

The Ecological Consequences of Complex Topology and Nested Structure in Pollination Webs

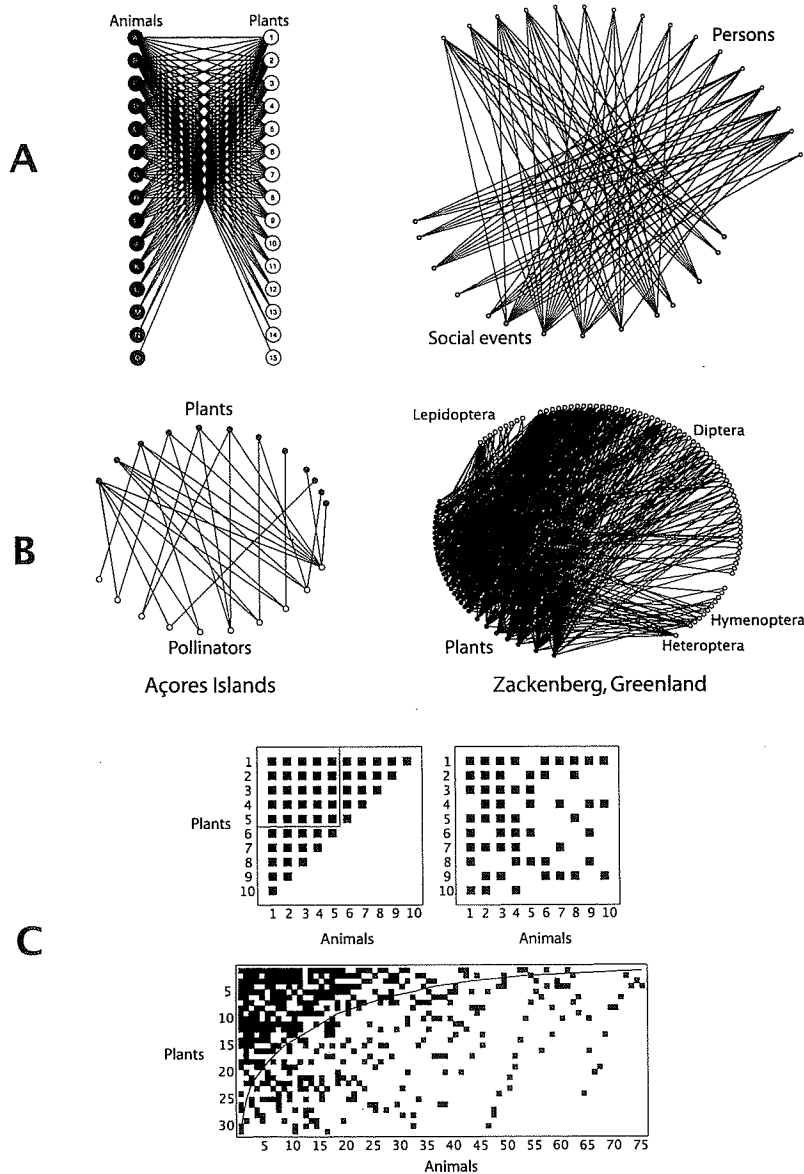
Pedro Jordano, Jordi Bascompte, and Jens M. Olesen

To me the most important thing in composition is disparity . . . Anything suggestive of symmetry is decidedly undesirable, except possibly where an approximate symmetry is used in a detail to enhance the inequality with the general scheme.

—Alexander Calder, “A Propos of Measuring a Mobile”

The extraordinary series of mobiles created by Alexander Calder provide a vivid illustration of how the dynamics of interconnected parts depends on the way they are connected or linked to each other. Calder's mobiles are complex structures of pieces of metal connected by wires or ropes that keep the massive sculptures in equilibrium while they move suspended in air (Calder and Davidson 1966). This equilibrium depends on both the number and the size of pieces and the way they are connected—not only pairwise, but collectively.

In nature, networks of species interactions are the architecture of biodiversity, because community dynamics rely deeply on the way species interact. Pollination by animals is the most common means of fertilization in higher plants, and the mutualism involved in the process illustrates the pervasiveness of complex networks of interaction. For example, tropical forests harbor woody floras in which more than 80% of species rely on animal pollinators for reproduction (Gentry 1982). Most pollination interactions are not specific and do not involve tight mutualisms between species pairs, yet pollination interactions are paradigmatic examples of coevolved interactions among animals and plants. Despite evidence for highly diversified interactions, the well-known precise adjustments between flowers and their pollinator visitors to ensure efficient pollination and adequate handling of the floral rewards led to the prevailing notion of highly specialized interactions. Darwin (1862) advanced a hypothesis of flower morphology evolution based on a highly specialized interaction between a long-spurred orchid and the specialized pollinator it ought to have, later found to be a long-tongued sphingid moth. Since then, textbooks have presented pollination interactions between animals and plants as paradigmatic of mutual speciali-



zation. However, when one considers communitywide patterns, for example, including all the flower species and all the pollinator taxa that interact in a particular location, a wide range of generalization in the mode of interaction emerges as a prevalent pattern. This illustrates the lasting debate about generalization versus specialization of pollination interactions. The debate stems from the difficulty of assessing the totality of biotic interactions within highly diversified communities, and it leads into the difficulties of quantifying generalization at

Figure 8.1 Bipartite graphs as representations of networks, illustrating plant–pollinator interaction networks. (A) Bipartite graph representation of the interactions among $A = 15$ pollinator taxa and $P = 15$ plant taxa, with $k = 120$ interactions. Species are nodes, or vertices, in such a graph, and the pairwise interactions among them are represented by lines connecting two nodes of different sets. Pollinator species A visits all 15 plants; plant species 15 is visited only by A. These bipartite networks are similar to, for example, sociological networks representing the relationships among people attending a series of social events (Davis et al. 1941). (B) Examples of the interaction patterns in relatively simple plant–pollinator webs in the Açores Islands (Olesen et al. 2002) and Zackenberg, Greenland (Olesen and Elberling, unpublished data). (C) Matrix representation of bipartite data. Rows represent plant species; columns represent pollinator species, and black boxes indicate actually documented pairwise interactions. The top left panel shows a perfectly nested matrix, where interactions of the more specialized species are a proper subset of the more generalized interactions; the top right panel shows a matrix of random interactions; and the bottom panel shows the actual dataset of Zackenberg, Greenland, in matrix form. The curved line shows the isocline of perfect nestedness; that is, all interactions (black boxes) would lie to the left of the isocline if the matrix were perfectly nested (see Bascompte et al. 2003).

the community level (Waser et al. 1996; Johnson and Steiner 2000; Olesen 2000). As stated by Thompson (1994), we need more than the analysis of pairwise interactions to understand the evolution of diversified mutualisms such as animal-mediated pollination.

Pairs of pollinator and plant species do not interact in an ecological vacuum, and the outcome of their interaction is best viewed within the network of community-level interactions. For instance, the possibility for a rare species to persist might depend on its ability to develop specialized interactions with a specialist pollinator or on the sharing of pollination services from generalists (Memmott and Waser 2002). The robustness of a network of interactions (i.e., the ability of the component species to persist given the extinction of a partner) may depend on the pattern of shared interactions, not uniquely on pairwise interaction with the extinct species. These issues, among others, require understanding of the web of plant–pollinator interactions.

The study of complex networks has flourished in recent years (Strogatz 2001; Albert and Barabási 2002), and general patterns are starting to emerge which point to interesting properties shared by many types of networks. Recent findings reveal consistent patterns in structure, irrespective of the type of network, for example, similarities between abiotic and biotic networks (Newman 2003). These networks share a fundamental structure or architecture of nodes (elements or parts) linked by connections (fig. 8.1). The frequency distribution of the number of links per node has generally been reported to decay as power-law (scale-free), broad-scale (i.e., truncated power-law), or faster-decaying functions (i.e., exponential; Amaral et al. 2000; Strogatz 2001). Power-law distributions of connectivity are characterized by a high frequency of nodes with few connections and a few highly connected nodes. These generalized patterns have implications for the evolution, stability, and resilience to perturbations of these networks (Barabási and Albert 1999; Albert and Barabási 2002; Dorogovtsev and

Mendes 2002). For example, exponential functions describe randomly assembled networks, whereas power-law distributions result from predictable build-up processes (Barabási and Albert 1999). Thus, the comparative statistical analysis of complex networks sheds lights on their dynamics. Similar patterns have been documented in the ecological literature in recent years, yet few data are available that provide sufficient resolution (Williams and Martinez 2000; Dunne et al. 2002; Montoya and Solé 2002). We have only a limited sample of the complex and diversified patterns of interaction among species in natural ecosystems because most of the previous work on ecological networks focused on food webs and predator-prey interactions. Mutualistic, parasite-host, facilitation, and commensalism interactions are best represented by bipartite graphs of species interactions (Jordano 1987; Poulin 1996; Poulin and Guegan 2000; Jordano et al. 2003) and share both topological (connectivity) and structural patterns (Bascompte et al. 2003) with great potential for influencing species coevolution.

