

Chapter <#> - Cover sheet

The ecological consequences of complex topology and nested structure in pollination webs

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"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."

"*A Propos of Measuring a Mobile*" by Alexander Calder
unpubl. MSS, 1943, The Calder Foundation, New York

Introduction

The extraordinary series of "mobiles" created by Alexander Calder provide a vivid illustration of how the dynamics of interconnected parts depend 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 sculpture in equilibrium while moving suspended in the air (Calder and Davidson 1966). This equilibrium depends on both the number and sizes of pieces and the way they are connected among them, not only pairwise, but collectively.

In nature, networks of species interactions are the architecture of biodiversity, because community dynamics deeply rely on the way species interact. Pollination by animals is one of the commonest ways 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 where >80 % of the 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 have been 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 assure 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 looked at pollination interactions between animals and plants as paradigmatic of mutual specialization. However, when one considers community-wide patterns,

e.g., 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 a lasting debate about how generalized or specialized are pollination interactions. The debate stems on the difficulty to assess completely the full range of biotic interactions within highly-diversified communities and unfolds into the difficulties of quantifying generalization at 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 interactions at the community level. For instance, the possibility for a rare species to persist within a diversified community might depend on a similar extent on its ability to develop specialized interactions with an specialist pollinator or on the sharing of pollination services from generalists. The robustness of a network of interactions (i.e., the ability of the component species to persist given the extinction of a partner) might depend on the pattern of shared interactions, and not uniquely on the 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 (Albert and Barabasi 2002; Strogatz 2001), and general patterns are starting to emerge pointing to interesting properties shared by many types of networks. Recent findings revealed consistent patterns in their structure, irrespective of the type of network, e.g., similarities between abiotic and biotic networks (Newman 2003). These networks share a structure of nodes (elements or parts) linked by connections among them. The links among nodes establish the fundamentals of the architecture of the network, the pattern of connectivity among nodes and the resulting relationships among them (Fig. 1). In general, the frequency distribution of the number of links per node has been reported to decay as a power-law (scale-free), broad-scale (i.e., truncated power-law distributions) or faster-decaying functions (i.e., exponential) (Amaral et al. 2000; Strogatz 2001). These generalized patterns have implications for the evolution, stability, and resilience to perturbations of these networks (Albert and Barabasi 2002; Barabasi and Albert 1999; Dorogovtsev and Mendes 2002). For example, exponential functions describe randomly-assembled networks, while power-law distributions result from predictable build-up processes (Barabasi 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 with sufficient resolution are available (Dunne et al. 2002; Montoya and Sole 2002; Williams and Martinez 2000). 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 to influence their coevolution. Considering plant-pollinator interactions at the community level is important for several reasons. First, the evolution of pollination adaptations in floral traits does not result from the sum of pairwise interactions between plant and animal species; rather, it results from community-level processes involving the interaction of groups of 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 way multi-species 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- illustrating the interactions among species (nodes or vertices) in the two sets of 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 the robustness to the loss of species. Taken together, these findings point to very general patterns of generalization-specialization gradients that pivot on shared topological and structural properties of how interactions in complex species assemblages are built.

Definitions and methods

Plant-pollinator records are typical two-mode data (Borgatti and Everett 1997) where the relations among two sets of entities (here, the sets of plant and pollinator species) are described

(Fig. 1A). Most, if not all the interactions included can be considered as mutualistic interactions, where both the animal and plant partners obtain a benefit; clearly, a gradient of types of effects exists (Thompson 1982) in such a diverse array of interactions, ranging from completely beneficial to close to antagonistic. In any case, 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 connecting 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 degree would represent the number of interactions per species. Bipartite graphs are the visualization of two-mode data, the relationships among nodes in two distinct sets, and they are properly described by means of interaction matrices (Fig. 1A). 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 describing 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 1, if an interaction has actually been recorded (Fig. 1A, C).

Thus, this matrix has k nonzero elements (a_{ij}) wherever plants are pollinated by flower-visiting animals that harvest pollen, nectar or fruits. The matrix R would have $A+P$ nodes or vertices (species) and k links among them (Fig. 1A, C). These are typically sparse matrices (Boisvert et al. 1997; Duff et al. 1986), i.e., matrices with a significant number of zero elements. The matrix of interactions captures the essence of interaction patterns at the species level within a given community. Whenever two species are recorded 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; also see Laska and Wotton 1998; Vázquez and Aizen 2004). Clearly,

any non-zero element of the matrix can be weighted by a value depending on the net effect of the interaction. In this case the matrix will 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. 2003; Vázquez and Aizen 2004). 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. 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 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, 2004).

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 non-random, well defined, subset (see Bascompte et al 2003). Thus, our first approach aims at establishing the number of interactions per species, and our second approach determines 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 been used previously 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 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 depending 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.- the count of the number of links present. This is usually normalized by dividing by the maximum possible, which for our bipartite graphs amounts to $A \times P$. This variable is frequently called connectivity or connectance of the network. Usually, large sparse matrices illustrating plant-pollinator interactions 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.- This measures different aspects of how a given network is centered on particular nodes, i.e., whether ‘central’ nodes exist to which others are connected. Generalist species represent nodes of plant-pollinator networks with high centrality; they show 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. Several measures of centrality can be considered and here we focus on two. 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 2-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 as 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 similar way as 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_i , fitting three different models: a) exponential, $P(k) \sim \exp(-\gamma k)$; b) power-law, $P(k) \sim k^{-\gamma}$; and c) 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. 3B). 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. 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. We examined the best fit to different models (Jordano et al. 2003) by examining the F values and associated adjusted- R^2 values. These distributions are not fully described by a characteristic scale and are called scale-free and broad-scale, respectively. They are more heterogeneous than random networks, since the cumulative distribution of k_i has longer tails. Thus, despite the fact the bulk of species have few interactions in these networks, a few species have much more interactions than randomly expected.

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

Centralization.- The previous variable of centrality characterizes the location of individual nodes or species. 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 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 so that they share more links among them than with the remaining of the 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 maximum 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., row-wise sorting the matrix); then we sort column-wise from the most generalist to the most specialized plant species (Fig. 1C). The way interactions are distributed among species yields nested patterns whenever species with fewer interactions appear 'included' within those with more generalized interactions (Fig. 1C). That is, the interactions of more specialized species tend to be a proper subset of the interactions already observed among the more generalists. Thus, the set of interactions recorded for any species is nested within any other more generalist species.

In order to measure nestedness one needs a quantitative measure and a benchmark to compare our observed value to check for significance. In relation to the quantitative measure, this was provided years ago 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 so that nestedness is maximal. In a situation of perfect nestedness, one could draw an isocline, separating the matrix in two parts. In the left-hand side of the matrix, all pairs of species would interact. On the right-hand side of the matrix, there would be no interactions at all (see Fig. 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 to the isocline of perfect nestedness of all the unexpected presences and absences, and it averages this value. Bascompte et al. (2003) use a value of nestedness which is inverse of the temperature T . Since temperature ranges from zero to 100, nestedness can be defined as $N = (100 - T)/100$. Thus, nestedness ranges between zero and one (Table 1). Nested patterns typically yield a core of species acting as a pivot cluster for other peripheral species (Fig. 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. In general, species with high eigenvector centrality are included in the core cluster of the network (Borgatti et al. 1999).

Network topologies

Plant-pollinator networks have typically sparse matrices as best descriptors of their topology (i.e., the way interactions are established among species) (Fig. 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 1; see 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). It seems as if super-generalists are hard

to find, so that the probability of encountering a species with k interactions drops as k increases. The mean number of interactions/species increases with increasing species richness across networks ($\langle k \rangle = -0.08 + 0.139 S$; for the log-transformed data; $F = 7.86$, $df = 1, 27$, $P = 0.009$), but the rate of increase is relatively low and even levels off beyond 150 species (Fig. 3A). This might suggest a bound on the number of potential k interactions a species develops and eventually explain the decrease in connectance with S (see Pimm 2002 for a discussion).

