

REPORT

Invariant properties in coevolutionary networks of plant–animal interactions

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Abstract

Plant–animal mutualistic networks are interaction webs consisting of two sets of entities, plant and animal species, whose evolutionary dynamics are deeply influenced by the outcomes of the interactions, yielding a diverse array of coevolutionary processes. These networks are two-mode networks sharing many common properties with others such as food webs, social, and abiotic networks. Here we describe generalized patterns in the topology of 29 plant–pollinator and 24 plant–frugivore networks in natural communities. Scale-free properties have been described for a number of biological, social, and abiotic networks; in contrast, most of the plant–animal mutualistic networks (65.6%) show species connectivity distributions (number of links per species) with a power-law regime but decaying as a marked cut-off, i.e. truncated power-law or broad-scale networks and few (22.2%) show scale-invariance. We hypothesize that plant–animal mutualistic networks follow a build-up process similar to complex abiotic nets, based on the preferential attachment of species. However, constraints in the addition of links such as morphological mismatching or phenological uncoupling between mutualistic partners, restrict the number of interactions established, causing deviations from scale-invariance. This reveals generalized topological patterns characteristic of self-organized complex systems. Relative to scale-invariant networks, such constraints may confer higher robustness to the loss of keystone species that are the backbone of these webs.

Keywords

Pollination, seed-dispersal, food web structure, coevolution, ecological networks, biodiversity.

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INTRODUCTION

Networks of interactions depict the essence of community assembly: relationships among component species that can take an enormous diversity of patterns and outcomes (Thompson 1982). However, we still have a limited understanding of the consequences of network patterns for ecosystem stability and evolution. Recent research on complex networks has revealed a striking invariance in their structure, with a frequency distribution of vertex connectivity (the number of links per node) that decays 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, specially the power-law (or scale-free) topologies lead to small-world patterns with important implications for the evolution, stability, and resilience to perturbations of these networks (Barabási & Albert 1999; Albert & Barabási

2002; Dorogovtsev & Mendes 2002). In the ecological literature very few data with reasonable accuracy and completeness are available, but the small-world structure, with average path length between species increasing linearly with the logarithm of the number of species (Watts & Strogatz 1998) has been reported repeatedly (Montoya & Solé 2002; Williams *et al.* 2002; but see Camacho *et al.* 2002; Dunne *et al.* 2002b). Both high clustering of species interactions (Montoya & Solé 2002) and low clustering (Camacho *et al.* 2002; Dunne *et al.* 2002b) were reported. However, the food-webs examined so far are community webs of directed links (Cohen 1978; Cohen *et al.* 1990; Pimm *et al.* 1991) illustrating the predominant patterns of trophic, predator–prey interactions, not including all types of web interactions in nature (mutualistic, parasite–host, facilitation, and commensalism interactions), best represented by bipartite graphs of species interactions (Jordano 1987). We thus have only a limited sample of the complex

and diversified patterns of interaction among species in natural ecosystems. Only by considering bipartite graphs (Strogatz 2001; Albert & Barabási 2002) – illustrating the interactions among species (nodes or vertices) in the two sets of animal and plant communities – can we address the potential for variations in network topology to influence coevolutionary processes in high-diversity mutualistic webs.

Plant–animal mutualistic interactions have a pervasive influence in community dynamics and diversity, where they play a central role in the reproduction of the plants and the life histories of the animals. In contrast to the complex food webs examined so far (Bersier *et al.* 1999; Dunne *et al.* 2002a; Williams *et al.* 2002), plant–animal mutualistic networks embed not only the trophic relationships among mutualistic partners (Jordano 1987), but also the complexities of the evolutionary effects on each other that drive coevolutionary processes (Thompson 1999). Thus, a comparative analysis of the topology and patterns of interaction in these networks might shed light on invariant patterns with deep implications for the stability and coevolutionary dynamics of these mutualistic assemblages. For instance, are specialization–generalization patterns consistent among different communities irrespective of the ecological setting and the component species (Waser *et al.* 1996; Olesen & Jordano 2002)? We address the following questions. (1) Are there shared patterns in the topology of plant–animal mutualistic networks, irrespective of whether they are pollination or seed dispersal networks? (2) Do these networks differ from highly complex abiotic and social (‘real-world’) networks in topological properties? (3) What are the implications and biological causes for these patterns?

METHODS

Here we examine the statistical properties of a large sample of well resolved plant–animal interaction networks, including 29 plant–pollinator and 24 plant–frugivore systems (Table 1, Appendix; for details see Jordano 1987 and unpubl. data; Olesen & Jordano 2002), adding to the scarce data on community food webs (Dunne *et al.* 2002a,b; Montoya & Solé 2002). Both pollination and seed dispersal are central stages in plant life, and in many species and habitat types they involve the mutualistic interaction with animal agents that transport pollen or seeds and benefit from plant rewards, such as nectar or fruit pulp (Futuyma & Slatkin 1983). A plant–animal interaction network is here defined as an adjacency matrix **R** describing trophic and reproductive interactions between communities of *P* plant species and *A* plant-visiting animal species (either pollinators or seed dispersers) within a well-defined habitat:

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

$$\text{where } a_{ij} = \begin{cases} 1, & \text{if } P_i \text{ and } A_j \text{ interact} \\ 0, & \text{otherwise} \end{cases}$$

Thus, this matrix has *k* nonzero elements (*a_{ij}*) wherever plants are pollinated or dispersed by flower- or fruit-visiting animals that harvest pollen, nectar or fruits. In contrast to the food web networks, made up by directed links among species, mutualistic interactions are two-mode networks with *S* = *P* + *A* vertices and *k_i* edges, or interactions, per vertex (Fig. 1).

