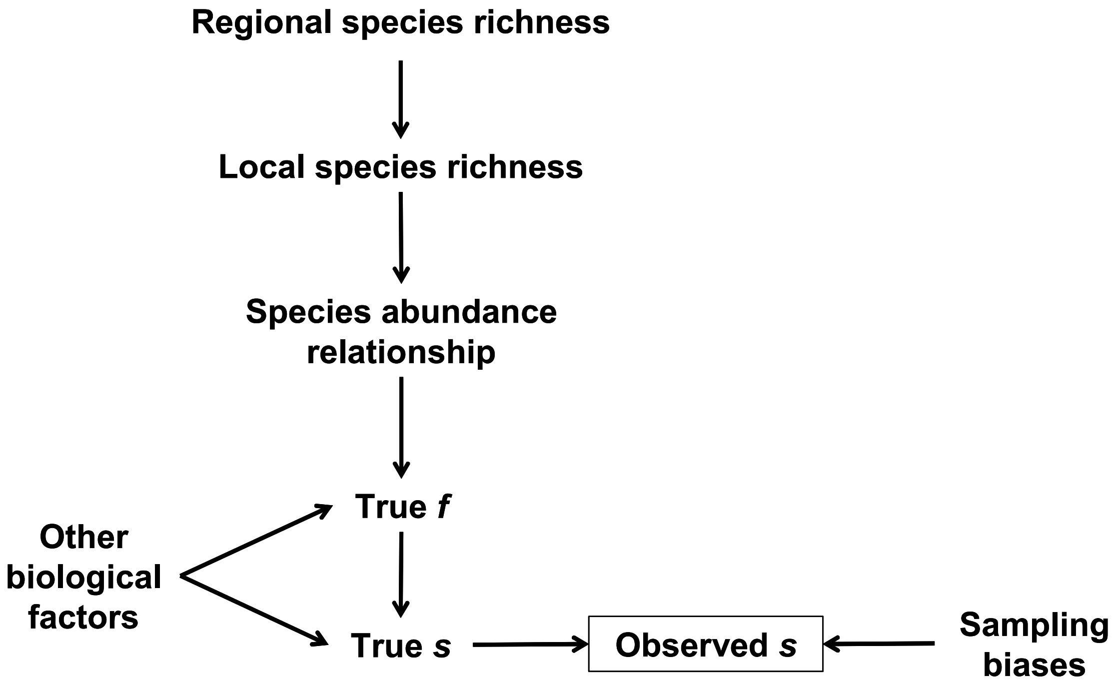
[Figure 9.3]


Plants
Pollinators
ln(d)
ln(m+n)
R^2 = 0.88; P < 0.0001
R^2 = 0.80; P < 0.0001
R^2 = 0.87; P < 0.0001
R^2 = 0.79; P < 0.0001
○ Expected
● Observed
0
1
2
3
4
5
6
3
4
5
6

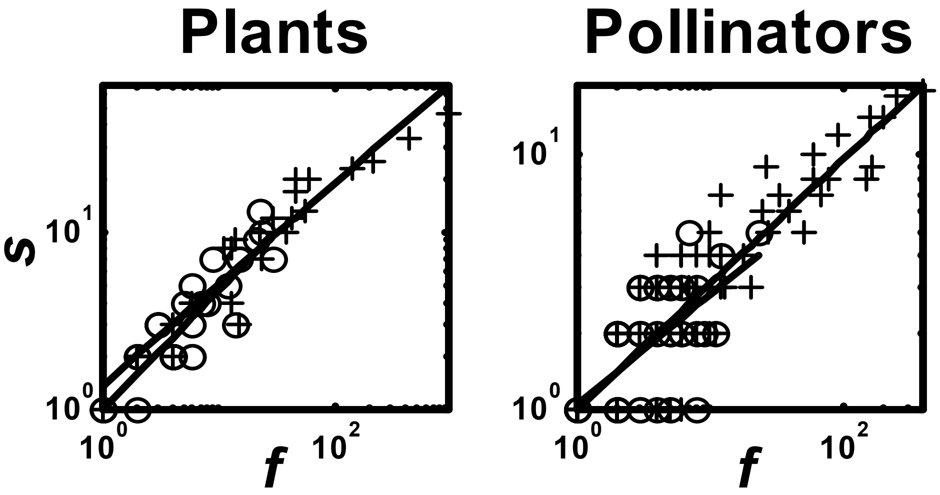
[Figure 9.4]



[Figure 9.5]



[Figure 9.6]



[Figure 9.7]