But super-generalists (species with very large k) do exist, and this differs from randomly-built networks, where nodes with large k values simply don't exist (Albert and Barabasi 2002, Vázquez and Aizen 2003). What biotic networks have special in contrast to other complex networks is that the frequency of these super-nodes, with an extremely large number of connections, is lower than expected if the network had a scale-free distribution of k values. Thus, the probability of finding a species with k interactions drops suddenly for a relatively large value of k (Fig. 3B; also see Fig. 2 in Jordano et al 2003). In fact, the upper limit for k (k_{max} ; Table 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., focusing on plant species and documenting the interaction patterns with pollinators. Although the plant-pollinator networks examined so far are reasonably robust to sampling artifacts (Jordano 1987; Vázquez and Aizen 2004) future research should focus on 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 due to variable completeness of the data (Olesen and Jordano 2002; see Golwasser and Roughgarden 1997; D. Vázquez, pers. comm.) and assumptions inherent to the analyses (Vázquez and Aizen 2004).

The distribution of the number of interactions/species is markedly skewed in these networks (Table 1). Most species have k_a or k_p values < 5 and this makes these networks to share a general pattern of a dense core of species which interact with each other surrounded by many species with few interactions, established with those in the core (Fig. 2). We found a number of networks fitting power-law distributions of k values (Table 1; e.g., KAT1 in Fig. 3B) but most were better described by a truncated power-law model (Jordano et al 2003). In a truncated power-law distribution, the probability of a given k value for a species drops with increasing k following a power law function; then, beyond a certain k_x value, the observed data depart from the power law pattern and show a steep decay beyond the k_x cut-off (Fig. 3B, ABIS network; Amaral et al. 2000).

Therefore, from the perspective of the distribution of connectivity, plant-pollinator networks share many aspects and patterns irrespective of the ecological setting. These patterns 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 assembled in the mutualistic assemblages. Irrespective of the size of the network, plant-pollinator mutualisms pivot 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. 2). The pattern not only depends on the distribution of k values among individual species, but also on “structural” patterns that define the distribution of interactions throughout the network (see below).

Biological patterns: beyond the topology of interactions

The truncated distributions of $P(k)$ are not exclusive of these networks and they 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 expected for a scale-free network (Mossa et al. 2002). The ubiquity of truncation in the distribution of the number of interactions/species in plant-pollinator and plant-disperser mutualisms led us to suggest (Jordano et al. 2003) that biological constraints are the main factor explaining the prevalence of truncated distributions. 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. This translates into the interaction matrices in the form of ‘structural’ zeroes, i.e., pairwise interactions that will never be recorded despite intensive study. We can thus expect a sizeable fraction of the non-observed interactions to be caused by these types of constraints. We defined these non-observable 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 frequency distributions of degree? We recently provided evidence for generalized truncation in plant-animal mutualistic networks (Jordano et al. 2003) and argued that whenever a complex network evolves, i.e., by the addition of species, the new species entering the network are constrained in the way they setup their

pattern of interaction with partners. Species-specific traits set limits to the possibilities of successful interaction. This is readily evident from the typically sparse matrices that describe plant-pollinator networks (Fig. 2), so that the presence of actual interactions is 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. 3A). Therefore, forbidden interactions are a major component of the sparse interaction matrices (Fig. 4).

The example of the Snow and Snow (1972) dataset (Fig. 4) exemplifies well the ubiquity of forbidden interactions. They studied the interactions between hummingbirds and plants in Arima Valley (Trinidad; 10° 40' N) for almost 2 years. Connectance is relatively high ($C=0.354$), typical of sub-networks that only include a subset of the pollinator fauna (Jordano 1987). However, there are only 185 interactions out of 522 possible, with 337 interactions not recorded. Fig. 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. 4). This occurs chiefly 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 the pollinator (Fig. 4). Thus, 6 % of the interactions are not observed due to size restrictions, i.e., the beak too short relative to the corolla tube length; 4% can be attributed to the reward per flower too small relative to the size of the bird; and 3% to color restrictions- e.g., *Phaethornis guy* and *Glaucis hirsuta* only forage on red-flowered species.

Obviously, a sizeable fraction of the interactions not recorded cannot be accounted for, and might be related to unknown factors (U, 24 %; Fig. 4) which, among others, include limited sampling effort. In fact, for the Fig. 4 dataset, interactions recorded only once were excluded in the original table, so 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 pers. obs.). They might result simply from an extremely low probability of the interaction actually occurring in nature despite no obvious cause for it not to occur; for instance, when two species are very rare, their probability of interaction, holding other factors, has to be close to zero. We believe that future explorations on the cause of forbidden interactions can shed light to important

factors in the evolution of complex patterns of interaction in species-rich systems. A categorization of forbidden “types” might indicate repeated patterns which are independent of the ecological setting and might help to explain the invariant properties we document. It might 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 which are peculiar to these biotic interactions and that cause network patterns that severely deviate from other complex networks, especially the abiotic networks.

In the previous 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 1), quantify to what extent a particular species has a central role in the network, located as a central actor relative to others that link with it. The mean eigenvector centrality is negatively correlated across networks with species richness ($r = -0.581$, $P = 0.0009$, $N = 29$), meaning that increasingly diverse communities have a lower number of central species. Relatively simple communities have higher connectance and that means each species in one set is connected with a relatively large fraction of the species in the other set. This means that simple plant-pollinator networks tend to be less centralized (Fig. 5) and to be structured as a single core with no central actor. In most cases however (Fig. 5) a number of species can be identified having the highest density of interactions. CEP3 has 16 species (10 plants, 6 pollinators) with eigenvector centrality > 20.0 (Fig. 5; see Table 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, the other peripheral, such that it maximizes the fit to the expected situation where the density of links within each group is maximal and non-existent between groups (Borgatti and Everett 1997, 1999). Thus it 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 1, Fig. 5), a relatively small fraction of species forms the core. In ZACK there are 20 species out of 107 with eigenvector centrality > 20.0 that form the core. In PETA (Fig. 5) the core is composed by 42 species with eigenvector centralities > 10.0 . In CEP3 bees (chiefly syrphids) dominate the core and also *Bombus* sp.; the PETA network core is composed in roughly the same proportions by bees and flies. In the plant set, in general, the most abundant species are included in the core. The ZACK and PETA cores share also a similar structure: the

MDS ordination locates two distinct clusters within the core of plant species (groups of squares; Fig. 5), at each of the two sides of the pollinator cluster in the center (Fig. 5). Thus, presumably ecological factors such as phenological variation 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 previous sections we have described patterns in the connectivity distribution. This is a first step towards 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 randomly expected. However, nothing has been said about how likely two species, i.e., a generalist and specialist, will interact among themselves. 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 to look at their identity (Dicks et al 2002). This is related to one of the classic questions in community ecology, that is, whether networks of ecological interactions (e.g. food webs) are compartmentalized (Pimm and Lawton, 1980).