Table 1 Best fit models to the distributions of links per node in plant–animal mutualistic networks and other real networks

< <i>S</i> >	< <i>k</i> >	<γ>	Set	Truncated power-law	Power-law	Exponential	No fit
Plant–pollinator networks							
108 [22–952]	1.7 [0.8–4.3]	1.23 ± 0.04	Animal	13	14	1	1
		0.84 ± 0.04	Plant	21	4	4	0
Plant–seed disperser networks							
32 [17–110]	2.5 [1.3–4.2]	1.12 ± 0.13	Animal	22	4	3	4
		0.82 ± 0.12	Plant	8	1	3	1
Social networks							
5.20 × 10 ⁵	14.5 [1.9–287.8]	2.45 ± 0.15	–	3	14	1	0
Abiotic networks							
2.62 × 10 ⁷	2.1 [1.3–7.9]	2.27 ± 0.08	–	0	15	1	0

Plant–pollinator and plant–disperser networks are two-mode networks, and the fits are given for the plant and animal sets separately. Plant–pollinator networks (all of them are complete webs, not sub-webs): 29 webs including a total of 1271 plant species (range: 7–131) and 4575 animal species (range: 12–840) (Olesen & Jordano 2002). Plant–seed disperser networks: 24 webs including a total of 510 plant species (range: 5–170) and 247 animal species (range: 6–40), including 11 complete webs and 13 sub-webs (Jordano 1987; unpubl. data). Statistics for social and abiotic networks were obtained from published sources (Albert & Barabási 2002; Dorogovtsev & Mendes 2002). <*S*>, median number of interacting species (or nodes) and range; <*k*>, median number of edges per node and range (animal and plant species pooled); <γ>, mean ± 1 SE for the scaling exponent of the power-law fit. Figures for the model fits indicate the number of networks in each group that fit a particular model. For a small number of networks (‘No fit’) no model fitted the distributions of links per species well.

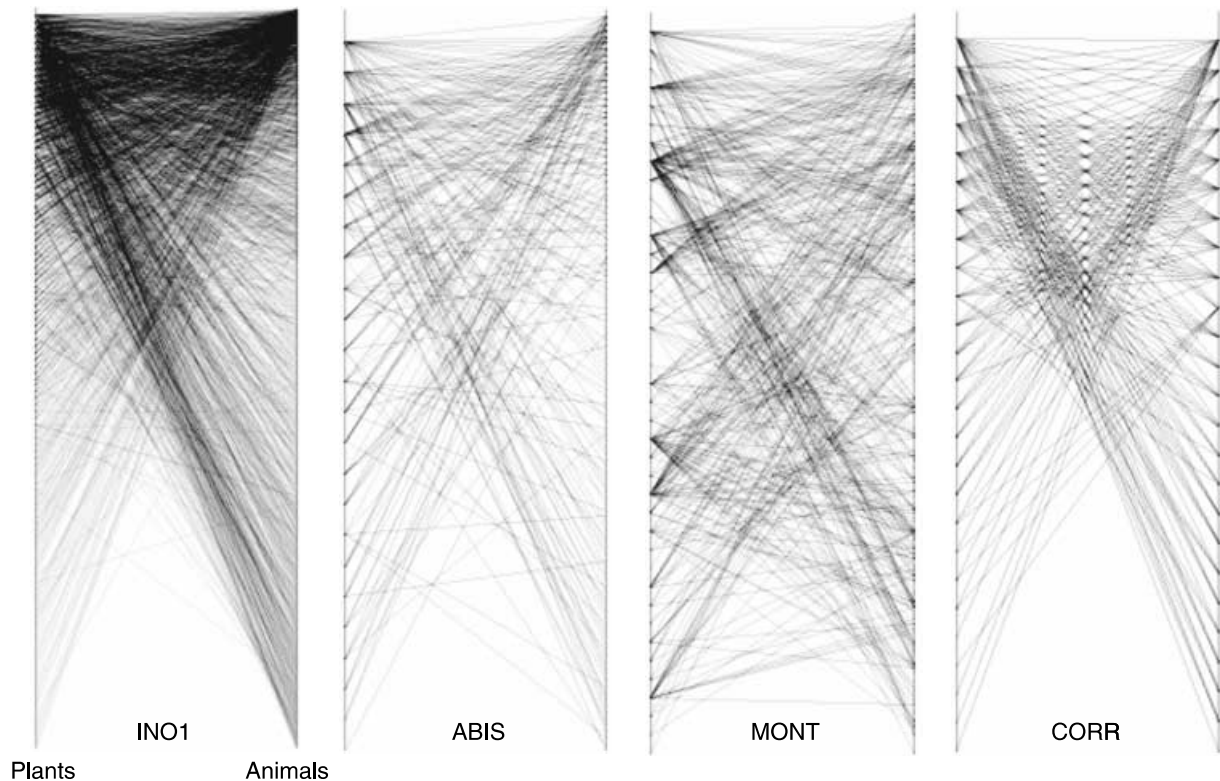


Figure 1 Bipartite graphs depicting two-mode networks characteristic of plant–animal mutualistic interactions. Species in each set (nodes arranged along the vertical lines and connected by thin oblique lines) are sorted in decreasing number of interactions per species. Plant–pollinator networks (Olesen & Jordano 2002): INO1, temperate forest, Kibune forest, Kyoto, Japan ($S = 952$, $k = 1876$); ABIS, arctic tundra, Abisko, Sweden ($S = 142$, $k = 242$). Plant–frugivore networks: MONT, neotropical montane rainforest, Monteverde, Costa Rica ($S = 210$, $k = 436$) (Wheelwright *et al.* 1984); CORR, high-elevation Mediterranean forest, Sierra de Cazorla, SE Spain ($S = 58$, $k = 148$) (P. Jordano, unpubl. data).