Considering plant-pollinator interactions at the community level is important for several reasons. First, the evolution of pollination adaptations in floral traits most likely results from community-level processes that involve the interaction of groups of species, and not exclusively from the sum of pairwise interactions between plant and animal species. Second, the evolutionary robustness of plant-pollinator interactions depends on properties best viewed at the community level, such as the resilience after extinctions of taxa or the resistance to invasions by exotic species. Third, the manner in which multispecies interactions are organized probably influences the possibilities of rare species for persistence (i.e., how they get reliable pollination services or floral rewards from other taxa). It is only by considering quantitative techniques for complex networks analysis—by characterizing the interactions among species (nodes or vertices) in animal and plant communities—that we can address the potential for variations in network topology to influence coevolutionary processes in high-diversity mutualistic webs.

In this chapter, we review recent advances in the analysis of complex interaction networks and apply them to the study of plant-pollinator interactions. In addition, we explore future avenues of research such as robustness to the loss of species. Taken together, these findings point to very general patterns of generalization-specialization gradients that rest on shared topological and structural properties of how interactions among complex species assemblages are built.

Definitions and Methods

Plant-pollinator records are typical two-mode data (Borgatti and Everett 1997), where the relations between two sets of entities (here, the sets of plant and pollinator species) are described (fig. 8.1A). Most, if not all, of the included interactions can be considered mutualistic interactions, where both animal and plant

partners obtain a benefit; of course, a gradient of types of effects exists (Thompson 1982) in such a diverse array of interactions, ranging from completely beneficial to almost antagonistic (see also Renner, chap. 6 in this volume). A community-level analysis of mutualism-driven coevolution has to account for the full range of interactions and their outcomes.

Entities contain nodes or vertices, which in our case are interacting species; vertices are also called actors in the sociological literature (Newman 2003). Lines that connect two vertices are called edges or links. In the ecological literature, nodes are species and links are interactions among them. The degree of a node is the number of edges connected to it (i.e., the number of interactions per species). The links in these networks only run between nodes of the different sets. A plant-pollinator interaction network is thus defined by an adjacency matrix R which describes the reproductive and trophic interactions between communities of P plant species and A plant-visiting animal species within a well-defined habitat (Jordano et al. 2003):

$$R = [a_{ij}]_{A \times P},$$

where $a_{ij} = 0$ if there is no interaction observed between species i and j , or $a_{ij} = 1$ if an interaction has actually been recorded (figs. 8.1A, 8.1C, 8.2).

Thus, this matrix has k nonzero elements (a_{ij}) wherever plants are pollinated by flower-visiting animals that harvest pollen or nectar. The matrix R would have $A + P$ nodes or vertices (species) and k links among them (figs. 8.1A, 8.1C). These typically are sparse matrices (Duff et al. 1986; Boisvert et al. 1997); that is, matrices with a significant number of zero elements (fig. 8.2). The matrix of interactions captures the essence of interaction patterns at the species level within a given community. Whenever two species are recorded as interacting, the elements $a_{ij} = 1$ when only the qualitative interaction is recorded. If quantitative information is available (e.g., frequency of visitation), for elements with $a_{ij} \neq 0$, we have some estimate of reliance of the pollinator on the plant (e.g., fraction of the pollinator's visits to the plant species relative to the total number of visits) or reliance of the plant on the pollinator (e.g., fraction of visits by the pollinator relative to the total visits by all pollinators or fruit set level resulting from pollinator visitation; Jordano 1987; see also Laska and Wootton 1998; Vázquez and Aizen, chap. 9 in this volume). In this case, the matrix would be valued and, in the case of a bipartite graph representation, would have two values, one describing the dependence or strength of the plant on the pollinator and another one for the pollinator on the plant (see Jordano 1987; Dicks et al. 2002; Vázquez and Aizen, chap. 9 in this volume). Such networks can evolve over time, with links among plants and pollinators appearing and disappearing according to phenological variation or even changing in their strength values.

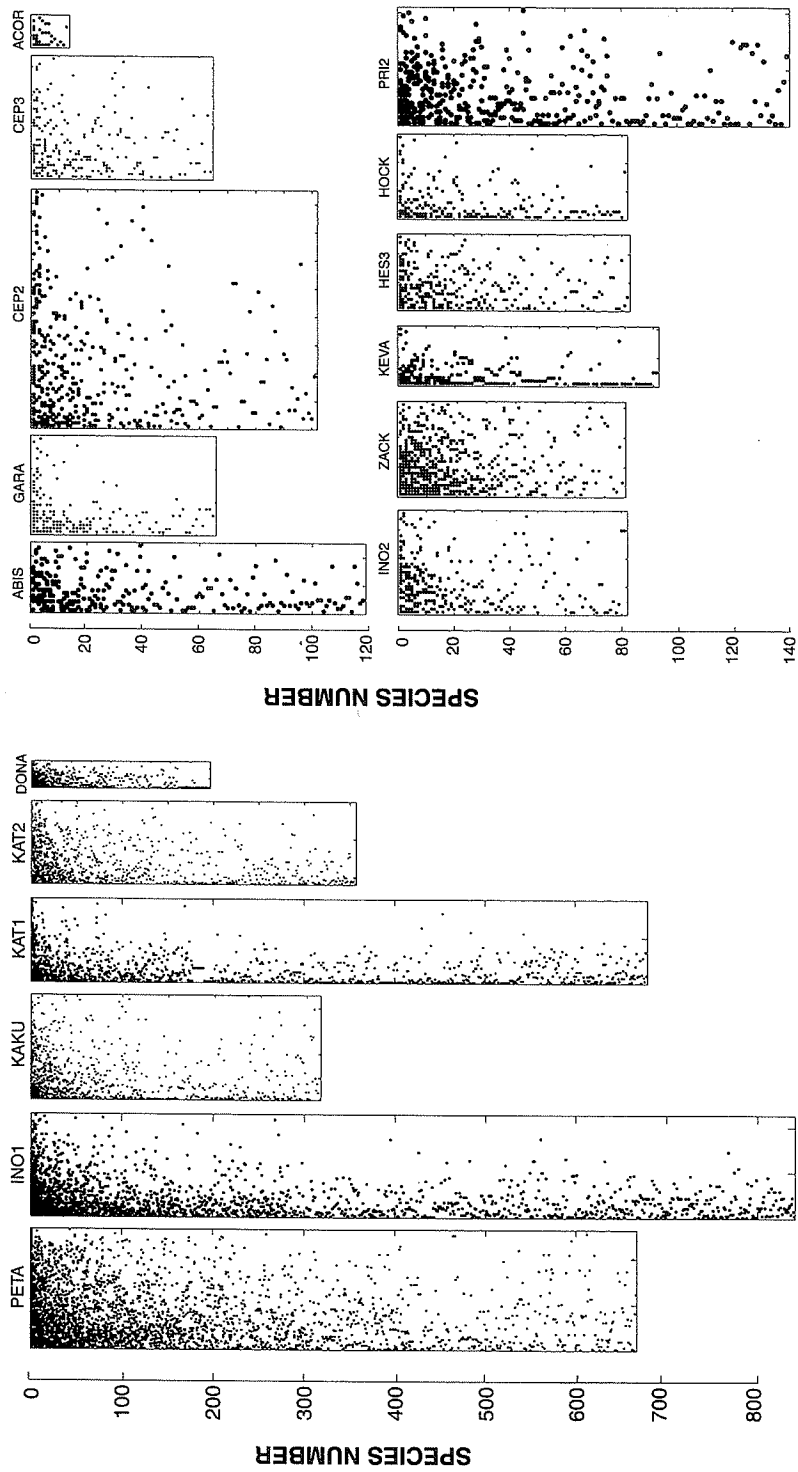


Figure 8.2 Examples of community matrices of plant-pollinator interactions. In each matrix, rows represent pollinator species and columns represent plant species. Dots indicate the presence of a particular pairwise interaction between pollinator species i and plant species j ; that is, dots represent the nonzero elements of the interaction matrices (fig. 8.1C). Matrices are sorted by column and row in decreasing number of interactions per species. These are typical sparse matrices, with a significant number of elements, $a_{ij} = 0$. Abbreviations for each network are as shown in table 8.1. The left axis indicates the scale of the matrices in terms of number of species, by either row or column.

Here we examine total networks, generally compiled during the whole reproductive season and thus including a reasonably complete representation of the interactions. Compared to data available for food webs (Goldwasser and Roughgarden 1997; Bersier et al. 1999; Pimm 2002), these bipartite webs have very high resolution—down to the species level. However, potential biases introduced by variation in sampling effort have been discussed in detail by Jordano (1987), Olesen and Jordano (2002), and Vázquez and Aizen (2003; chap. 9 in this volume).