One concept that captures network structure has been brought recently to the study of mutualisms: nestedness. The concept of nestedness is, however, not new in ecology. It was developed in the context of island biogeography to describe a specific, non-random pattern by which a set of species is distributed within a set of islands (Atmar and Patterson 1993). Bascompte et al (2003) have brought this concept to the study of mutualistic interactions by imaging that plants are “islands” in which 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 Fig. 1A-C, specialist species tend to interact with the most generalist species (see also Vázquez and Aizen 2004). Second, nestedness implies that there is a core of taxa with a high density 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”. Techniques from complex networks allow us to detect this core. For example, in Fig. 5 we plot the plant and animal species which constitute the core of specific mutualistic networks. As noted, a few species contain the bulk of interactions and build cohesively 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 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 a community is? 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 by chance, then there is no biological pattern to explain. Answering this question depends on having an appropriate null model. Null models have been used widely 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 generalism and specialism are higher than expected by chance (see Vázquez and Aizen, this book; Vázquez and Aizen, 2003). 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). Each replicate, on average, 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 previous section we have seen that the degree 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 the ones used by 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 have to have at least one

interaction. Their null model 2 has also a specific probability of interaction for each pair of species. In their case, this probability is also 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.” Since there is a strong relationship between degree and abundance of visits (Vázquez and Aizen 2003, 2004; D. Vázquez, personal communication; also see Jordano 1987), then null model 2 is essentially the same than in Bascompte et al. (2003). However, from a conceptual point of view Vázquez and Aizen (2003) define their null model at the level of the individual, instead of at the level of species. That is, individuals are the key elements involved in mutualisms. In general, the ideal situation would be to test significance of results in front a suite of null models with increasing level of complexity. This exercise would tell us what is important and what irrelevant in producing an observed pattern.

The study by Bascompte et al. (2003) proved that the bulk of mutualistic networks are highly nested. Also, a large fraction of these matrices are significantly nested, that is, they are much more structured than similar, randomly constructed networks (for both null models) (Fig. 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 previous 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 both the point of view of community assembly and coevolution. From the point of view of community assembly, they unambiguously show that these mutualistic networks are neither randomly assembled nor compartmentalized. This is probably the best evidence for a pattern in networks of ecological interactions. The non-random 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, while 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 got fixed, and posterior papers have looked for compartmentalization in real food webs, with poorly results. For example, both Pimm and Lawton (1980) and Raffaelli and Hall (1992) have failed to find compartmentalization, although some evidence exists (e.g. Dicks et al 2002). Nestedness can be understood as the most significant and widely observed non-random 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. First, since specialist (and generally rare species) interact with generalist (and generally abundant species), nestedness provides higher chances for the persistence of rare species. Second, since 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/species that we report, which seems a general pattern in plant-animal interaction networks (Jordano et al. 2003). In general, networks with broad-scale distributions of connectivities are thought to be more robust to loss of highly connected nodes than scale-free networks (Amaral et al. 2000). Fig. 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 connectance preserved, as a fraction of the original connectance. The results show that increasing the fraction of nodes removed can affect dramatically the connectivity of the network and its persistence. removal of a relatively small fraction of the most connected nodes (< 20 %) can cause a collapse of the network (KAT1, Fig. 6) or the loss of almost 50 % of the interactions (CEP3, Fig. 6). In both cases, the network is more robust to the loss of pollinator species and more sensitive to loss of plant species. It is interesting that, confirming expectations of models for abiotic networks (Albert and Barabasi 2002; Albert et al. 2000; Barabasi and Albert 1999; Barabasi et al. 2000; Jeong et al. 2000), KAT1, a scale-free network was less robust to the loss of plant species. 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 to e.g., agricultural practices or human intervention

(Kearns et al. 1998; Memmott and Waser 2002).

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 non-random pattern we found is largely consistent, invariant, in different ecological settings. This reveals very general patterns in the way interactions are assembled in these communities and suggest 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 the pollinator and plant sets that becomes organized in a complex way. This organization has both topological and structural aspects relevant to understand its evolution.

First, a wide range of number of interactions/species occurs but it is 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. So, it is unlikely to find super-generalists, but they do exist. The presence of these highly-connected nodes is less frequent than 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 fitting the power-law distribution of k values, and this was generally for the pollinator interactions, not the plants interactions. So, probably biases due to sampling design (e.g., plant centered vs pollinator centered) 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 pair-wise interactions as the ones expected for symbiotic mutualisms, nor organized as a “diffuse” assembly that precludes any analytic approximation. Traditionally, scientists have

assumed to find the pattern of pair-wise specialization observed in symbiotic mutualisms when dealing with non-symbiotic 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 which does not correspond to any of these two extreme views. The core of interactions may drive the coevolution of the rest of the species which are attached to it. It is a coevolutionary “vortex” sensu Thompson (1994). Bascompte et al (2003) have clearly found 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 just obtained by counting how many species are specialists and how many are generalists. Thus, viewed from a network perspective, the centrality of a given species does not only relate to its own generalization level, but also to how central are the other species with which it interacts. Together with the results on the connectivity distribution (Jordano et al. 2003), this draws a scenario in which plant-pollinator communities are highly structured. The pattern observed 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 the coevolutionary interactions. While in the geographic mosaic the emphasis 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 bring 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 (that is, among communities) and the local (within communities) nested pattern is related and contributes 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 even with the loss of a small fraction of species, specially if these are plants. Therefore, understanding the geographic variation of interaction matrices will contribute enormously to clarify potential effects of fragmentation on plant-pollinator communities. Techniques for rapid assessment of plant-pollinator interaction matrices will be rewarding for designing conservation priorities for preserving the whole network of interactions. Differential robustness to the loss of plants or pollinators can be ultimately 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 are perhaps themselves the architecture of biodiversity.

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Figures

Figure 1. Bipartite graphs as representations of networks, illustrating plant-pollinator interaction networks. A, bipartite graph representation of the interactions among $A = 15$ pollinator taxa, $P = 15$ 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 the 15 plants; plant species #15 is visited only by A. These bipartite networks are similar to e.g., 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 (Açores Islands; Olesen et al. 2002 ; Zackenberg, Greenland, Olesen and Elberling, unpubl.). C, matrix representation of bipartite data. Rows are plant species; columns are pollinator species. Black boxes indicate those pairwise interactions actually documented. C, top left, a perfectly nested matrix, where interactions of the more specialized species are a proper subset of the more generalists' interactions. Top right, a matrix of random interactions. C, bottom, the actual dataset of Zackenberg, Greenland in matrix form. Curve line shows the isocline of perfect nestedness; i.e., all interactions (black boxes) would lie to the left of the isocline if the matrix were perfectly nested (see Bascompte et al 2003).

Figure 2. Examples of community matrices of plant-pollinator interactions. In each matrix, rows are pollinator species; columns are plant species. Dots indicate the presence of a particular pairwise interaction between pollinator species i and plant species j , i.e., dots represent the non-zero elements of the interaction matrices (Fig. 1C). Matrices are sorted column- and row-wise in decreasing number of interactions/species. These are typical sparse matrices, with a significant number of elements $a_{ij} = 0$. Abbreviations for each network, as in Table 1. The axis to the left indicates the scale of the matrices in terms of number of species, either row- or column-wise.

Figure 3. A. Relationship between the mean number of interactions/species, $\langle k \rangle$, and the total number of species (species richness, S) in plant-pollinator networks (Table 1). Dots, tropical communities; +, arctic; open circles, alpine; x, Mediterranean; squares, temperate. Line is the least-squares fit to the log-transformed data. B. Cumulative distributions of the number of interactions/species, or degree, k_i , for the ABIS and KAT1 networks (see Table 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 fit of the distribution to a power-law or truncated power-law models is represented by continuous or dashed lines, respectively. The best fit for the networks analyzed is given in Table 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 k_x value, $k_x < k$, so that there is a “truncation” at large k values.

Figure 4. Patterns of forbidden interactions in a plant-hummingbird sub-network (Snow and Snow 1972). Rows are hummingbird species ($A=9$) and columns are their foodplants ($P=58$). Forbidden interactions are those never observed in interaction matrices i.e., 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 non-observed interactions ($a_{ij}=0$), letters indicate the potential cause for not encountering that interaction: S, size restrictions; H, habitat restrictions, due to habitat uncoupling of birds and plants; R, reward limitation; C, flower colour restrictions; U, unknown reason (see text for detailed descriptions). In general, there are 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 case of migratory pollinators; or when the size of the pollinator mouthparts restricts access to the nectar and pollen.