We examine the cumulative distributions $P(k)$ of the number of interactions per species, k , 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. 2).

RESULTS

A selection of the model-fits to several representative plant–animal assemblages (Fig. 2) shows the predominant pattern of truncated power-law distributions (Table 1), when fitted separately for the animal and plant species sets. Pollination and dispersal networks (considering both sets of animal and plant species together) differ in the frequencies of best-fitted model ($\chi^2 = 12.1$, d.f. = 3, $P = 0.005$), pollination systems showing a higher than expected frequency of power-law fits due to the higher than expected fits of the animal pollinator distributions to this model (Table 1). Good power-law fits to the data were frequent, especially in the range of 5–30 interactions per species (Fig. 2), but then had a sharp cut-off

for a higher number of interactions (Amaral *et al.* 2000). The power-law fits simply describe a characteristic feature of the specialization–generalization levels in these communities: a large number of species with few interactions coexist with a relatively small number of super-generalists. If the network did not fit this power-law, or scale-free distribution (e.g. a random network), then a single value of k would characterize the distribution, thus having a characteristic scale (single-scale). The truncation of the power-law fits indicates that super-generalist taxa are rarer than would be expected were the network build-up with a scale-free distribution of the number of interactions per species (in the random network such super-generalist, heavily connected nodes, simply do not exist).

The γ exponents for the power-law fits to the plant and animal distributions in pollination and dispersal networks differed significantly (Table 1), plant distributions consistently showing $\gamma < 1.0$, and animal distributions, $\gamma > 1.0$ (Table 1, Appendix). Abiotic and social networks (Table 1) show $\gamma \approx 2.1$ – 2.4 (Watts & Strogatz 1998; Amaral *et al.* 2000; Strogatz 2001; Albert & Barabási 2002; Dorogovtsev

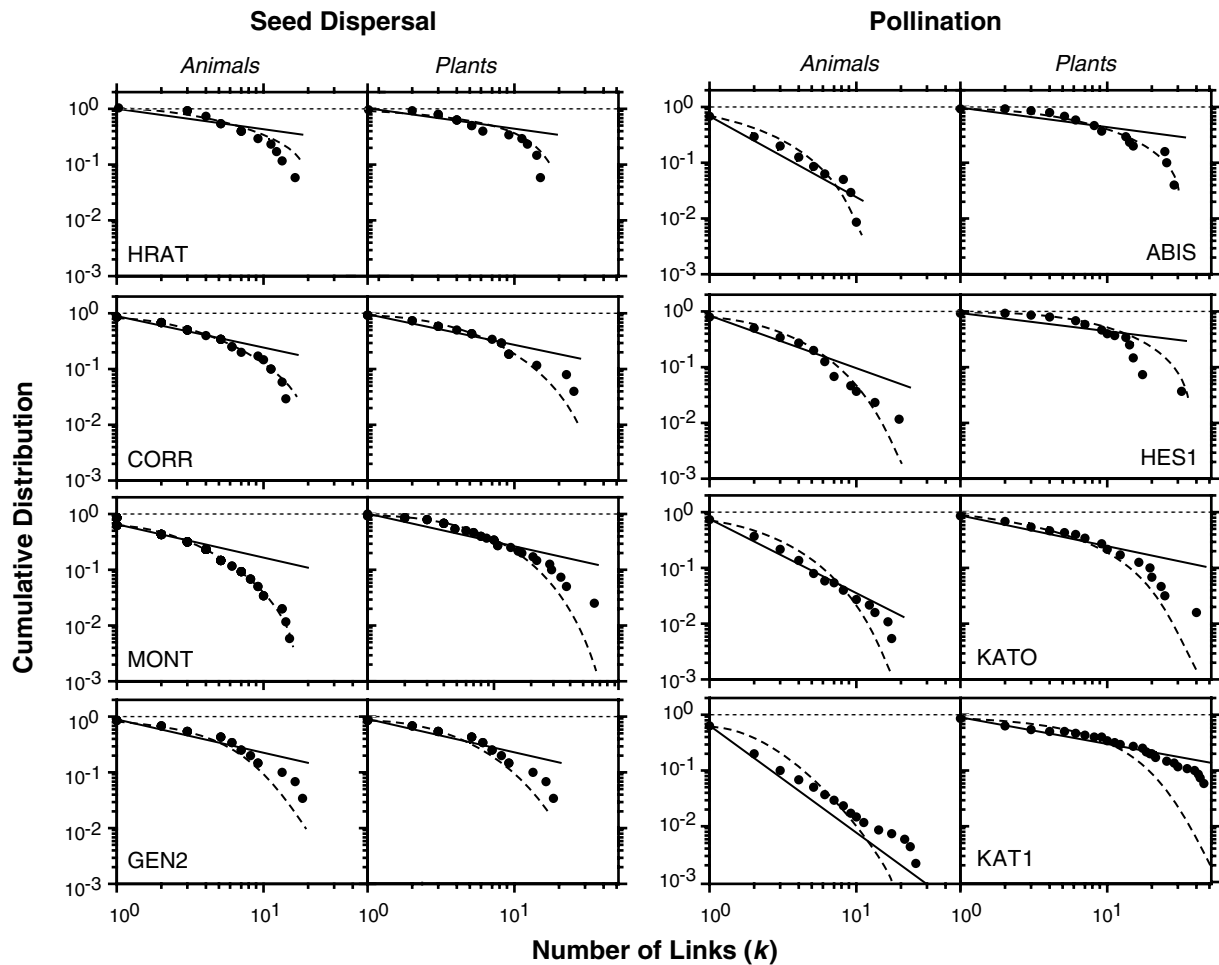


Figure 2 Cumulative distribution of connectivities (number of links per species, k , or degree) for different examples of the plant–animal interaction networks analysed (pollination and seed-dispersal mutualisms; Jordano 1987; Olesen & Jordano 2002). For these two-mode networks (see Fig. 1 for examples of the bipartite graphs) the distributions of links, $P(k)$, for the animal and plant species sets are given separately. Panels show the log-log plots of the cumulative distributions of species with 1, 2, 3, ..., k links (dots), power-law fits (solid lines) and truncated power-law fits (dotted lines). The distributions depart in most cases from the power-law beyond cut-off values, k_x .