We use additional variables to characterize the interaction matrices and associated graphs. First, we analyze topological patterns defined by the way interactions are distributed among species—the so-called connectivity distribution (i.e., the probability density function of the number of interactions per species; Jordano et al. 2003). Second, we study structural patterns in the networks, mainly their nested structure and the presence of different compartments (i.e., whether the identity of interacting species is randomly established or defines a nonrandom, well-defined, subset; see Bascompte et al. 2003). Thus, our first approach aims to establish the number of interactions per species, and our second approach to determine the identity of each species' partners. Extending the latter, we also examine where the most-connected species are in the network and how they are connected with other generalists.

In general, multivariate methods have previously been used to represent sparse matrices such that the distances between rows and columns (vertices of the graphs) are meaningful in describing the pattern of presence/absence of interactions in the original matrix. The approach is to compute the geodesic distances between all pairs of nodes in the matrix and to subject the resulting distance matrix to ordination techniques. We used multidimensional scaling (MDS) to represent the pattern of relations among the species in the matrices, such that groupings that depend on the pattern of interactions can be visualized; however, we used the MINLEN modification routine to improve visualization (Borgatti and Everett 1997). We used both PAJEK (Batagelj and Mrvar 2003) and UCINET (Borgatti et al. 1999) packages to analyze the plant–pollinator network datasets; the main variables used were the following.

Density

Density involves the count of the number of links present. This is usually normalized by dividing by the maximum possible number of links, which for our bipartite graphs amounts to $A \times P$. This variable is frequently called connectivity or connectance of the network (see also Petanidou and Potts, chap. 10 in this volume; Medan et al., chap. 11 in this volume). Large sparse matrices illustrating plant–pollinator interactions usually have low density (i.e., only a small fraction of all possible interactions is actually recorded), even in intensively and adequately sampled studies.

Centrality and Connectivity Distribution

Centrality and connectivity distribution are used to measure different aspects of how a given network is centered on particular nodes—whether “central” nodes exist to which others are connected. Generalist species represent nodes of plant–pollinator networks with high centrality; they exhibit many interactions, both with other generalists (nodes which also have high k values) and with specialists (nodes with low k values), thus resulting in high centrality. Here we focus on two measures of centrality. First, the degree centrality of a node is the number of edges incident on (connected to) that node; thus, the degree of a pollinator is the number of plant species it pollinates. In the case of bipartite graphs, the maximum degree of a node is the number of nodes in the opposite set; therefore, degrees are normalized and we used the two-mode normalization proposed by Borgatti and Everett (1997). Second, the eigenvector centrality of a node is its associated eigenvector of the interaction matrix describing the network; it can be considered a weighted degree measure in which the centrality of a node is proportional to the sum of the centralities of the nodes it is connected to. Thus, a species with higher eigenvector centrality will be a generalist interacting with other generalists, located at a more central position of the network, if compared with more specialized species. We sort out the central species in a given network by examining the largest eigenvector centralities in a way similar to how we examine the largest eigenvalues of a multivariate dataset to sort out the main variables influencing covariation.

In a previous paper (Jordano et al. 2003), we examined the cumulative distributions $P(k)$ of the number of interactions per species, k , by fitting three different models: (1) exponential, $P(k) \sim \exp(-\gamma k)$; (2) power law, $P(k) \sim k^{-\gamma}$; and (3) truncated power law, $P(k) \sim k^{-\gamma} \exp(-k/k_x)$, where γ is the fitted constant (degree exponent) and k_x is the truncation value (see fig. 8.3B). The variable k_x is a critical number of interactions/species beyond which $P(k)$ decays faster than expected from a power-law function; k_x can be visualized (fig. 8.3B) as the k value in the abscissa beyond which $P(k)$ departs from the straight-line fit to the power law. In general, the cumulative distributions of connectivity, or degree distributions, reveal interesting patterns of the way networks are built. Random networks have characteristically exponential degree distributions; they are single-scale distributions because the distribution of links per node can be fully characterized by a single value, or scale: the mean number of links/node. Complex networks deviate markedly from this pattern and show link distributions that fit either power-law or truncated power-law models. These distributions are not fully described by a characteristic scale and are called scale-free and broad-scale distributions, respectively. They are more heterogeneous than random networks, because the cumulative distributions of k have longer tails. Thus, despite the fact that the bulk of species has few interactions in these networks, a few species have many more interactions than randomly expected. We found the best fit to different models

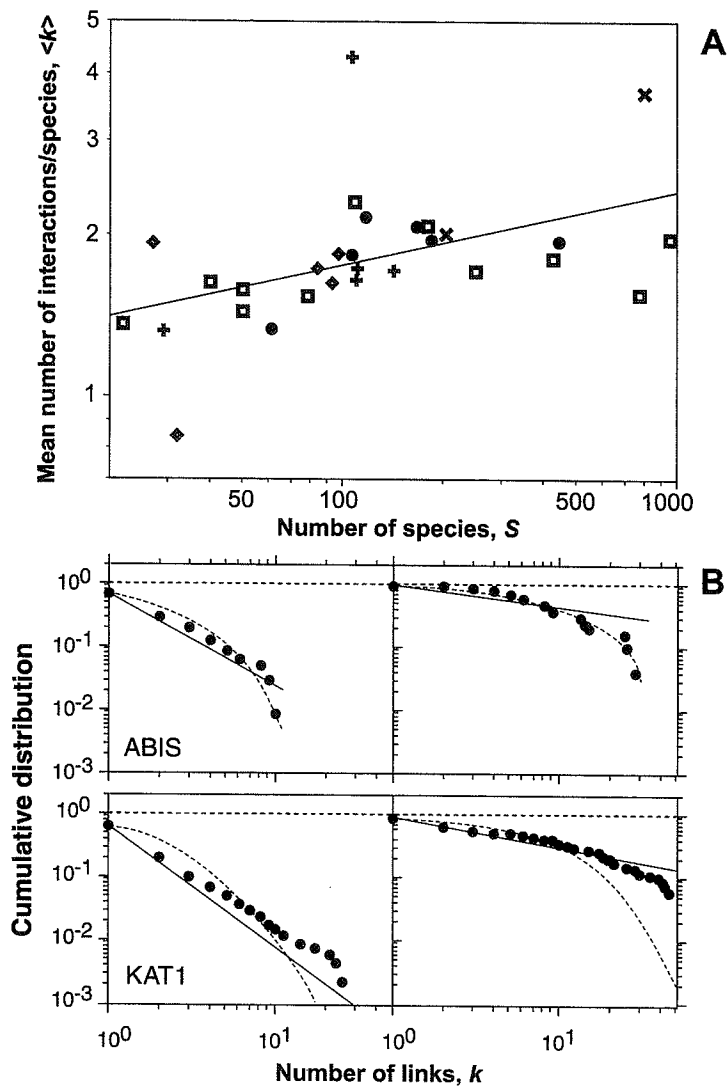


Figure 8.3 (A) Relationship between the mean number of interactions per species, $\langle k \rangle$, and the total number of species (species richness, S) in plant–pollinator networks (table 8.1). Data are presented for tropical (●), arctic (+), alpine (◆), Mediterranean (×), and temperate (□) communities. The line is the least-squares fit to the log-transformed data. (B) Cumulative distributions of the number of interactions per species, or degree, k , for the ABIS and KAT1 networks (see table 8.1). The distributions of interactions are given separately for the pollinator and plant sets of species (left and right panels, respectively). Plots show the decay in the probability $P(k)$ of finding a species with k interactions as k increases. The observed data are plotted as dots, then the fits of the distribution to a power-law or truncated power-law model are represented by continuous or dashed lines, respectively. The best fit for the analyzed networks is given in table 8.1 (see also Jordano et al. 2003). Typically, the distributions of $P(k)$ depart from the straight-line fit to the power law beyond a certain value of k_x ($k_x < k$), so that there is a “truncation” at large values of k .

(Jordano et al. 2003) by examining the F values and associated adjusted R^2 values.

We also examine three additional structural properties of the plant-pollinator networks, namely, centralization, k -cores or cliques, and nestedness.

Centralization

The preceding variable of centrality characterizes the location of individual nodes or species, whereas the measure of centralization (Everett and Borgatti 1999) gives the extent to which a network has a highly central node or species around which peripheral species collect. A network with a high centralization value would resemble a star (e.g., a community with a single pollinator species interacting with all the plant species).

k -Cores

There are many ways to identify the internal heterogeneity of the network (i.e., the extent to which groups of nodes exist that share more links among themselves than with the remaining nodes). In the ecological and sociological literature, these have been called cliques (Pimm 2002) or cores (Everett and Borgatti 1999); k -cores are subsets of nodes with at least k interactions among them. Larger k -cores identify larger components of the network—groups of species that show a maximum number of interactions among them in comparison with other species. We used the k -cores routines in PAJEK and UCINET to identify subgroups of taxa in the plant-pollinator networks.