Figure 5. Examples of plant-pollinator networks with the core of species outlined, as identified by the eigenvector centrality value (2-mode normalized) of each node. Species with eigenvector centrality > 10.0 (PETA network) or > 20.0 (in CEP3 and ZACK networks) are outlined with larger symbols. Circles, pollinator species; squares, plant species. The three networks have cores with 42, 16 and 20 species, respectively. 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 1 for a description of the networks.

Figure 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_i value, starting with the most generalist species. The ordinate represents how well the original connectivity of the network is preserved, 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 but they illustrate the most general pattern; CEP3, Cordón del Cepo, in the Andes, Chile, with $S= 107$ species ($A= 64$, $P= 43$); KAT1, Ashu, Kyoto in temperate Japan, with $S= 770$ species ($A= 679$, $P= 91$).

Table 1. Summary statistics of plant-pollinator interaction networks. 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; $\langle k \rangle$, mean number of interactions/species (degree); $\langle k_a \rangle$, mean number of interactions/pollinator species); $k_{max} A$, degree of most connected pollinator species; $\langle k_p \rangle$, mean number of interactions/plant species; $k_{max} P$, degree of most connected plant species; $\gamma_{Pollinators}$, 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); Centrality, network centrality value; C , connectance, or density of the network; N , nestedness. See Olesen and Jordano (2002), Jordano et al (2003), Bascompte et al (2003) for details.

No.	Code	S	A	P	M	k	$\langle k \rangle$	$\langle k_a \rangle$	$k_{max} A$	$\langle k_p \rangle$	$k_{max} P$	$\gamma_{Pollinators}$	Fit	γ_{Plants}	Fit
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	94080	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	35482	774	1.81	2.46	26	6.85	68	-1.25	a	-0.85	b
16	KAT1	770	679	91	61789	1193	1.55	1.76	25	13.11	188	-1.62	a	-0.62	a
17	KAT2	446	356	90	32040	865	1.94	2.43	24	9.61	65	-1.26	a	-0.79	b
18	KATO	251	187	64	11968	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	87246	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

Table 1 (continued)

No.	Eigenvector	Centralization	<i>C</i>	<i>N</i>		Locality	Source ¹
1	4.01	20.35	0.0854	0.8602	*	Latnjajaure, Abisko, Sweden	Elberling & Olesen 1999
2	26.01	48.68	0.2500	0.6707	ns	Flores, Açores Islands	Olesen unpubl.
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 Natl. Park, Spain	J. 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 Isl., 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, USA	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 & 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

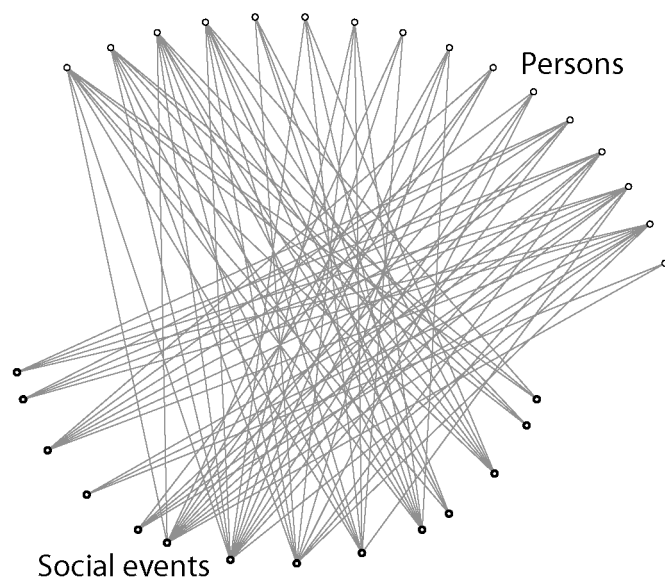
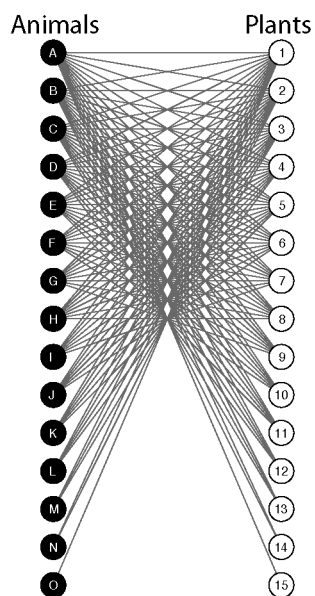
17	2.02	19.97	0.0270	0.9746	**	Mt Kushigata, Japan	Kato et al. 1993
18	2.79	21.88	0.0359	0.9551	**	Nakaikemi, Japan	Kato & Miura 1996
19	9.82	65.25	0.1044	0.9550	**	Hazen Camp, Canada	Kevan 1970
20	11.77	28.45	0.2857	0.8743	**	Mauritius Island	Eskildsen et al. Unpubl.
21	6.29	18.08	0.1919	0.7808	ns	Melville Island, Canada	Mosquin & 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 Nat. Park, Venezuela	Ramirez 1989
28	8.98	50.04	0.2814	0.8668	**	Brownfield, Illinois, USA	Schemske et al. 1978
29	5.37	9.66	0.1935	0.7420	**	Zackenberg, Greenland	Elberling & Olesen MS

Fit: a: Power law, b: Truncated power-law, c: Exponential, d: not available. Best fit determined by the highest *F* and adjusted-*R*² values.

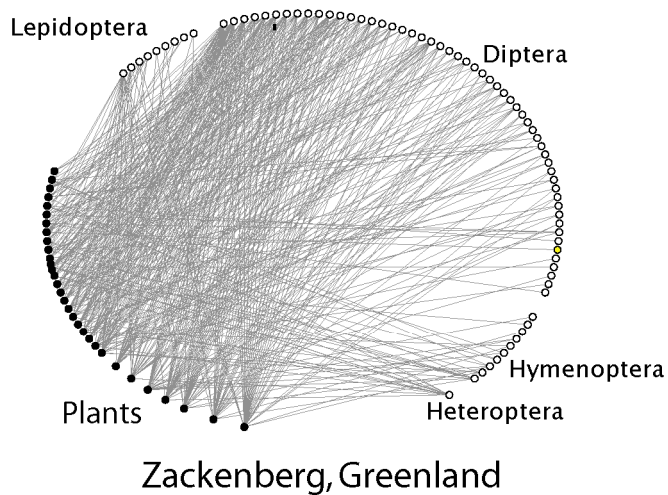
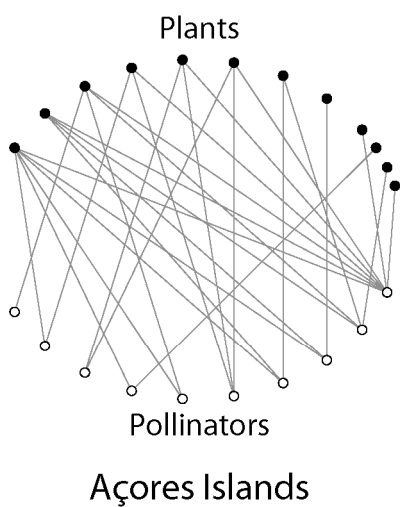
Significance of the nestedness value: *, $P < 0.05$; **, $P < 0.01$; ns, not significant.

¹ For reference list, see Bascompte et al. 2003 and Jordano et al. 2003.