& Mendes 2002), the differences being highly significant when compared to the mutualistic networks ($F = 106.31$, d.f. = 2, 119; $P < 0.0001$).

DISCUSSION

Large, sparse networks, both biotic and abiotic, typically show scale-invariant topology, probably as a pervasive consequence of the dynamics of network build-up that involves properties of both growth and preferential attachment of new nodes (Barabási & Albert 1999; Albert & Barabási 2002). The prevalence of truncated power-law and power-law fits to our data indicates that these two ingredients are involved in the evolution of mutualistic bipartite networks. Most food webs examined so far display single-scale distributions of k (Dunne *et al.* 2002b). This

result contrasts with the mutualistic networks examined here and could be related to the higher taxonomic resolution of the mutualistic webs (Bersier *et al.* 1999), thus deserving further investigation. Biotic webs in natural ecosystems strongly differ from abiotic webs by the nature of the biological constraints that limit the possible links formed when species add up to the net. A scale-free topology automatically emerges whenever new species add preferentially to pre-existing ones with a probability proportional to the number of interactions of the target species (see Barabási & Albert 1999). Highly diversified, non-symbiotic, mutualistic interactions among animals and plants involve the addition and loss of partners over evolutionary time (Thompson 1994), contrasting with symbiotic mutualisms, where the interactions are much more fixed over time. However, we know very little about

the mechanisms and causes of species additions to these mutualistic assemblages.

In seed-dispersal networks where the relative abundance of both animal and plant species have been quantified, k -values were significantly correlated with abundance (Jordano 1987), suggesting that the process of abundance-related addition of links is at work. If this were the only process of link addition and network build-up, we should expect generalized power-law distributions of interaction frequencies. Instead, we find over-represented the truncated power-law distributions, indicative of more homogeneous networks and less connected arrays of species. Finite size artifacts (Keitt & Stanley 1998) or constraints in the addition of links (Amaral *et al.* 2000) are two possible reasons. Despite the fact that broad-scale fits are shown by small networks (Table 1), the two types of fit span the entire range of network sizes. This suggests that constraints for the addition of new links exist, resulting in the generalized broad-scale patterns.

Constraints for the establishment of new links chiefly arise from the biological attributes of the species: no link can be established between a plant and an animal mutualist differing in phenology, i.e. the seeds of a winter-ripening plant cannot be dispersed by a frugivore that is a summer stopover migrant (Jordano 1985). In addition, the phenotypic traits of species, largely a product of their patterns of shared ancestry and phylogenetic relations, dictate generalization and specialization patterns, limiting the number of species in the community with which they actually interact. For instance, short-tongued pollinators cannot successfully reach the nectar in long-corolla flowers and pollinate them efficiently (Nilsson 1988; Johnson & Steiner 1997). Constraints result in 'forbidden links' that *a priori* we cannot observe when assembling the pattern of $[a_{ij}]_{A \times P}$ interactions (Fig. 1), 'filtering the information' (Mossa *et al.* 2002) for potential nodes and limiting the growth of scale-free topologies. To our knowledge, no one has examined the causes beyond these forbidden links or unobserved interactions in natural communities, despite their relevance in dictating preferential attachment. For the Hato Ratón network (17 frugivore species and 16 fleshy-fruit producing plants in Mediterranean scrubland, Jordano 1987; unpubl. data), we recorded 141 interactions out of $P \times A = 272$ possible; the remaining 131 (48.16%) were not observed. The phenological uncoupling of the plants' fruiting period and animal presence in the community accounted for 51.13% of these unrecorded links; size restrictions (uncoupling of fruit size and frugivore size causing inability to handle fruits) accounted for 23.66%; structural constraints of the plants (i.e. branch architecture or fruit display mode limiting accessibility to the fruits), 6.11%. The remaining 19.0% of the links not recorded were not assignable to a particular cause.

The forbidden links constitute a constraint on network growth that limits the preferential attachment, and explain the generalized truncation of the power-law behaviour that we document here for the first time (Fig. 2). Our work in progress suggests that forbidden links are a universal property of ecological interaction networks. Most networks have cut-off degrees, $k_x < k$ (Fig. 2) giving rise to a gradient of variation from scale-free to broad-scale and to single-scale distributions (Table 1). If those constraints on network evolution and build-up were general to the bipartite networks examined here, we should expect variation of the degree distribution (Fig. 2) to be independent of scale considerations (Keitt & Stanley 1998; Mossa *et al.* 2002), i.e. of differences in S , degree of overall generalization in the participating species ($< k >$), and k . Most of the networks considered here, specially those that fit to power-law or truncated power-law distributions of links, collapse to a universal scaling form (Mossa *et al.* 2002):

$$P(k, f, S) \propto k^{-\gamma} F\left(\frac{k}{k_x}\right) \quad (1)$$

where k is the degree (number of links per species), f is the fraction of nodes 'filtered', S is the number of species (nodes) in the network, and k_x is the cut-off value. $F(y)$ is approximately constant for $y \ll 1$; and $F(y) \sim e^{-y}$ for $y \gg 1$ (Mossa *et al.* 2002).