Nestedness

Imagine that we sort the interaction matrix from the most generalist pollinator species to the most specialist (i.e., matrix sorting by row); then we sort by column from the most generalist to the most specialized plant species (fig. 8.1C). The distribution of interactions among species yields nested patterns whenever species with fewer interactions appear to be “included” within those with more generalized interactions (fig. 8.1C); that is, the interactions of the more specialized species tend to be a proper subset of (i.e., nested within) the interactions already observed among the more generalized species.

To measure nestedness, one needs a quantitative measure and a benchmark to compare an observed value to check for significance. A quantitative measure was provided by Atmar and Patterson (1993). Their nestedness calculator provides a measure of disorder understood as a physical measure of “temperature.” When temperature is zero, the system is totally ordered; in this case, species would be organized in the matrix to achieve maximum nestedness. In a situation of perfect nestedness, one could draw an isocline that separates the matrix into two parts. In the left-hand side of the matrix, all pairs of species would interact;

on the right-hand side of the matrix, no interactions at all would occur (see fig. 8.1C). Now imagine that temperature (or randomness) increases. Random noise would move some interaction away and we would depart from the perfect nested scenario to a random one in which all interactions are randomly distributed. The nested calculator measures the global distance to the situation of perfect nestedness: it works by calculating the distance of all the unexpected presences and absences to the isocline of perfect nestedness, and it averages this value. Bascompte et al. (2003) use a value of nestedness which is the inverse of the temperature T . Because temperature ranges from zero to one hundred, nestedness can be defined as $N = (100 - T)/100$; thus, nestedness ranges between zero and one (table 8.1). Nested patterns typically yield a core of species acting as a pivot cluster for other peripheral species (fig. 8.1C).

We used the **FACTIONS** and **GENFAC2** routines in the **UCINET** package to identify the central and peripheral groups of species according to the distributions of interactions. Species with high eigenvector centrality are generally included in the core cluster of the network (Borgatti et al. 1999).

The Complexity of Plant–Pollinator Interaction Networks

Network Topologies

Plant–pollinator networks typically have sparse matrices, which best describe their topology (i.e., the way interactions occur among species; fig. 8.2). Thus, most interactions are simply not observed and only a fraction of the maximum possible number actually occurs. The connectance varies widely among networks and is strongly and negatively associated to species richness (see table 8.1; Olesen and Jordano 2002). Interactions rarify with increasing species richness and connectance decreases despite the fact that, when comparing networks, the number of interactions increases with the number of species (Jordano 1987; Olesen and Jordano 2002; Bascompte et al. 2003). Supergeneralists are hard to find; therefore, the probability of encountering a species with k interactions drops as k increases. The mean number of interactions per species increases with increasing species richness across networks ($\langle k \rangle = -0.08 + 0.139S$; for the log-transformed data, $F_{1,27} = 7.86, P = .009$), but the rate of increase is relatively low and even levels off beyond 150 species (fig. 8.3A). This may suggest a bound on the number of potential interactions a species can develop and may ultimately explain the decrease in connectance with S (see Pimm 2002 for discussion).

But supergeneralists (species with very large k) do exist; this differs from randomly built networks, where nodes with large k values simply do not exist (Albert and Barabási 2002; Vázquez and Aizen 2003). What biotic networks have that is special in contrast to other complex networks is that the frequency of these supernodes, with an extremely large number of connections, is lower than expected if the network has a scale-free distribution of k values. Thus, the proba-

Table 8.1 Summary statistics of plant–pollinator interaction networks

No.	Code	S	A	P	M	k	<k>	<k _a >	k _{max} A	<k _p >	k _{max} P	γ _{Pollinators}	Fit ^a	γ _{Plants}	Fit ^a
1	ABIS	142	118	24	2832	242	1.70	2.05	10	10.08	28	-1.35	a	-0.89	b
2	ACOR	22	12	10	120	30	1.36	2.50	6	3.00	8	-1.02	b	-1.26	c
3	CEP1	61	25	36	900	81	1.33	3.24	34	2.25	25	-1.01	a	-0.97	b
4	CEP2	185	101	84	8484	361	1.95	3.57	15	4.30	7	-0.93	a	-1.24	b
5	CEP3	107	64	43	2752	196	1.83	3.06	16	4.56	14	-1.13	b	-0.92	b
6	DONA	205	179	26	4654	412	2.01	2.30	17	15.85	86	-1.33	a	-0.68	b
7	GALA	32	22	10	220	27	0.84	1.23	4	2.70	6	-1.76	b	-0.83	b
8	GARA	84	55	29	1595	145	1.73	2.64	16	5.00	24	-1.14	a	-0.76	a
9	HES1	50	40	10	400	79	1.58	1.98	7	7.90	17	-1.45	b	-0.78	b
10	HES2	50	42	8	336	72	1.44	1.71	5	9.00	17	-1.51	d	-0.83	c
11	HES3	108	82	26	2132	249	2.31	3.04	19	9.58	31	-1.10	b	-0.92	b
12	HOCK	110	81	29	2349	179	1.63	2.21	10	6.17	40	-1.46	b	-0.74	a
13	INO1	952	840	112	94,080	1876	1.97	2.23	37	16.75	119	-1.36	b	-0.62	b
14	INO2	117	81	36	2916	253	2.16	3.12	21	7.03	25	-1.08	a	-0.47	b
15	KAKU	428	314	113	35,482	774	1.81	2.46	26	6.85	68	-1.25	a	-0.85	b
16	KAT1	770	679	91	61,789	1193	1.55	1.76	25	13.11	188	-1.62	a	-0.62	a
17	KAT2	446	356	90	32,040	865	1.94	2.43	24	9.61	65	-1.26	a	-0.79	b
18	KATO	251	187	64	11,968	430	1.71	2.30	17	6.72	40	-1.36	a	-0.77	b
19	KEVA	111	91	20	1820	190	1.71	2.09	7	9.50	60	-1.39	b	-0.58	b
20	MAUR	27	13	14	182	52	1.93	4.00	12	3.71	8	-0.89	b	-1.23	b
21	MOSQ	29	18	11	198	38	1.31	2.11	7	3.45	9	-1.22	a	-0.90	b
22	PERC	97	36	61	2196	178	1.84	4.94	31	2.92	13	-1.00	b	-1.10	b
23	PETA	797	666	131	87,246	2933	3.68	4.40	104	22.39	124	-0.99	a	-0.89	b
24	PRI1	78	60	18	1080	120	1.54	2.00	9	6.67	12	-1.44	b	-0.89	b
25	PRI2	180	139	41	5699	374	2.08	2.69	16	9.12	43	-1.22	b	-0.73	b
26	PRI3	167	118	49	5782	346	2.07	2.93	26	7.06	43	-1.11	a	-1.00	c
27	RAMI	93	46	47	2162	151	1.62	3.28	17	3.21	10	-1.01	a	-1.24	c
28	SCHE	40	33	7	231	65	1.63	1.97	6	9.29	23	-1.33	b	-0.52	a
29	ZACK	107	76	31	2356	456	4.26	6.00	20	14.71	32	-0.89	c	-1.36	b

bility of finding a species with k interactions drops suddenly for a relatively large value of k (fig. 8.3B; see also fig. 2 of Jordano et al. 2003). In fact, the upper limit for k (k_{max} ; table 8.1) is much lower for pollinator species than for plant species, although this might relate to the fact that plant–pollinator records are typically obtained with “phytcentric” surveys (i.e., surveys focused on plant species and documenting their interactions with pollinators). Although the plant–pollinator networks examined thus far are reasonably robust to sampling artifacts (Jordano 1987; Vázquez and Aizen, chap. 9 in this volume), future research should explore potential biases derived from sampling designs focused on particular sets of these bipartite networks. In addition, caution should be taken in the interpretation of results because of variable completeness of the data (Olesen and Jordano 2002; see Goldwasser and Roughgarden 1997; D. Vázquez, personal communication) and assumptions inherent to the analyses (Vázquez and Aizen, chap. 9 in this volume).