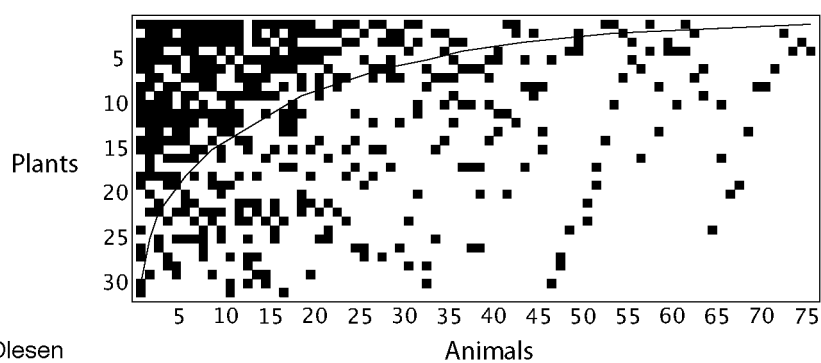
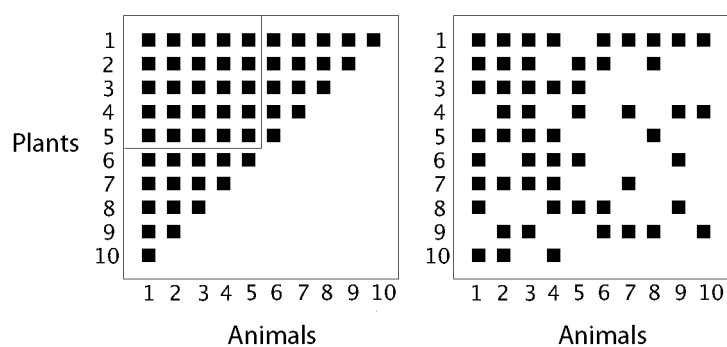
A