The plot of the scaled cumulative distribution $k^\gamma P(k)$ vs. the scaled degree k/k_x (Fig. 3) collapses reasonably well for these networks, with scatter due to the fact that the degree distribution incorporates sampling error and that characteristic small size (Table 1) hinders the precise estimation of statistical parameters (Albert & Barabási 2002). Despite this, all networks cluster around the scaling function, revealing a shared pattern of internal topology independent of scaling considerations (Sugihara *et al.* 1989; Bersier & Sugihara 1997; Bersier *et al.* 1999; also see Melián & Bascompte 2002).

Our results show that, in addition to ageing and cost-related constraints (two properties of evolving networks yielding truncation of the power-law fits; Amaral *et al.* 2000), information filtering imposed by the biological properties of plant-animal mutualisms limits the growth of these interaction networks due to the existence of forbidden links, and confers them a broad-scale behaviour. Broad-scaling suggest that, compared to abiotic networks with scale-free behaviour, these networks are very robust to the loss of keystone, highly connected nodes (species) which are the backbone of the interactions (see also Dunne *et al.* 2002a). However, for two-mode networks like plant-animal mutualisms, this property also has important implications for coevolutionary processes in high-diversity assemblages because of the possibility for coevolved interactions to be re-shaped as individual species enter the

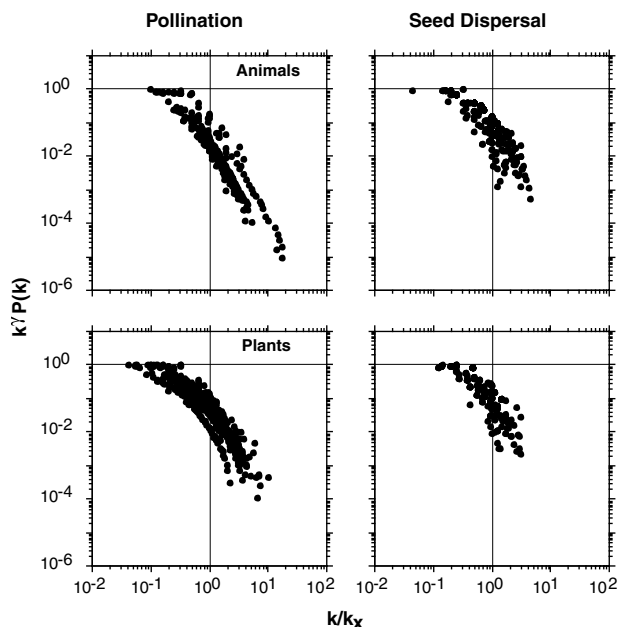


Figure 3 Data collapse to a scaling function (eqn 1) when plotting the scaled cumulative distributions of links/species, $k^\gamma P(k)$ vs. the scaled links per species (k/k_x), where k_x is the cut-off value of each distribution (the k -value where the distribution departs from the power-law fit). Complete networks: $N = 21$, pollination; $N = 11$, seed dispersal. A collapse suggests invariant topologies of web organization despite variation in size and number of links.

assemblage or go extinct. Coevolved interactions within highly diversified non-symbiotic mutualisms are not simply 'diffuse' in these networks (Thompson 1994), and result from more than simply an addition of pairwise interactions. They characteristically show broad-scale or scale-free distributions of the number of interactions per species, that define distinct generalization–specialization levels. Thus, no single value (scale) can be used to characterize how generalized or specialized is a particular mutualistic assemblage. Despite their obvious heterogeneity, these diverse two-mode networks share invariant topological patterns typical of larger complex systems capable of self-organization, a property with far-reaching implications for the coevolution of interactions and the conservation of plant–animal mutualisms. Our understanding of coevolutionary processes in highly diversified communities will rest on a solid knowledge of the network structure of these interactions.

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APPENDIX

Summary of data sources for the analyses. Entries are community data for plant–frugivore and plant–pollinator interactions summarizing the number of species, n ; number of interactions, k ; median number of interactions per species, $\langle k \rangle$; gamma exponent for the fitting model (see text), γ ; truncation value of k (i.e. the k value beyond which the cumulative distribution departs from a power-law fit, see text); the best fitted model and its characteristic type of scale; and the literature sources for the data. The data are summarized separately for the seed-dispersal and the pollination mutualisms; for each of them, the data are available for the plant and animal species separately. NA, not available