The distribution of number of interactions per species is markedly skewed in pollination networks (table 8.1). Most species have k_a or k_p values greater than 5; these networks share a general pattern of a dense core of species which interact

Table 8.1 (continued)

No.	Eigenvector	Centralization	C	N	p	Locality	Source ^b
1	4.01	20.35	0.0854	0.8602	*	Latnjajaure, Abisko, Sweden	Elberling and Olesen 1999
2	26.01	48.68	0.2500	0.6707	ns ^c	Flores, Açores Islands	J. M. Olesen, unpublished data
3	14.25	9.86	0.0900	0.9604	**	Cordón del Cepo, Chile	Arroyo et al. 1982
4	6.90	27.67	0.0425	0.9098	**	Cordón del Cepo, Chile	Arroyo et al. 1982
5	9.95	19.02	0.0712	0.9250	**	Cordón del Cepo, Chile	Arroyo et al. 1982
6	6.84	50.38	0.0885	0.9114	**	Doñana National Park, Spain	Herrera 1988
7	15.92	12.79	0.1227	0.7016	ns	Galapagos Islands	McMullen 1993
8	5.49	30.72	0.0909	0.9523	**	Garajonay, Gomera Island, Spain	Olesen MS/laurisilva
9	7.57	43.52	0.1975	0.6279	ns	Hestehaven, Denmark	Olesen MS/bog
10	7.60	29.08	0.2143	0.5938	ns	Hestehaven, Denmark	Olesen MS/forest
11	5.08	24.42	0.1168	0.8283	**	Hestehaven, Denmark	Olesen MS/fallow
12	4.62	40.96	0.0762	0.9454	**	Hazen Camp, United States	Hocking 1968
13	0.49	0.55	0.0199	—		Kibune, Kyoto, Japan	Inoue et al. 1990
14	9.29	20.46	0.0868	0.9041	*	Snowy Mountains, Australia	Inouye and Pyke 1988
15	2.04	23.11	0.0218	—		Kyoto City, Japan	Kakutani et al. 1990
16	0.62	38.12	0.0193	—		Ashu, Kyoto, Japan	Kato et al. 1990
17	2.02	19.97	0.0270	0.9746	**	Mt. Kushigata, Japan	Kato et al. 1993
18	2.79	21.88	0.0359	0.9551	**	Nakaikemi, Japan	Kato and Miura 1996
19	9.82	65.25	0.1044	0.9550	**	Hazen Camp, Canada	Kevan 1970
20	11.77	28.45	0.2857	0.8743	**	Mauritius Island	Eskildsen et al., unpublished data
21	6.29	18.08	0.1919	0.7808	ns	Melville Island, Canada	Mosquin and Martin 1967
22	10.38	36.01	0.0810	0.9254	**	Jamaica	Percival 1974
23	3.11	14.69	0.0336	—		Daphní, Athens, Greece	Petanidou 1991
24	5.85	23.55	0.1111	0.9397	**	Arthur's Pass, New Zealand	Primack 1983, AP
25	3.53	30.79	0.0656	0.9252	**	Cass, New Zealand	Primack 1983, Cass
26	7.56	35.30	0.0598	0.7363	**	Craigieburn, New Zealand	Primack 1983, Craigieb.
27	8.61	25.17	0.0698	0.8710	*	Canaima National Park, Venezuela	Ramirez 1989
28	8.98	50.04	0.2814	0.8668	**	Brownfield, Illinois, United States	Schemske et al. 1978
29	5.37	9.66	0.1935	0.7420	**	Zackenbergl, Greenland	Elberling and Olesen MS

Source: See Olesen and Jordano 2002; Jordano et al. 2003; and Bascompte et al. 2003 for details.

Note: Column headings are as follows: (S) species richness; (A) number of pollinator species; (P) number of plant species; (M) matrix size (total number of potential interactions); (k) number of interactions recorded; (<k>) mean number of interactions per species (degree); (<k_p>) mean number of interactions per pollinator species; (k_{max}A) degree of most-connected pollinator species; (<k_p>) mean number of interactions per plant species; (k_{max}P) degree of most-connected plant species; (γ_{Pollinators}) gamma exponent for the fit of the cumulative frequency distribution of P(k) for pollinator species; (γ_{Plants}) gamma exponent for the fit of the cumulative frequency distribution of P(k) for plant species; (Fit) best fit of the cumulative frequency distribution of P(k) to a model; (Eigenvector) mean eigenvector centrality of the species (plants and pollinators pooled); (Centralization) network centrality value; (C) connectance, or density of the network; (N) nestedness.

*Power law (a); truncated power law (b); exponential (c); not available (d). Best fit determined by the highest F and adjusted-R² values.

^bFor reference list, see Bascompte et al. 2003 and Jordano et al. 2003.

^cNo significance.

*p < .05; **p < .01

with each other, surrounded by many species with few interactions, connected with those in the core (fig. 8.2). We found a number of networks that fit power-law distributions of k values (table 8.1; e.g., KAT1 in fig. 8.3B), but most were better described by a truncated power law (Jordano et al. 2003). In a truncated power-law distribution, the probability of a given value of k for a species drops with increasing k following a power-law function; then, beyond a certain value of k , the observed data depart from the power law and show a steep decay (ABIS network in fig. 8.3B; Amaral et al. 2000).

Therefore, from the perspective of connectivity distribution, plant-pollinator networks share many features irrespective of the ecological setting. These features are also shared with other plant-animal mutualisms (Jordano et al. 2003) and other complex networks (Newman 2003) and probably reveal very basic processes of the way species are arranged in mutualistic assemblages. Irrespective of the size of the network, plant-pollinator mutualisms center around a core of generalist species with a high density of interactions. The interactions of the core involve not only other generalists but also the more specialist species, and this pattern gives the characteristic aspect to the sparse matrices that describe these interactions (fig. 8.2). The pattern depends not only on the distribution of k values among individual species but also on “structural” patterns that define the distribution of interactions throughout the network, as described next.

Biological Patterns: Beyond the Topology of Interactions

The truncated distributions of $P(k)$ are not exclusive to pollination networks but occur whenever constraints are imposed in the way nodes establish links. In the presence of constraints, highly connected nodes would be less likely to occur than the frequency expected for a scale-free network (Mossa et al. 2002). The ubiquity of truncation in the distribution of the number of interactions per species in plant-pollinator and plant-disperser mutualisms led us to suggest (Jordano et al. 2003) that biological constraints are the main factor explaining truncation. Constraints occur because of the biological attributes of the species; if a plant and a pollinator differ in phenology (e.g., an early blooming herb and a late-summer migratory pollinator), their interaction cannot occur (see also Medan et al., chap. 11 in this volume). This translates into “structural” zeros in the interaction matrices, that is, pairwise interactions that will never be recorded despite intensive study. We can thus expect a sizeable fraction of the nonobserved interactions to be caused by these types of constraints. We defined these nonobservable interactions as “forbidden interactions” and hypothesized that they are the main cause of the patterns we observe in the distributions of $P(k)$ in plant-animal interaction networks in general.

What is the reason behind truncation of the cumulative degree distributions? We recently provided evidence for generalized truncation in plant-animal mu-

tualistic networks (Jordano et al. 2003) and argued that, whenever a complex network evolves (i.e., by the addition of species), the new species are constrained in the way they set up interaction with partners. Species-specific traits set limits to the possibilities of successful interaction. This is readily evident from the sparse matrices that typically describe plant–pollinator networks (fig. 8.2): actual interactions are relatively “rare.” Moreover, the number of interactions observed increases with species richness, but at a relatively low rate that results in a low fraction of the possible interactions realized at high species-richness values (fig. 8.3A). Therefore, forbidden interactions are a major component of the sparse interaction matrices (fig. 8.4).

The example of the Snow and Snow (1972) dataset (fig. 8.4) exemplifies the ubiquity of forbidden interactions. These authors studied interactions between hummingbirds and plants in Arima Valley, Trinidad (10°40' N), for almost two years. Connectance is relatively high ($C = 0.354$), which is typical of subnetworks that only include a subset of the pollinator fauna (Jordano 1987). However, there are only 185 interactions out of 522 possible, with 337 not recorded; figure 8.4 outlines the reasons for not observing these 337 pairwise interactions. In most cases (29%), habitat uncoupling between the plant species and the pollinator causes the interaction not to occur (matrix elements marked H in fig. 8.4). This chiefly occurs between subcanopy foragers like the hermit hummingbird species (*Phaethornis* spp. and *Glaucis hirsuta*) and canopy trees, and among *Anthracothorax nigricollis* and *Florisuga mellivora*, which avoid lower strata (Snow and Snow 1972). A relatively small fraction (13%) of forbidden interactions is due to uncoupling of corolla or flower characteristics (tube length, reward, or color) and pollinator (fig. 8.4). Thus, 6% of the interactions are not observed because of size restrictions (i.e., beak is too short relative to the corolla tube length), 4% can be attributed to the reward per flower being too small relative to the size of the bird; and 3% can be attributed to apparent color restrictions (e.g., *Phaethornis guy* and *G. hirsuta* only forage on red-flowered species).