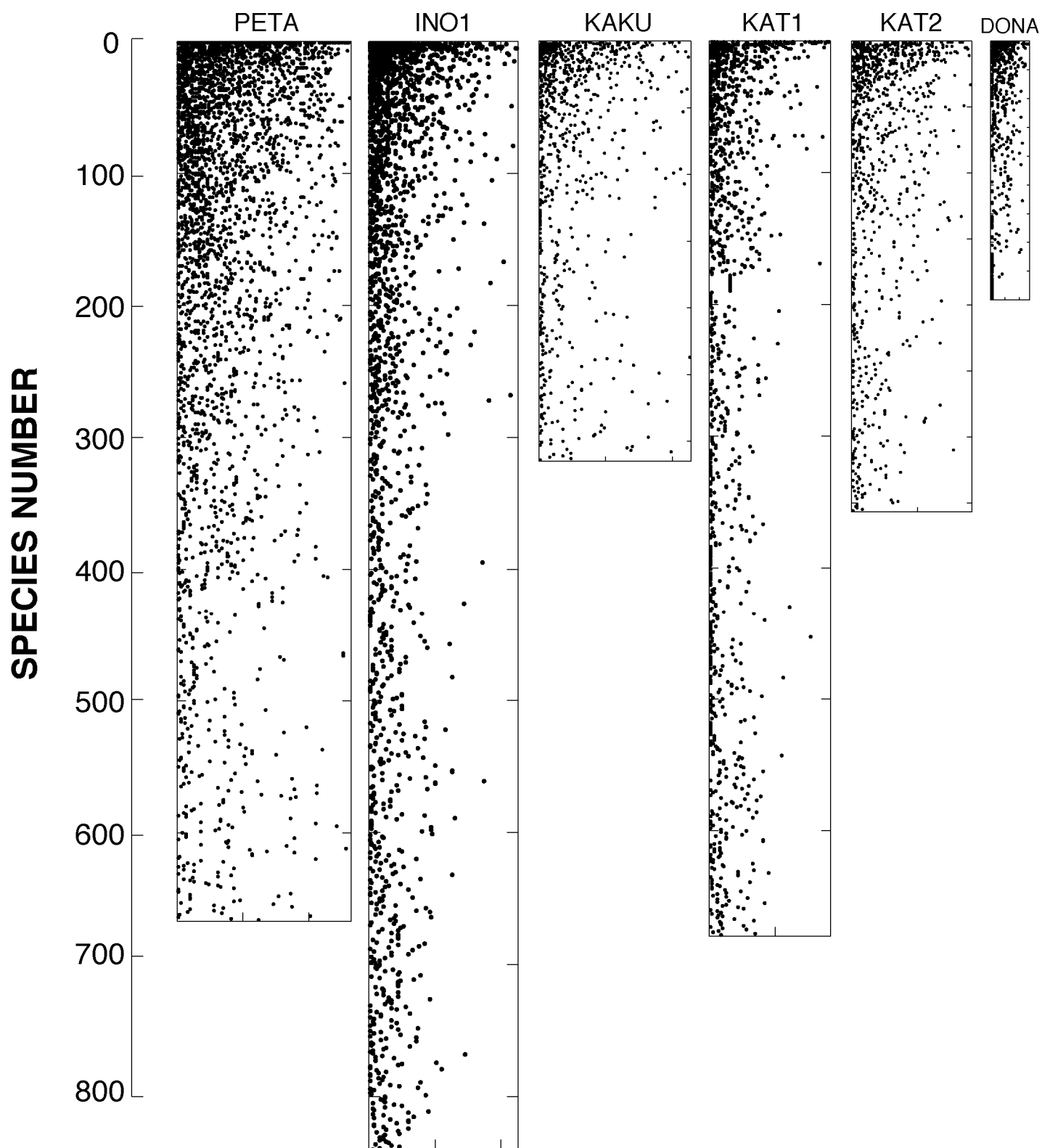


B

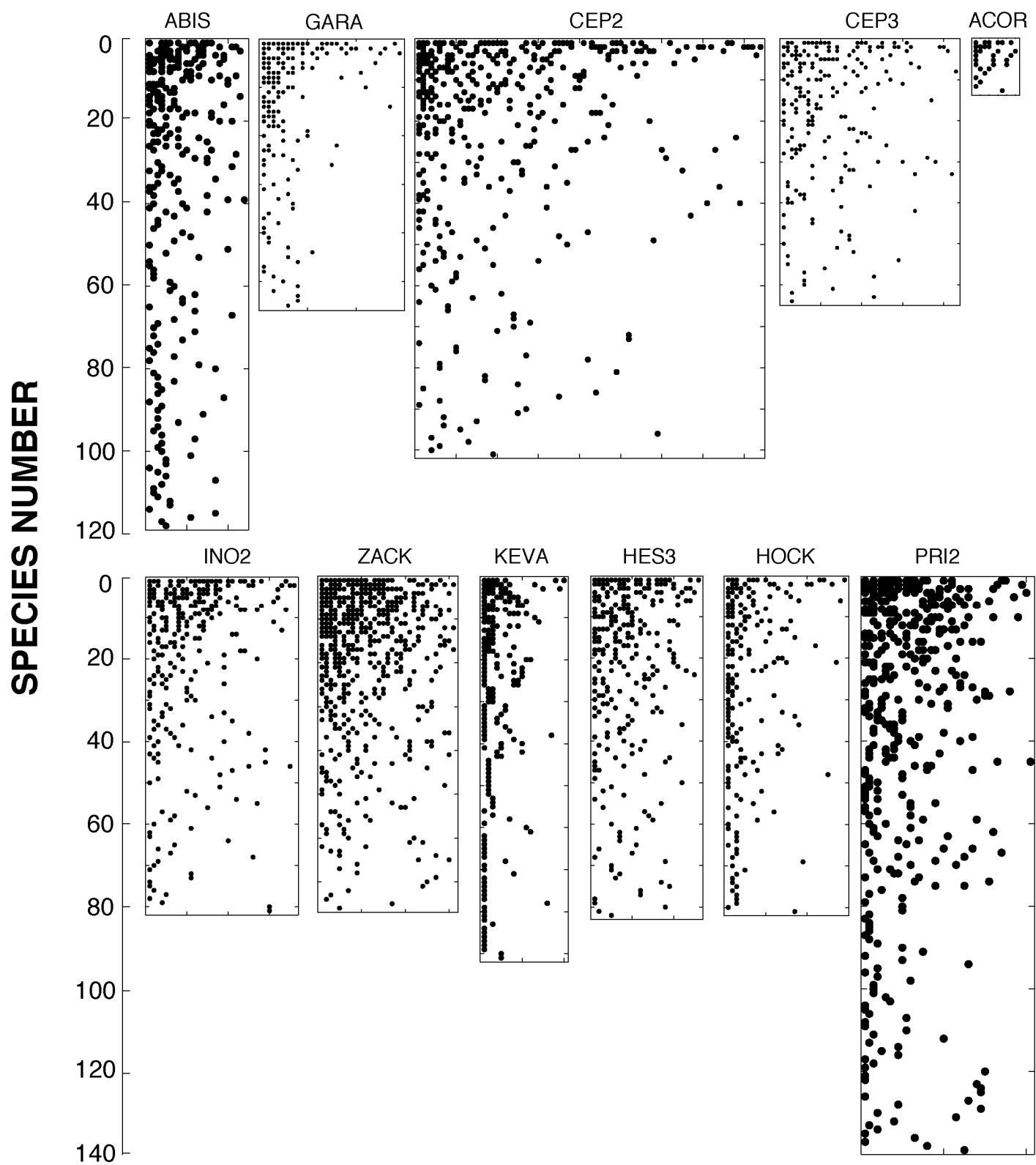


C

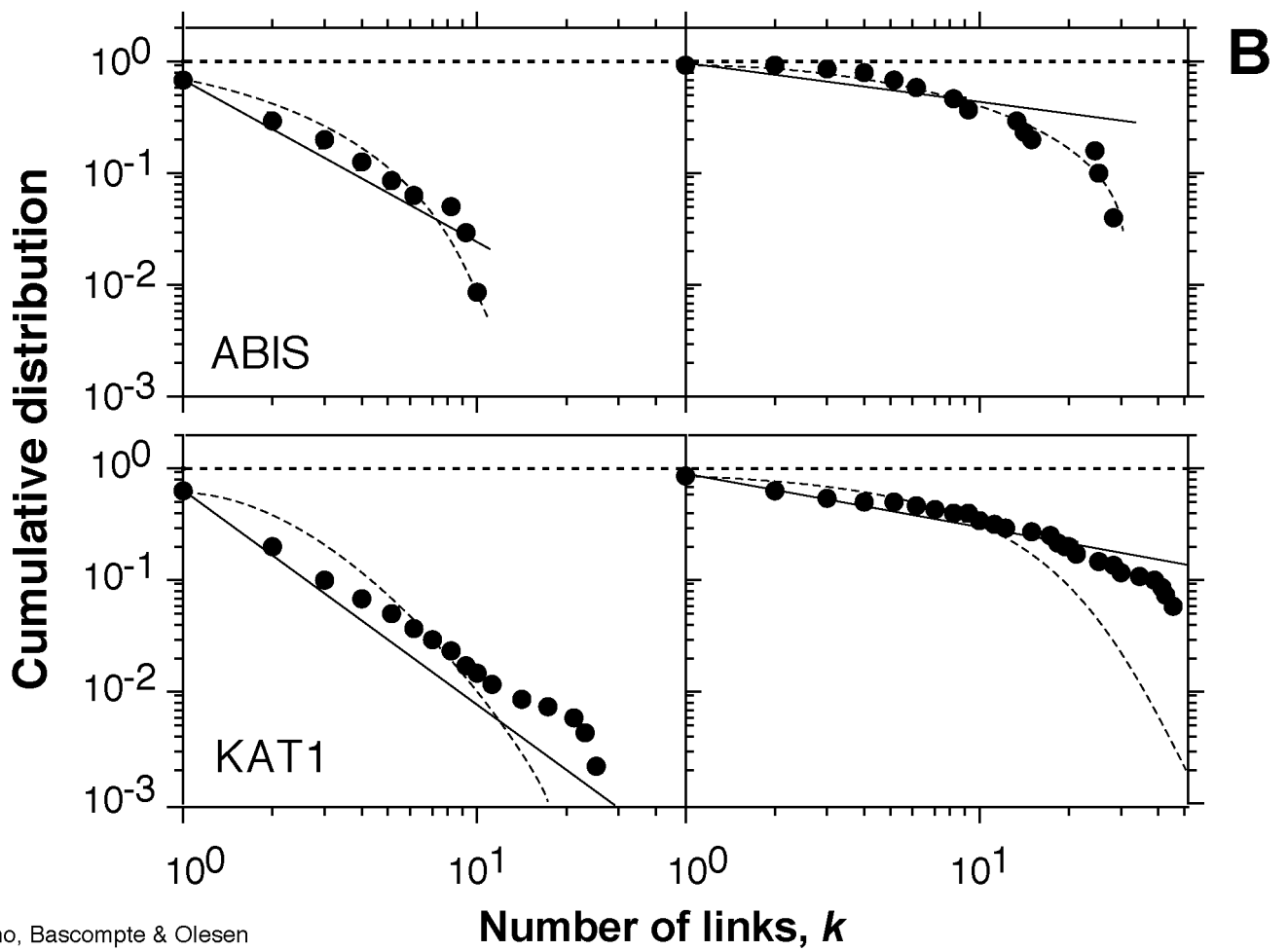
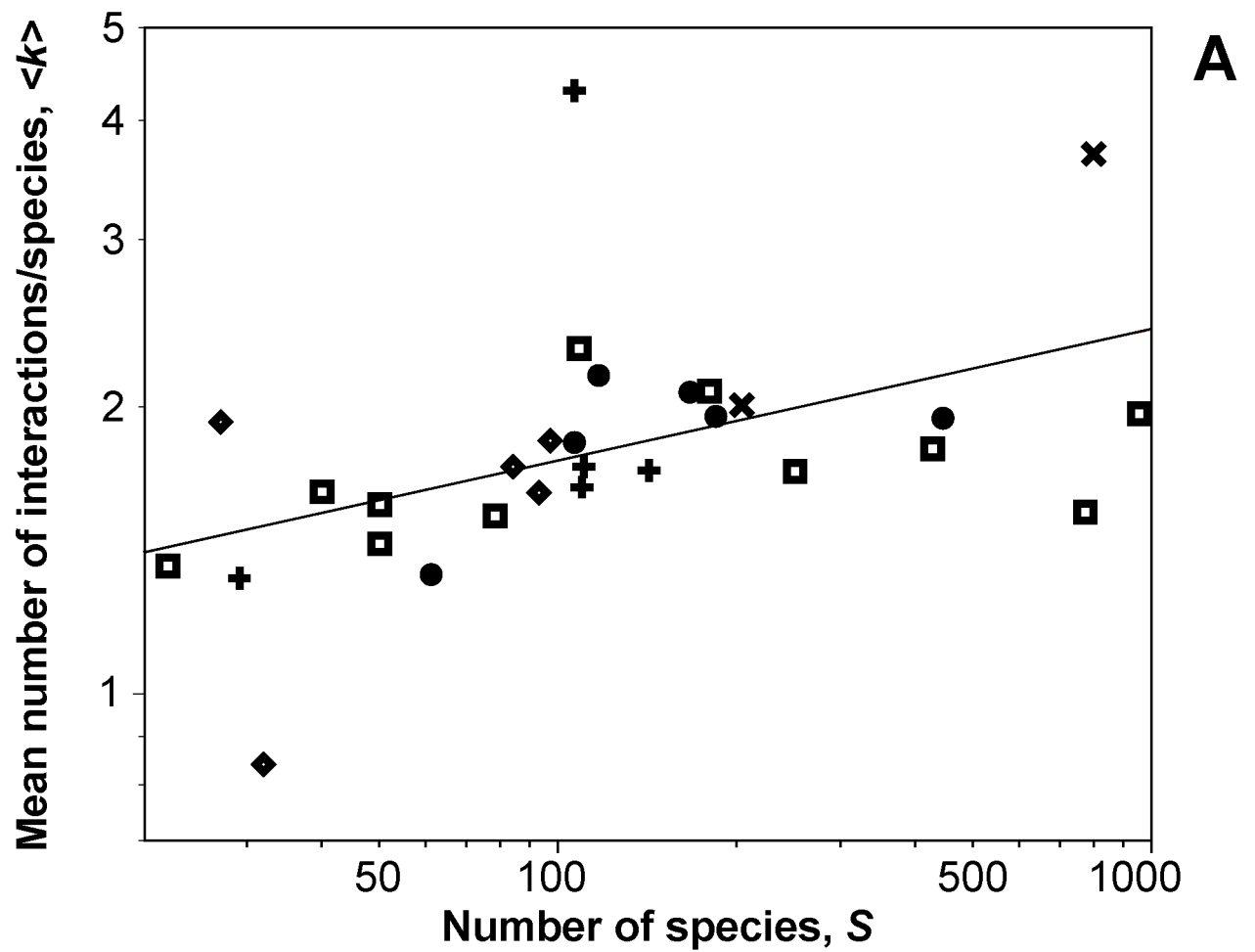