CODE	n	k	$\langle k \rangle$	γ	k_{tr}	Best fit	Scale	Reference
Seed dispersal – animal species								
BEEH	40	119	2.98	1.050	11.91	Truncated power-law	Broad scale	Beehler, B. (1983) Frugivory and polygamy in birds of paradise. <i>Auk</i> , 100, 1–11.
SORE	17	22	1.29	1.520	3.01	Truncated power-law	Broad scale	Sorensen, A.E. (1981) Interactions between birds and fruit in a temperate woodland. <i>Oecologia (Berl.)</i> , 50, 242–249.
FROS	26	110	4.23	1.430	11.00	Truncated power-law	Broad scale	Frost, P.G.H. (1980) Fruit–frugivore interactions in a South African coastal dune forest. In: <i>Acta XVII Congressus Internationalis Ornithologici</i> (ed. Noring R), pp. 1179–1184. Deutsche Ornithologische Ges., Berlin, Germany.
GUIT	19	40	2.11	1.610	5.95	Truncated power-law	Broad scale	Gutián, J. (1983) Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera cantábrica occidental. Unpubl. PhD Thesis, Univ. Santiago, Spain.
GEN1	25	38	1.52	1.040	5.01	Exponential	Single scale	Galetti, M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. <i>Ararajuba, Rev. Brasil. Ornitol.</i> , 4, 71–79.
GEN2	66	147	2.23	0.850	5.95	Truncated power-law	Broad scale	Galetti, M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. <i>Ararajuba, Rev. Brasil. Ornitol.</i> , 4, 71–79.
KANT	32	86	2.69	1.740	3.01	NA	NA	Kantak, G.E. (1981) Temporal feeding patterns of some tropical frugivores. <i>Condor</i> , 83, 185–187.
WYTH	25	47	1.88	1.320	3.01	NA	NA	Snow, B.K. & Snow D.W. (1988) <i>Birds and Berries</i> , Calton, England.
LOPE	27	75	2.78	1.780	10.00	Truncated power-law	Broad scale	Tutin, C.E.G., Ham R.M., White L.J.T. & Harrison M.J.S. (1997) The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. <i>Am. J. Primatol.</i> , 42, 1–24.
SAPF	35	60	1.71	0.560	6.94	Power-law	Scale free	Noma, N. (1997) Annual fluctuations of sap fruits production and synchronization within and inter species in a warm temperate forest on Yakushima Island, Japan. <i>Tropics</i> , 6, 441–449.
MONT	210	436	2.08	0.320	3.98	Truncated power-law	Broad scale	Wheelwright, N.T., Haber W.A., Murray K.G. & Guindon C. (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. <i>Biotropica</i> , 16, 173–192.
CROM	80	142	1.78	0.440	21.96	Truncated power-law	Broad scale	Crome, F.H.J. (1975) The ecology of fruit pigeons in tropical Northern Queensland. <i>Aust. Wildl. Res.</i> , 2, 155–185.
SNOW	64	234	3.66	1.400	2.98	Truncated power-law	Broad scale	Snow, B.K. & Snow D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. <i>Auk</i> , 88, 291–322.
CORR	58	148	2.55	0.940	5.01	Truncated power-law	Broad scale	Pedro, Jordano, unpublished data. Mediterranean montane forest, SE Spain.
HRAT	33	121	3.67	1.410	5.01	Truncated power-law	Broad scale	Jordano, P. (1985) El ciclo anual de los passeriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. <i>Ardeola</i> , 32, 69–94.

VISO	24	65	2.71	1.220	5.01	Truncated power-law	Broad scale	Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. <i>Ecol. Monogr.</i> , 54, 1–23.
Pollination – animal species								
CEP1	185	361	1.95	0.930	7.94	Power-law	Scale free	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
CEP2	107	196	1.83	1.130	2.98	Truncated power-law	Broad scale	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
CEP3	61	81	1.33	1.010	7.94	Power-law	Scale free	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
ABIS	142	242	1.70	1.350	9.08	Power-law	Scale free	Elberling, H. & Olesen J.M. (1999) The structure of a high latitude plant–flower visitor system: the dominance of flies. <i>Ecography</i> , 22, 314–323.
ZACK	107	456	4.26	0.890	10.00	Exponential	Single scale	Elberling, H. & Olesen J.M., unpublished data. Arctic tundra, Greenland.
MAUR	27	52	1.93	0.890	2.98	Truncated power-law	Broad scale	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
DONA	205	412	2.01	1.330	6.94	Power-law	Scale free	Herrera, J. (1988) Pollination relationships in Southern Spanish Mediterranean shrublands. <i>J. Ecol.</i> , 76, 274–287.
HOCK	110	179	1.63	1.460		Truncated power-law	Broad scale	Hocking, B. (1968) Insect–flower associations in the high Arctic with special reference to nectar. <i>Oikos</i> , 19, 359–387.
INO1	952	1876	1.97	1.360	2.03	Truncated power-law	Broad scale	Inoue, T., Kato, M., Kakutani, T., Suka, T., & Itino, T. (1990) Insect–flower relationship in the temperate deciduous forest of Kibune, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> 27, 377–463.
INO2	117	253	2.16	1.080	11.01	Power-law	Scale free	Inouye, D.W. & Pyke, G.H. (1988) Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado. <i>Aust. J. Ecol.</i> 13, 191–210.
KAKU	428	774	1.81	1.250	22.82	Power-law	Scale free	Kakutani, T., Inoue, T., Kato, M. & Ichihashi, H. (1990) Insect–flower relationship in the campus of Kyoto University, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> 27, 465–521.
KATO	251	430	1.71	1.360	3.98	Power-law	Scale free	Kato, M. & Miura R. (1996) Flowering phenology and anthophilous insect community at a threatened natural lowland marsh at Nakaikemi in Tsuruga, Japan. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 29, 1–48.
KAT1	770	1193	1.55	1.620		Power-law	Scale free	Kato, M., Kakutani, T., Inoue, T. & Itino, T. (1990) Insect–flower relationship in the primary beech forest of Ashu, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 27, 309–375.
KAT2	446	865	1.94	1.260	19.95	Power-law	Scale free	Kato, M., Matsumoto M. & Kato T. (1993) Flowering phenology and anthophilous insect community in the cool-temperate subalpine forests and meadows at Mt. Kushigata in the Central part of Japan. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 28, 119–172.