Obviously, a sizeable fraction of the unrecorded interactions cannot be accounted for and might be related to unknown factors (U , 24%; fig. 8.4) which, among others, include chance effects and limited sampling effort. In fact, for the figure 8.4 dataset, interactions recorded only once were excluded in the original table; this might explain the relatively high frequency of U values. These unknowns are also found in other well-studied systems (Jordano et al. 2003; P. Jordano, unpublished data). They may simply result from an extremely low probability that the interaction actually occurs in nature despite an obvious cause. For instance, when two species are very rare, their probability of interaction is likely to be low. We believe that future explorations of the cause of forbidden interactions will shed light on important factors in the evolution of complex patterns of interaction in species-rich systems. A categorization of forbidden “types” may indicate repeated patterns that are independent of the ecological setting and

Plant species

Plant species	1	2	3	4	5	6	7	8	9
<i>Isertia pariflora</i>	H	H	H						
<i>Calliandra guildingii</i>		H	H						
<i>Heliconia bihnai</i>		H	H						
<i>Norantea guianensis</i>	H	H	H						
<i>Palaourea crocea</i>		H	H						
<i>Samanea saman</i>		H	H						
<i>Costus spiralis</i>		H	H						
<i>Erythrina micropteryx</i>		H	H						
<i>Gravisia aquilega</i>		H	H						
<i>Gourania spinulosa</i>		H	H						
<i>Inga venosa</i>		H	H						
<i>Justicia sp.</i>		H	H						
<i>Symphonia globulifera</i>		H	H						
<i>Doxantha unguis-cati</i>									
<i>Heliconia hirsuta</i>									
<i>Inga ingoides</i>									
<i>Mandevilla hirsuta</i>									
<i>Pachystachys coccinea</i>									
<i>Psychotria sp.</i>									
<i>Ryania speciosa</i>									
<i>Warszewiczia coccinea</i>									
<i>Cephaelis muscosa</i>									
<i>Citrus sp.</i>									
<i>Cordia bicolor</i>									
<i>Cordia curassavica</i>									
<i>Dugenia hirsuta</i>									
<i>Erythrina glauca</i>									
<i>Guzmania monostachya</i>									
<i>Inga sp.</i>									
<i>Listanthus chelonoides</i>									
<i>Pithecellobium lupunba</i>									
<i>Tabernaemontana psychotriifolia</i>									
<i>Brownea latifolia</i>									
<i>Centropogon surinamensis</i>									
<i>Aechmea nudicaulis</i>									
<i>Clathrotophis brachypetala</i>									
<i>Erythrina corallodendron</i>									
<i>Eugenia jambos</i>									
<i>Hamelia erecta</i>									
<i>Marcravia sp.</i>									
<i>Psychotria tobagensis</i>									
<i>Renalmia sp.</i>									
<i>Tabebuia stenocalyx</i>									
<i>Tillandsia utriculata</i>									
<i>Vitex divaricata</i>									
<i>Arrabidaea inaequalis</i>									
<i>Aechmea duchlamydea</i>									
<i>Aechmea fendleri</i>									
<i>Billbergia pyramidalis</i>									
<i>Costus sp.</i>									
<i>Heliconia psittacorum</i>									
<i>Heliconia sp.</i>									
<i>Ischnosiphon arouma</i>									
<i>Lantana camara</i>									
<i>Tabebuia serratifolia</i>									
<i>Tillandsia fasciculata</i>									
<i>Vrhesia procera</i>									
<i>Aegiphila perplexa</i>									

Hummingbird species

1. *Saurornis tobaci*
2. *Phaethornis longuemareus*
3. *Chlorestes notatus*
4. *Amazilia chionopectus*
5. *Phaethornis guy*
6. *Glaucis hirsuta*
7. *Chrysolampis mosquitus*
8. *Anthracoceros nigricollis*
9. *Florisuga mellivora*

Figure 8.4 Patterns of forbidden interactions in a plant–hummingbird subnetwork (Snow and Snow 1972). Rows indicate hummingbird species ($A = 9$) and columns are their foodplants ($P = 58$). Forbidden interactions are those never observed in interaction matrices; that is, for each zero element of the interaction matrix, we note the potential cause for not having recorded that particular pairwise interaction. Black cells are the observed interactions in the matrix ($a_{ij} = 1$). For the nonobserved interactions ($a_{ij} = 0$), letters indicate the potential cause for not encountering that interaction: size restrictions (S); habitat restrictions (H), due to habitat uncoupling of birds and plants; reward limitation (R); flower color restrictions (C); and unknown reason (U; see text for detailed descriptions). There are general reasons for the actual interaction between a pair of plant and pollinator species being impossible to record in a given habitat, for instance, when the flowering period of the plant does not match the period of presence of the pollinator in the area, as in the case of migratory pollinators, or when the size of the pollinator mouthparts restricts access to the nectar and pollen.

may help to explain the invariant properties we document. It may also be possible to tease apart the relative importance of phylogenetic composition of the interaction partners and their ecological traits in causing forbidden interactions. In any case, forbidden interactions illustrate the types of constraints that are peculiar to these biotic interactions and that cause network patterns that severely deviate from other complex networks, especially the abiotic networks.

In the preceding section, we argued that the distribution of interactions among species indicates the presence of a central core of taxa showing the highest density of interactions. The centrality parameters, such as the eigenvector centrality (table 8.1), quantify to what extent a particular species has a central role in the network, that is, located as a central actor relative to others that link with it. The mean eigenvector centrality is negatively correlated across networks with species richness ($r = -0.581, P = .0009, N = 29$), meaning that increasingly diverse communities have a lower number of central species. Relatively simple communities have higher connectance, which means each species in one set is connected with a relatively large fraction of the species in the other set. This also means that simple plant–pollinator networks tend to be less centralized (fig. 8.5) and to be structured as a single core with no central actor. In most cases, however (fig. 8.5), a number of species can be identified as having the highest density of interactions. CEP3 has 16 species (10 plants, 6 pollinators) with eigenvector centrality greater than 20.0 (fig. 8.5; see table 8.1); among these, 9 species define a central core as identified by clustering algorithms in UCINET. This algorithm takes the bipartite graph and uses a combinatorial procedure to assign nodes to two clusters, one central and the other peripheral, such that it maximizes the fit to the expected situation where the density of links within each group is maximal and nonexistent between groups (Borgatti and Everett 1997, 1999). Thus, the algorithm finds the two groups of nodes that maximize the separation between a core and a periphery within the network. In larger networks, such as ZACK and PETA (table 8.1; fig. 8.5), a relatively small fraction of species forms the core. In ZACK, there are 20 species out of 107 with an eigenvector centrality

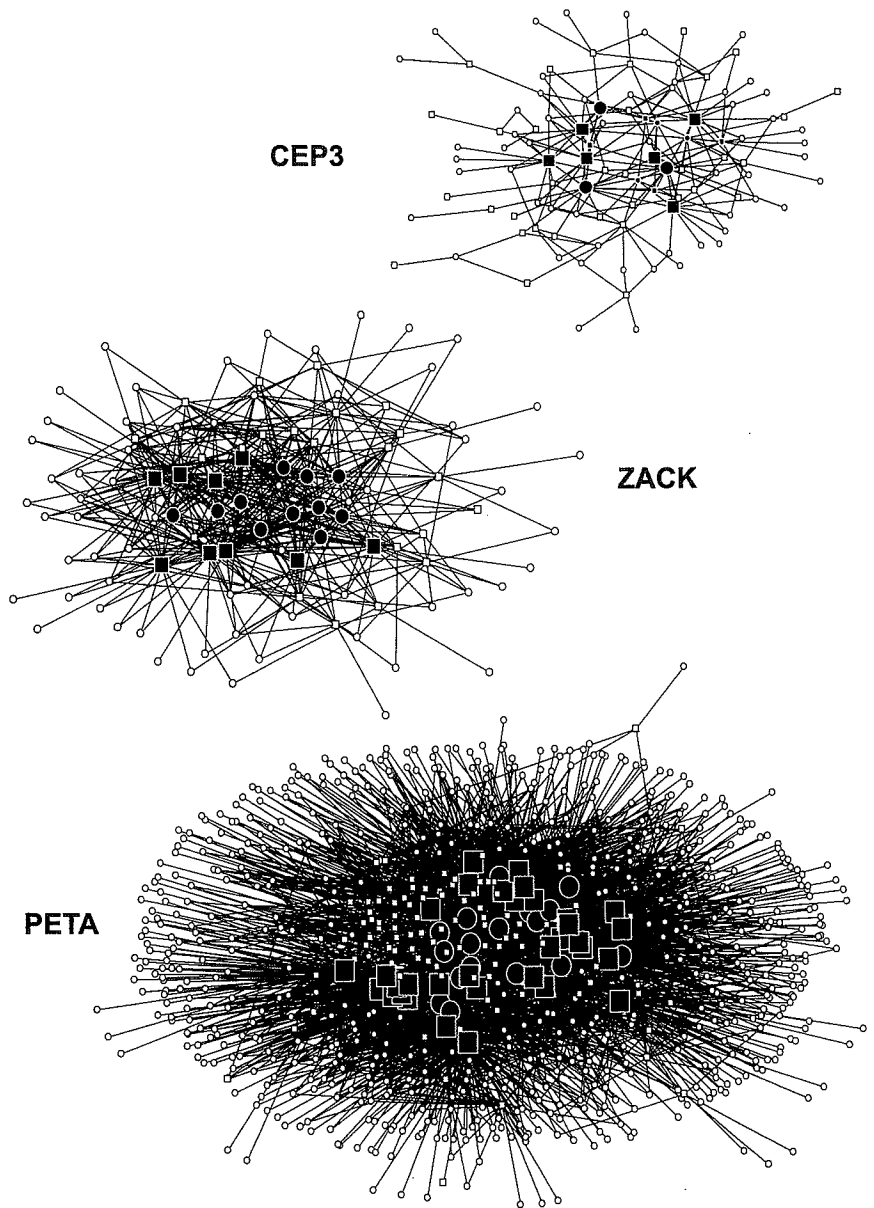


Figure 8.5 Examples of plant–pollinator networks with the core of species outlined, as identified by the eigenvector centrality value (two-mode normalized) of each node. Species with eigenvector centrality greater than 10.0 (PETA network) or greater than 20.0 (in CEP3 and ZACK networks) are outlined with larger symbols: circles indicate pollinator species; squares indicate plant species. The three networks have cores with 42 (PETA), 16 (CEP3), and 20 (ZACK) species. A pollinator’s centrality is proportional to the sum of centralities of the plants it interacts with. A central pollinator species is more central by being a generalist—interacting with other generalist plants but also with specialized species. See table 8.1 for a description of the networks.