Jordano, Bascompte & Olesen
Figure 2



Jordano, Bascompte & Olesen
Figure 2 (Continued)



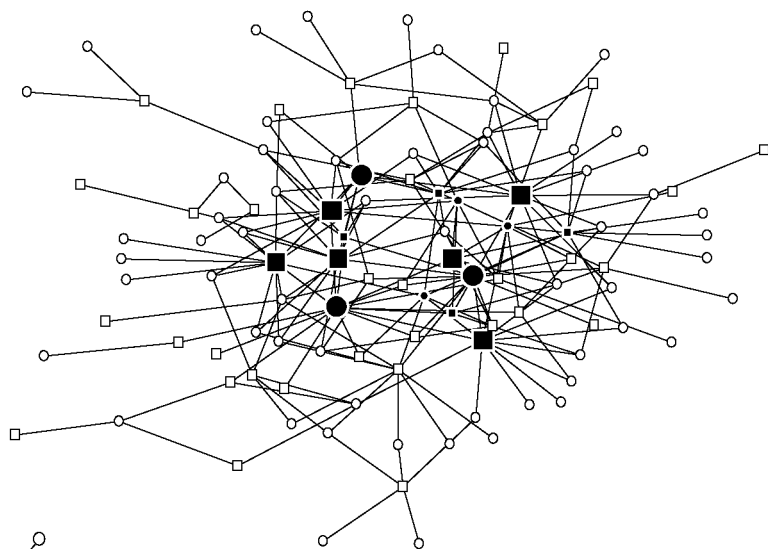
Plant species

	1.	2.	3.	4.	5.	6.	7.	8.	9.	Species
					R			H	H	<i>Iseria parviflora</i>
							C	H	H	<i>Calliandra guildingii</i>
								H		<i>Heliconia bihai</i>
										<i>Norantea guianensis</i>
										<i>Palicourea crocea</i>
										<i>Samanea saman</i>
										<i>Costus spiralis</i>
										<i>Erythrina micropteryx</i>
										<i>Gravisia aquilega</i>
										<i>Gurania spinulosa</i>
										<i>Inga venosa</i>
										<i>Justicia</i> sp.
										<i>Symphonia globulifera</i>
										<i>Doxantha unguis-cati</i>
										<i>Heliconia hirsuta</i>
										<i>Inga ingoides</i>
										<i>Mandevilla hirsuta</i>
										<i>Pachystachys coccinea</i>
										<i>Psychotria</i> sp.
										<i>Ryania speciosa</i>
										<i>Warszewiczia coccinea</i>
										<i>Cephaelis muscosa</i>
										<i>Citrus</i> sp.
										<i>Cordia bicolor</i>
										<i>Corida curassavica</i>
										<i>Duguea hirsuta</i>
										<i>Erythrina glauca</i>
										<i>Guzmania monostachia</i>
										<i>Inga</i> sp.
										<i>Lisianthus chelonoides</i>
										<i>Pithecellobium jupunba</i>
										<i>Tabernaemontana psychotrifolia</i>
										<i>Brownea latifolia</i>
										<i>Centropogon surinamensis</i>
										<i>Aechmea nudicaulis</i>
										<i>Clathrotropis brachypetala</i>
										<i>Erythrina coralodendron</i>
										<i>Eugenia jambos</i>
										<i>Hamelia erecta</i>
										<i>Marcravia</i> sp.
										<i>Psychotria tobagensis</i>
										<i>Renialmia</i> sp.
										<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</i> sp.
										<i>Heliconia psittacorum</i>
										<i>Heliconia</i> sp.
										<i>Ischnosiphon aroma</i>
										<i>Lantana camara</i>
										<i>Tabebuia serratifolia</i>
										<i>Tillandsia fasciculata</i>
										<i>Vriesia procera</i>
										<i>Aegiphila perplexa</i>

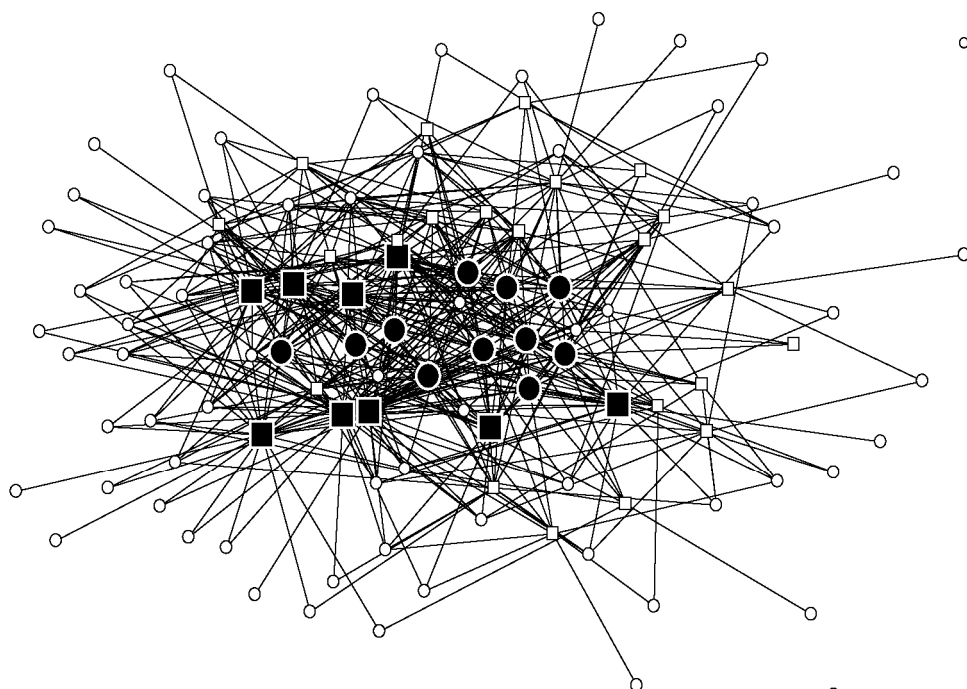
Hummingbird species

- | | | |
|------------------------------------|---------------------------------|--------------------------------------|
| 1. <i>Saurotia tobaci</i> | 4. <i>Amazilia chionopectus</i> | 7. <i>Chrysolampis mosquitus</i> |
| 2. <i>Phaethornis longuemareus</i> | 5. <i>Phaethornis guy</i> | 8. <i>Anthracothorax nigricollis</i> |
| 3. <i>Chlorestes notatus</i> | 6. <i>Glaucis hirsuta</i> | 9. <i>Florisuga mellivora</i> |