APPENDIX *continued*

CODE	<i>n</i>	<i>k</i>	$\langle k \rangle$	γ	k_x	Best fit	Scale	Reference
KEVA	111	190	1.71	1.390	3.01	Truncated power-law	Broad scale	Kevan, P. G. (1972) Insect pollination of high arctic flowers. <i>J. Ecol.</i> , 60, 831–847.
GALA	32	27	0.84	1.760		Truncated power-law	Broad scale	McMullen, C.K. (1993) Flower-visiting insects of the Galapagos Islands. <i>PanPacific Entomol.</i> , 69, 95–106.
MOSQ	29	38	1.31	1.220	1.99	Power-law	Scale free	Mosquin, T. & Martin, J.E. (1967) Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. <i>Can. Field Nat.</i> 81, 201–205.
HES1	108	249	2.31	1.100	5.01	Truncated power-law	Broad scale	J.M. Olesen, unpublished data. Fallow, Denmark.
GARA	84	145	1.73	1.140	5.96	Power-law	Scale free	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
HES2	50	79	1.58	1.450	3.01	Truncated power-law	Broad scale	J.M. Olesen, unpublished data. Bog, Denmark.
HES3	50	72	1.44	1.510	1.99	NA	NA	J.M. Olesen, unpublished data. Temperate forest, Denmark.
ACOR	22	30	1.36	1.020	3.01	Truncated power-law	Broad scale	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
PERC	97	178	1.84	1.000	2.98	Truncated power-law	Broad scale	Percival, M. (1974) Floral ecology of coastal scrub in southeast Jamaica. <i>Biotropica</i> , 6, 104–129.
PETA	797	2933	3.68	0.990	7.08	Power-law	Scale free	Petanidou, T. 1991. [Pollination ecology in a phryganic ecosystem]. Unpubl. PhD thesis, Aristotelian University, Thessaloniki.
PRI1	78	120	1.54	1.440	3.01	Truncated power-law	Broad scale	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
PRI2	180	374	2.08	1.220	3.98	Truncated power-law	Broad scale	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
PRI3	167	346	2.07	1.110	26.10	Power-law	Scale free	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
RAMI	93	151	1.62	1.010	5.96	Power-law	Scale free	Ramirez, N. (1989) Biología de polinización en una comunidad arbustiva tropical de la alta Guyana Venezolana. <i>Biotropica</i> 21, 319–330.
SCHE	40	65	1.63	1.330	3.01	Truncated power-law	Broad scale	Schemske, D., Willson, M.F., Melampy, M., Miller, L., Verner, L., Schemske, K. & Best, L. (1978) Flowering ecology of some spring woodland herbs. <i>Ecology</i> , 59, 351–366.
Seed dispersal – plant species								
BEEH	40	119	2.98	0.900	7.01	Truncated power-law	Broad scale	Beehler, B. (1983) Frugivory and polygamy in birds of paradise. <i>Auk</i> , 100, 1–11.
SORE	17	22	1.29	0.350	3.98	Truncated power-law	Broad scale	Sorensen, A.E. (1981) Interactions between birds and fruit in a temperate woodland. <i>Oecologia (Berl.)</i> , 50, 242–249.
FROS	26	110	4.23	1.290	6.94	Truncated power-law	Broad scale	Frost, P.G.H. (1980) Fruit–frugivore interactions in a South African coastal dune forest. In: <i>Acta XVII Congressus Internationalis Ornithologici</i> (ed. Noring R), pp. 1179–1184. Deutsche Ornithologische Ges., Berlin, Germany.

GUIT	19	40	2.11	0.970	3.98	NA	NA	Gutián, J. (1983) Relaciones entre los frutos y los passeriformes en un bosque montano de la cordillera cantábrica occidental. Unpubl. PhD Thesis, Univ. Santiago, Spain.
GEN1	25	38	1.52	1.620	4.06	Truncated power-law	Broad scale	Galetti, M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. <i>Ararajuba, Rev. Brasil. Ornitol.</i> , 4, 71–79.
GEN2	66	147	2.23	0.940	5.01	Truncated power-law	Broad scale	Galetti, M. & Pizo M.A. (1996) Fruit eating birds in a forest fragment in southeastern Brazil. <i>Ararajuba, Rev. Brasil. Ornitol.</i> , 4, 71–79.
KANT	32	86	2.69	1.260	18.13	NA	NA	Kantak, G.E. (1981) Temporal feeding patterns of some tropical frugivores. <i>Condor</i> , 83, 185–187.
WYTH	25	47	1.88	1.000	3.98	Truncated power-law	Broad scale	Snow, B.K. & Snow D.W. (1988) <i>Birds and Berries</i> , Calton, England.
LOPE	27	75	2.78	1.130	3.98	Truncated power-law	Broad scale	Tutin, C.E.G., Ham R.M., White L.J.T. & Harrison M.J.S. (1997) The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. <i>Am. J. Primatol.</i> , 42, 1–24.
SAPF	35	60	1.71	0.280		Power-law	Scale free	Noma, N. (1997) Annual fluctuations of sapfruits production and synchronization within and inter species in a warm temperate forest on Yakushima Island, Japan. <i>Tropics</i> , 6, 441–449.
MONT	210	436	2.08	0.070	6.94	Truncated power-law	Broad scale	Wheelwright, N.T., Haber W.A., Murray K.G. & Guindon C. (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. <i>Biotropica</i> , 16, 173–192.
CROM	80	142	1.78	0.770	2.02	Truncated power-law	Broad scale	Crome, F.H.J. (1975) The ecology of fruit pigeons in tropical Northern Queensland. <i>Aust. Wildl. Res.</i> , 2, 155–185.
SNOW	64	234	3.66	1.170	18.13	Truncated power-law	Broad scale	Snow, B.K. & Snow D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. <i>Auk</i> , 88, 291–322.
CORR	58	148	2.55	0.130	7.94	Truncated power-law	Broad scale	Pedro, Jordano, unpublished data. Mediterranean montane forest, SE Spain.
HRAT	33	121	3.67	1.100	5.01	Truncated power-law	Broad scale	Jordano, P. (1985) El ciclo anual de los passeriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. <i>Ardeola</i> , 32, 69–94.
VISO	24	65	2.71	0.770	6.94	Truncated power-law	Broad scale	Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. <i>Ecol. Monogr.</i> , 54, 1–23.
Pollination – plant species								
CEP1	185	361	1.95	1.240	3.98	Truncated power-law	Broad scale	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
CEP2	107	196	1.83	0.920	5.01	Truncated power-law	Broad scale	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
CEP3	61	81	1.33	0.970	5.96	Truncated power-law	Broad scale	Arroyo, M.T.K., Primack R. & Armesto J. (1982) Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. <i>Am. J. Bot.</i> , 69, 82–97.
ABIS	142	242	1.70	0.890	7.94	Truncated power-law	Broad scale	Elberling, H. & Olesen J.M. (1999) The structure of a high latitude plant–flower visitor system: the dominance of flies. <i>Ecography</i> , 22, 314–323.