greater than 20.0 that form the core. In PETA, the core is composed of 42 species with eigenvector centralities greater than 10.0. In CEP3, flies (chiefly syrphids) dominate the core and also *Bombus* spp.; the PETA network core is composed of flies and bees in roughly the same proportions. In the plant set, in general, the most abundant species are included in the core. The ZACK and PETA cores also share a similar structure: the MDS ordination locates two distinct clusters within the core of plant species (groups of squares in fig. 8.5) at each of the two sides of the pollinator cluster in the center. Thus, ecological factors such as phenological variation presumably contribute to the location of a particular species within the complex network of interactions. A future research line would be to explore the ecological correlates of differences in these locations among species and whether there are predictable traits shared by the core species.

Network Structure: Nested Patterns

In the preceding sections, we have described patterns in connectivity distribution. This is a first step toward a description of the structure of plant-pollinator networks. To some extent, this has revolved around the level of generalization and specialization in these networks. As noted, the pollination webs are more heterogeneous than random webs; that is, there are species more connected than what would be expected to randomly occur. However, nothing has been said about the likelihood of interaction between two species (i.e., a generalist and specialist). For example, consider two focal species and their interactions. Are the interactions common in both subsets? Our next step in the description of the pattern of plant-pollinator assembly is not just to quantify the number of connections but also to look at their identity (Dicks et al. 2002). This is related to one of the classic questions in community ecology: whether networks of ecological interactions (e.g., food webs) are compartmentalized (Pimm and Lawton 1980).

One concept that captures network structure, and that recently has been introduced to the study of mutualisms, is nestedness. However, the concept of nestedness is not new in ecology. It was developed in the context of island biogeography to describe a specific, nonrandom pattern by which a set of species is distributed within a set of islands (Atmar and Patterson 1993). Bascompte et al. (2003) introduced this concept to the study of mutualistic interactions by imagining that plants are "islands" that a certain number of animal species "inhabit."

Nested matrices are organized as in Chinese boxes, with sets of species within larger sets of species. This nested structure has two important features. First, it generates highly asymmetric interactions. This can be seen by the fact that, as indicated in figures 8.1A–8.1C, specialist species tend to interact with the most generalist species (see also Minckley and Roulston, chap. 4 in this volume; Vázquez and Aizen, chap. 9 in this volume; Petanidou and Potts, chap. 10 in this volume). Second, nestedness implies that there is a core of taxa with a high den-

sity of interactions. In other words, generalist plants and generalist animals tend to interact among themselves. Thus, nestedness implies asymmetry at the level of specialists but symmetry at the level of generalists. The fact that generalist species interact among themselves creates a very cohesive structure—understood as a structure with redundancy, that is, multiple ways to connect the species within this “core.” In figure 8.5, we plot the plant and animal species that constitute the core of specific mutualistic networks. As noted, a few species contain the bulk of interactions and cohesively build the rest of the network around themselves; they are “central” to the network and, thus, have high centrality values.

Our quantitative measures of nestedness for natural networks are summarized in table 8.1 (see Bascompte et al. 2003). Nestedness values range between 0 and 1, as measured with the nestedness calculator (Atmar and Patterson 1993). Once a measure is provided to characterize each community, we have to put this measure in context. How nested is a given community? Is it more nested than expected? Or is its value of nestedness similar to what we would expect for a randomly assembled matrix? This is a crucial question. If the value of nestedness is nothing more than what we would expect to occur by chance, then there is no biological pattern to explain. Answering this question depends on having an appropriate null model. Null models have been widely used in community ecology as a way to check whether an observed level of structure can be reproduced by simple rules (Gotelli 2000). Null models have been used in the context of plant–pollinator networks to explore whether levels of generalization and specialization are higher than expected by chance (see Vázquez and Aizen 2003, chap. 9 in this volume). Two different null models have been used to test the significance of the nested patterns. In null model 1 (the one provided by the nestedness calculator), all cells in the matrix have the same probability of being occupied—a probability estimated as the number of interactions divided by the total number of possible interactions (i.e., the connectivity). On average, each replicate will have the same number of connections but these will be randomly distributed. Note that this null model assumes that each species has the same probability of having an interaction; clearly this is not the case in plant–pollinator networks. In the preceding section, we have seen that the degree of distribution is highly skewed. How can we incorporate this fact into a null model? In null model 2, the probability of two particular species interacting is the average of the probability of interaction of both the plant and the animal; that is, the probability of a link is proportional to the degree of both plant and animal species. These two null models are very similar to those of Vázquez and Aizen (2003). Null model 1 is the same with the small difference that Vázquez and Aizen (2003) have the additional constraint that all species must have at least one interaction. Their null model 2 also has a specific probability of interaction for each pair of species—an average of the “presence” of both species. However, they use the frequency of visits by each species (as opposed to the degree) as a measure of “abundance.”

Because there is a strong relationship between degree and frequency of visits (Vázquez and Aizen 2003, chap. 9 in this volume; D. Vázquez, personal communication; see also Jordano 1987), their null model 2 is essentially the same as that of Bascompte et al. (2003). However, from a conceptual point of view, Vázquez and Aizen (2003) define their null model at the individual level instead of at the species level; that is, individuals are the key elements involved in mutualisms. Generally the ideal situation would be to test significance of results with a suite of null models with increasing levels of complexity. This exercise would tell us what is important and what is irrelevant in producing an observed pattern.

The study by Bascompte et al. (2003) showed that the bulk of mutualistic networks are significantly nested; that is, they are much more structured than similar, randomly constructed networks based on either null model (fig. 8.2). Second, there were no significant differences between the level of nestedness for both plant–pollinator and plant–disperser networks, which, together with the result outlined in preceding sections about the pattern of connectivity distributions, suggests invariant properties in these two types of mutualisms. That is, there are conservative patterns of network assembly independent of the biological detail of the interaction, network size, latitude, and other differences—these patterns are very robust.

The implications of the nested pattern can be seen from the points of view of both community assembly and coevolution. From the point of view of community assembly, these patterns unambiguously show that mutualistic networks are neither randomly assembled nor compartmentalized. This is probably the best evidence for a pattern in networks of ecological interactions. The nonrandom pattern of these webs may be very relevant. From the pioneering work by May (1972) and Pimm and Lawton (1980), it was clear that the structure of food webs highly affects their stability. May (1972) used randomly assembled food webs in his influential study about the relationship between stability and complexity. However, at the end of the paper, he assumed that real food webs are probably not random and suggested that they may be organized in compartments. This structure assumes that species within the compartments are highly interactive, whereas there are almost no interactions among different compartments.

May (1972) explored compartmentalized food webs and concluded that they were more stable than random ones—a result challenged by Pimm and Lawton (1980), who found the opposite result when food webs are more realistically built. Interestingly enough, the concept of compartmentalization became entrenched, and subsequent papers have looked for compartmentalization in real food webs, but with poor results. For example, both Pimm and Lawton (1980) and Raffaelli and Hall (1992) failed to find compartmentalization, although some limited evidence exists (e.g., Dicks et al. 2002; Corbet, chap. 14 in this volume). Nestedness can be understood as the most significant and widely observed nonrandom pattern in networks of ecological interactions.