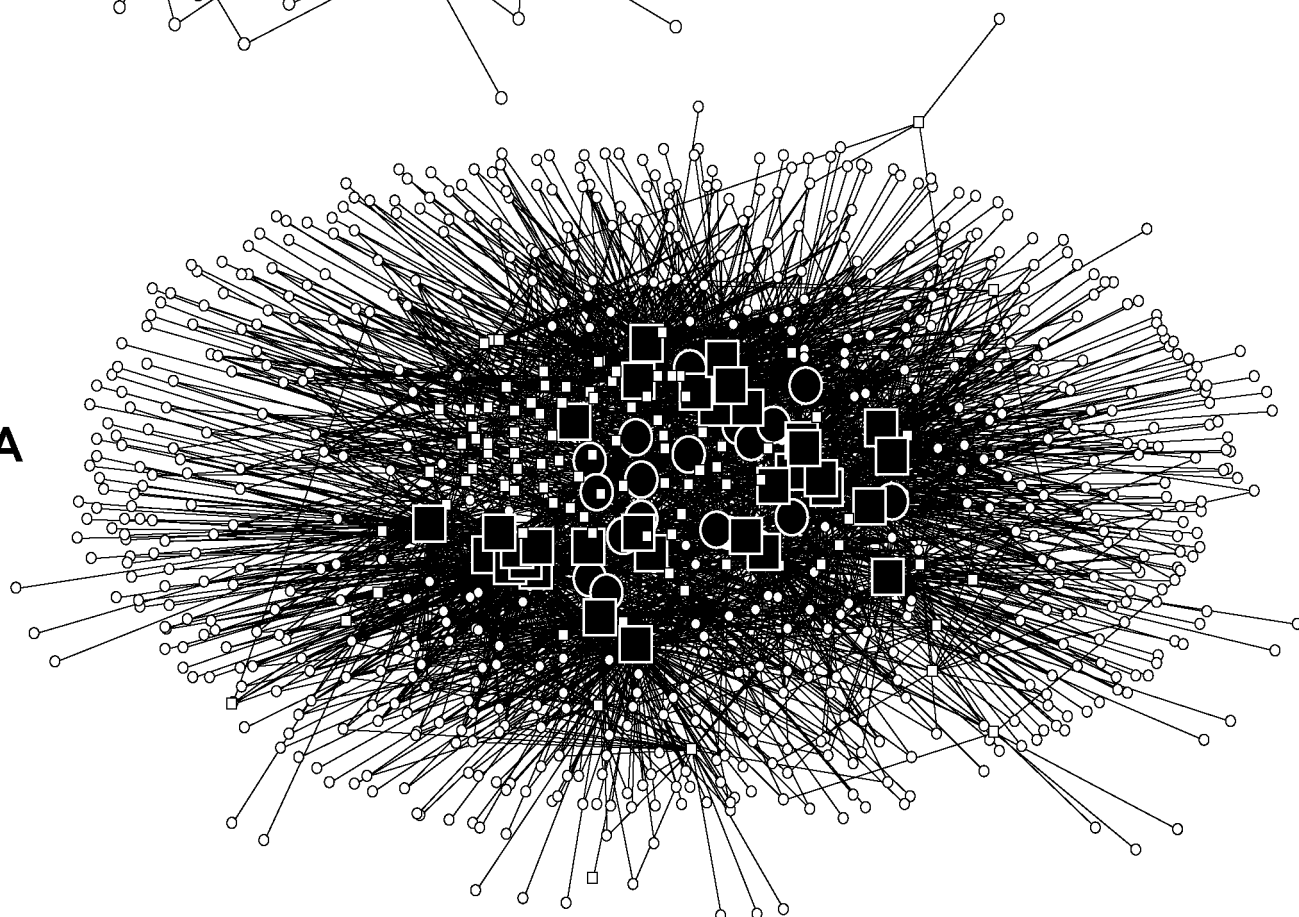
CEP3

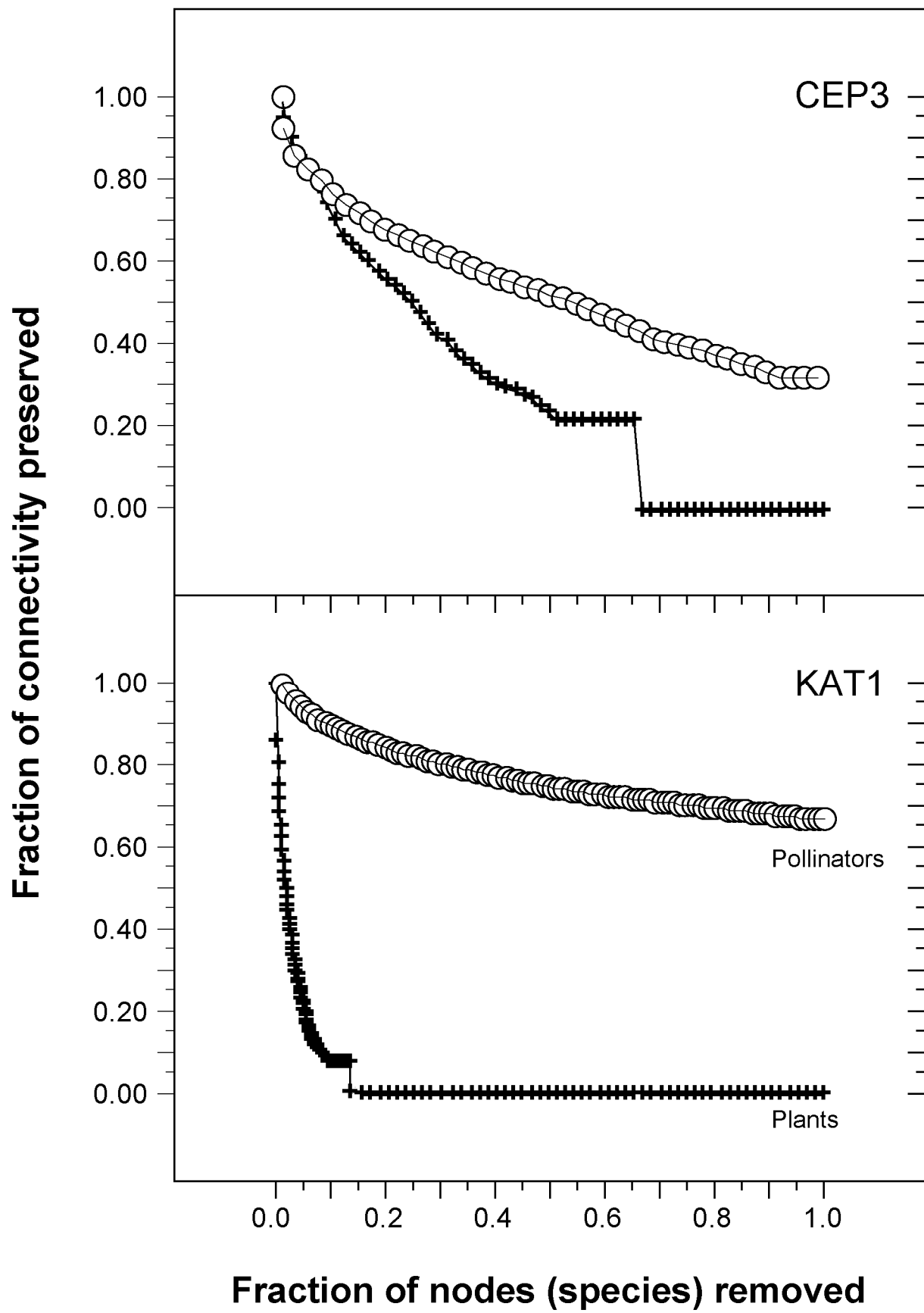


ZACK



PETA





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Figure 6