APPENDIX *continued*

CODE	<i>n</i>	<i>k</i>	$\langle k \rangle$	γ	k_x	Best fit	Scale	Reference
ZACK	107	456	4.26	1.360	13.86	Truncated power-law	Broad scale	Elberling, H. & Olesen J.M., unpublished data. Arctic tundra, Greenland.
MAUR	27	52	1.93	1.230	3.01	Truncated power-law	Broad scale	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
DONA	205	412	2.01	0.680	17.11	Truncated power-law	Broad scale	Herrera, J. (1988) Pollination relationships in Southern Spanish Mediterranean shrublands. <i>J. Ecol.</i> , 76, 274–287.
HOCK	110	179	1.63	0.740	6.94	Power-law	Scale free	Hocking, B. (1968) Insect–flower associations in the high Arctic with special reference to nectar. <i>Oikos</i> , 19, 359–387.
INO1	952	1876	1.97	0.620	23.04	Truncated power-law	Broad scale	Inoue, T., Kato, M., Kakutani, T., Suka, T., & Itino, T. (1990) Insect–flower relationship in the temperate deciduous forest of Kibune, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 27, 377–463.
INO2	117	253	2.16	0.470	9.08	Truncated power-law	Broad scale	Inouye, D. W. & Pyke, G. H. (1988) Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado. <i>Aust. J. Ecol.</i> 13, 191–210.
KAKU	428	774	1.81	0.850	9.08	Truncated power-law	Broad scale	Kakutani, T., Inoue, T., Kato, M. & Ichihashi, H. (1990) Insect–flower relationship in the campus of Kyoto University, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 27, 465–521.
KATO	251	430	1.71	0.770	9.09	Truncated power-law	Broad scale	Kato, M. & Miura R. (1996) Flowering phenology and anthophilous insect community at a threatened natural lowland marsh at Nakaikemi in Tsuruga, Japan. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 29, 1–48.
KAT1	770	1193	1.55	0.620	17.78	Power-law	Scale free	Kato, M., Kakutani, T., Inoue, T. & Itino, T. (1990) Insect–flower relationship in the primary beech forest of Ashu, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. <i>Contrib. Biol. Lab., Kyoto Univ.</i> 27, 309–375.
KAT2	446	865	1.94	0.790	10.00	Truncated power-law	Broad scale	Kato, M., Matsumoto M. & Kato T. (1993) Flowering phenology and anthophilous insect community in the cool-temperate subalpine forests and meadows at Mt. Kushigata in the Central part of Japan. <i>Contrib. Biol. Lab., Kyoto Univ.</i> , 28, 119–172.
KEVA	111	190	1.71	0.580	10.00	Truncated power-law	Broad scale	Kevan, P. G. (1972) Insect pollination of high arctic flowers. <i>J. Ecol.</i> , 60, 831–847.
GALA	32	27	0.84	0.830	5.01	Truncated power-law	Broad scale	McMullen, C.K. (1993) Flower-visiting insects of the Galapagos Islands. <i>PanPacific Entomol.</i> , 69, 95–106.
MOSQ	29	38	1.31	0.900	5.01	Truncated power-law	Broad scale	Mosquin, T. & Martin, J. E. (1967) Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. <i>Can. Field Nat.</i> 81, 201–205.
HES1	108	249	2.31	0.920	11.01	Truncated power-law	Broad scale	J.M. Olesen, unpublished data. Fallow, Denmark.

GARA	84	145	1.73	0.760	14.96	Power-law	Scale free	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
HES2	50	79	1.58	0.780	5.96	Truncated power-law	Broad scale	J.M. Olesen, unpublished data. Bog, Denmark.
HES3	50	72	1.44	0.830	11.22	Exponential	Single scale	J.M. Olesen, unpublished data. Temperate forest, Denmark.
ACOR	22	30	1.36	1.260	3.01	Exponential	Single scale	Olesen, J.M., Eskildsen, L.I. & Venkatasami, S. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. <i>Diversity and Distributions</i> , 8, 181–192.
PERC	97	178	1.84	1.100	3.98	Truncated power-law	Broad scale	Percival, M. (1974) Floral ecology of coastal scrub in southeast Jamaica. <i>Biotropica</i> , 6, 104–129.
PETA	797	2933	3.68	0.890	18.30	Truncated power-law	Broad scale	Petanidou, T. 1991. [Pollination ecology in a phryganic ecosystem]. Unpubl. PhD thesis, Aristotelian University, Thessaloniki.
PRI1	78	120	1.54	0.890	7.94	Truncated power-law	Broad scale	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
PRI2	180	374	2.08	0.730	10.00	Truncated power-law	Broad scale	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
PRI3	167	346	2.07	1.000	5.96	Exponential	Single scale	Primack, R.B. (1983) Insect pollination in the New Zealand mountain flora. <i>New Zealand J. Bot.</i> , 21, 317–333.
RAMI	93	151	1.62	1.240	2.98	Exponential	Single scale	Ramirez, N. (1989) Biología de polinización en una comunidad arbustiva tropical de la alta Guyana Venezolana. <i>Biotropica</i> , 21, 319–330.
SCHE	40	65	1.63	0.520	1.99	Power-law	Scale free	Schemske, D., Willson, M.F., Melampy, M., Miller, L., Verner, L., Schemske, K. & Best, L. (1978) Flowering ecology of some spring woodland herbs. <i>Ecology</i> , 59, 351–366.