The two properties of nestedness (asymmetry and the core of interactions) may greatly affect the robustness of the mutualistic networks (see also Memmott et al. 2004). First, because specialist (and generally rare) species interact with generalist (and generally abundant) species, nestedness provides higher chances for the persistence of rare species. Second, due to the cohesive role of the core of species, with its redundancy of interactions, nestedness provides alternative routes for system responses after perturbations such as the elimination of a species or a link. Another element for robustness is the generalized broad-scale distribution of the number of interactions per species that we report, which seems to be a general pattern in plant–animal interaction networks (Jordano et al. 2003). Networks with broad-scale distributions of connectivities are generally thought to be more robust to loss of highly connected nodes than scale-free networks (Amaral et al. 2000). Figure 8.6 shows a simple simulation of the effects of species loss on the persistence of connectivity patterns in two plant–pollinator networks. We simulated loss of either plants or pollinators in decreasing order of their number of interactions (i.e., in decreasing order of their eigenvalue centrality). For each node (species) removed, we estimated the preserved connectance as a fraction of the original connectance. The results show that increasing the fraction of nodes removed can dramatically affect the connectivity of the network and its persistence. Removal of a relatively small fraction of the most connected nodes (more than 20%) can cause a collapse of the network (KAT1, fig. 8.6) or the loss of almost 50% of the interactions (CEP3, fig. 8.6). In both cases, the network is more robust to loss of pollinator species and more sensitive to loss of plant species. It is interesting that KAT1, a scale-free network, was less robust to the loss of plant species, confirming expectations of models for abiotic networks (Barabási and Albert 1999; Albert et al. 2000; Barabási et al. 2000; Jeong et al. 2000; Albert and Barabási 2002). CEP3, a broad-scale network, appeared more robust, especially to the loss of plant species. These preliminary results suggest ways to explore the robustness of plant–pollinator networks to species loss, to invasion by exotics, or to overall simplification due, for example, to agricultural practices or human intervention (Kearns et al. 1998; Memmott and Waser 2002; Memmott et al. 2004).

Concluding Remarks

Plant–pollinator networks are complex webs that share many properties with other types of networks, both abiotic and biotic. The most characteristic property is that interactions among species are not distributed at random, but, surprisingly, the nonrandom pattern we found is largely invariant across different ecological settings. This reveals very general patterns in the way interactions are assembled in these communities and suggests important clues to understand their evolution. Moreover, it demonstrates that these networks are more than the addition of pairwise interactions: it is the whole set of pairs of species in both

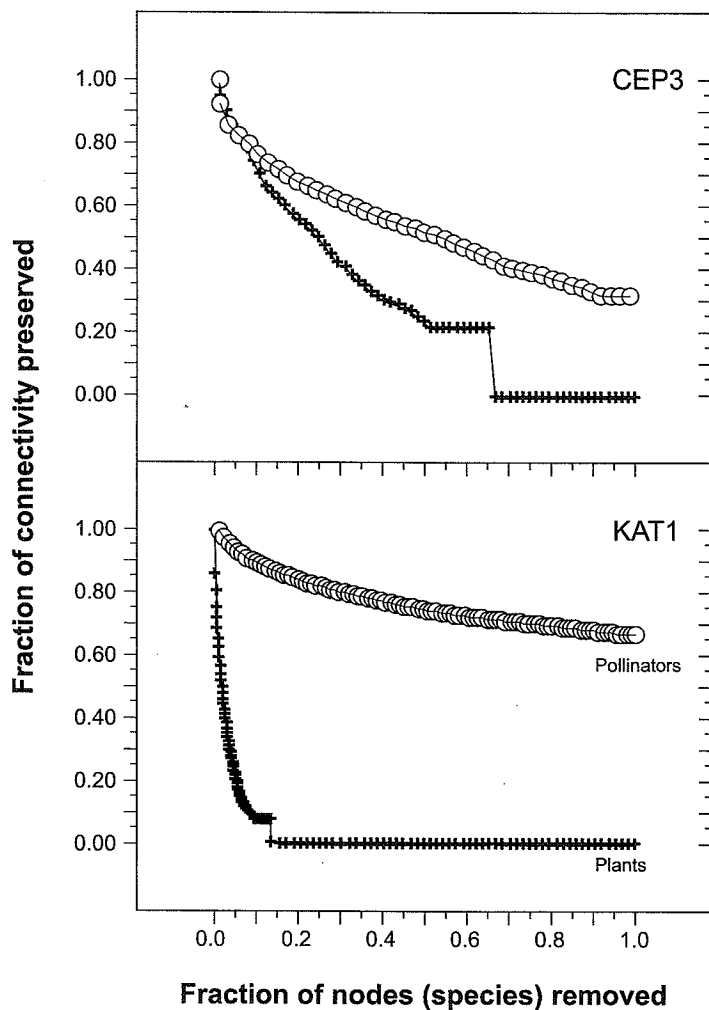


Figure 8.6 Decay in connectance as a function of removal of species in plant-pollinator networks. We simulate the loss of an increasing fraction of either plant (+) or pollinator (o) species (abscissa) by removing species, step by step, according to their decreasing k , value, starting with the most generalist species. The ordinate represents how well the original connectivity of the network is preserved; it is estimated as the fraction of the actual connectance (degree) that the network would have after the loss of a given fraction of species (nodes). We use two examples of networks which illustrate the most general pattern: CEP3—Cordón del Cepo, in the Andes, Chile—with $S = 107$ species ($A = 64$, $P = 43$); and KAT1—Ashu, Kyoto, in temperate Japan—with $S = 770$ species ($A = 679$, $P = 91$).

the pollinator and plant sets that becomes organized in a complex way. This organization has both topological and structural aspects relevant to understanding its evolution.

First, a wide range of interactions per species occurs, but these interactions are predictably distributed according to truncated power-law or power-law models.

That is, the probability of finding a particular species interacting with k other species decays as k increases. Therefore, it is unlikely to find supergeneralists, but they do exist. The presence of these highly connected nodes is less frequent than what would be expected had plant-pollinator networks evolved similarly to other complex abiotic networks. Whenever such a network evolves by preferentially attaching new nodes to the already well-connected ones, a power-law (scale-free) distribution of connectivities emerges. But plant-pollinator networks differ from these because the probabilities for the most-generalist species lie below those expected from a scale-free network. We found few plant-pollinator networks that fit the power-law distribution of k values, and this was generally for the pollinator interactions, not the plant interactions. Therefore, biases due to sampling design (e.g., plant centered vs. pollinator centered) probably should be taken into account in future studies.

Second, a pervasive feature of complex plant-pollinator networks is that they are not randomly built but show a characteristic distribution of interactions throughout the matrix: interactions pivot around a core of species generated by the fact that interactions show a markedly nested pattern. From the point of view of coevolution, the nested assembly has very important implications. It clearly shows that mutualistic interactions are neither organized in specific pairwise interactions, as the ones expected for symbiotic mutualisms, nor organized as a "diffuse" assembly that precludes any analytic approximation. Traditionally, scientists have expected to find the pattern of pairwise specialization observed in symbiotic mutualisms when dealing with nonsymbiotic mutualisms. The lack of such evidence has led to the alternative view that plant-pollinator systems are "diffuse." Nestedness illustrates a highly structured assembly pattern that does not correspond to either of these two extreme views. The core of interactions may drive the coevolution of the rest of the species attached to it. It is a coevolutionary "vortex" sensu Thompson (1994). Bascompte et al. (2003) have reported a pattern in which specialists interact with generalists and generalists in turn interact among themselves. The finding of a nested pattern greatly advances the knowledge of plant-pollinator systems obtained simply by counting how many species are specialists and how many are generalists. Thus, viewed from a network perspective, the centrality of a given species relates not only to its own generalization level but also to how central are the other species with which it interacts. Combined with the results on the connectivity distribution (Jordano et al. 2003), this creates a scenario in which plant-pollinator communities are highly structured. The observed pattern delineates their "topology" and "architecture."

The nested structure of mutualisms contributes to other recent approaches, such as the geographic mosaic of coevolution (Thompson 1994), to bring tractability to the complexity of coevolutionary interactions. Whereas the emphasis in the geographic mosaic theory is in the geographic structure, with possible specific interactions at local scales but global interactions with a larger

number of species at a global scale, our results indicate structure within local communities. Both views are in fact related, nestedness being eminently a geographic idea (Patterson and Atmar 1986). Further studies should elucidate how the geographic (i.e., among communities) and the local (within communities) nestedness patterns are related and contribute to the maintenance of biodiversity.

A future avenue for research should explore the phenotypic and phylogenetic correlates of variation in k among species, the phylogenetic diversity of core species, and whether there are repeated patterns among networks. For instance, are the species at the core of interactions, with the highest centrality, a random subset of the morphospace in the community? Thus, do the species at the core define a distinct morphological type, either in the range of corolla or pollinator morphologies? In addition, a network-based approach to plant–pollinator interactions could increase our predictive power for the effects of exotic species in the networks and in the evolutionary dynamics of these communities (Memmott and Waser 2002). These aspects are central to our understanding of the resilience of these mutualisms to species loss. Our simple simulations showed that networks might collapse with the loss of even a small fraction of species, especially if these are plants (for a somewhat contrasting view see Memmott et al. 2004). Therefore, understanding the geographic variation of interaction matrices will greatly contribute to clarifying potential effects of fragmentation on plant–pollinator communities. Techniques for rapid assessment of plant–pollinator interaction matrices will be rewarding for the design of conservation priorities for preserving the whole network of interactions. Differential robustness to the loss of plants or pollinators can ultimately be related to their positions within the network and their role as core species in these mutualisms. All these findings point to interactions as a major component of ecosystem biodiversity—indeed, they themselves are perhaps the architecture of biodiversity.

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