

# The smallest of all worlds: Pollination networks

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## Abstract

A pollination network may be either 2-mode, describing trophic and reproductive interactions between communities of flowering plants and pollinator species within a well-defined habitat, or 1-mode, describing interactions between either plants or pollinators. In a 1-mode pollinator network, two pollinator species are linked to each other if they both visit the same plant species, and vice versa for plants. Properties of 2-mode networks and their derived 1-mode networks are highly correlated and so are properties of 1-mode pollinator and 1-mode plant networks. Most network properties are scale-dependent, i.e. they are dependent upon network size. Pollination networks have the strongest small-world properties of any networks yet studied, i.e. all species are close to each other (short average path length) and species are highly clustered. Species in pollination networks are much more densely linked than species in traditional food webs, i.e. they have a higher density of links, a shorter distance between species, and species are more clustered.

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## 1. Introduction

Recently, network analysis (see e.g. Barabási et al., 2000; Albert and Barabási, 2001) has been applied to two types of ecological webs, viz. food webs (Dunne et al., 2002; Montoya and Solé, 2002; Williams et al., 2002) and mutualistic networks (Jordano et al., 2003). Network properties of these two types of webs have, however, never been compared. Such a comparison is important in our efforts to achieve a broader understanding of the topology and dynamics of ecological webs and also if we want to generalize to molecular networks, or even to non-biological networks. Such an analysis is, however, hampered by the fact that food webs and mutualistic networks are so-called 1- and 2-mode networks, respectively, i.e. depicting interactions within either one set of species or between two sets of species. In this study, we transform a large set of 2-mode mutualistic networks to their 1-mode relatives and compare these latter ones with a set of food webs earlier analysed by Dunne et al. (2002). These authors compared

food webs with non-ecological networks and found that food webs were more complex. Complexity was measured as link density or connectance, i.e. the fraction of possible links realized. In general, networks with short distance or path length between their nodes and highly clustered nodes are termed small worlds (for definitions see later). Although path length between taxa in food webs is short, food webs do not truly qualify as small worlds because their taxa are not highly clustered (Dunne et al., 2002; Williams et al., 2002). We extend this analysis to include non-food webs, mutualistic networks, in order to make broad generalizations about ecological webs.

Recently, several authors have analysed mutualistic networks (e.g. Memmott, 1999; Memmott and Waser, 2002; Olesen and Jordano, 2002; Ollerton and Cranmer, 2002; Bascompte et al., 2003; Jordano et al., 2003; Ollerton et al., 2003; Vázquez and Aizen, 2003). As an example of mutualistic networks we focus upon pollination networks. The aims of our study are: (1) to compare structural properties of 1- and 2-mode pollination networks, (2) to analyse level of scale-dependency of pollination network properties, i.e. to relate properties to network size, (3) to compare 1-mode pollinator networks to 1-mode plant

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networks, (4) to analyse if these 1-mode networks are small-worlds, and (5) to discuss similarities and differences between 1-mode pollination networks and traditional food webs.

**2. Material and methods**

Thirty-seven pollination networks from 22 published studies and seven unpublished ones were analysed (Table 1).

We included all “total” networks to which we had access. “Total” does not, of course, indicate that networks are completely sampled with respect to species and links, but only refers to sampling width, i.e. all species involved in biotic pollination are included irrespective of taxonomic or functional affinity (Olesen and Jordano, 2002). All networks are also “temporarily cumulative” (*sensu* Schoenly and Cohen, 1991), i.e. data are from one site, but sampled over a

Table 1  
Characteristics of 1-mode pollination networks

Source	A	P	S	I	Pollinators			Plants			Pollinators			Plants		
					$d_A$	$m_A$	$\langle k_A \rangle$	$d_P$	$m_P$	$\langle k_P \rangle$	$\langle c_A \rangle$	$\langle c_P \rangle$	$\langle l_A \rangle$	$D_A$	$\langle l_P \rangle$	$D_P$
1 Inoue et al. (1990)	840	112	952	1876	0.11	38687	92.1	0.42	2605	46.5	0.86	0.81	1.94	4	1.61	3
2 Petanidou (1991)	666	131	797	2933	0.16	35345	106.1	0.79	6748	103.0	0.77	0.91	1.85	3	1.20	2
3 Kato et al. (1990)	679	91	770	1193	0.13	30905	91.0	0.33	1349	29.6	0.90	0.78	1.97	4	1.72	4
4 Kato (2000)	619	107	726	1109	0.08	14810	47.9	0.19	1093	20.4	0.87	0.74	2.19	5	2.01	4
5 Kato et al. (1993)	356	90	446	865	0.12	7273	40.9	0.35	1389	30.9	0.84	0.72	2.08	4	1.72	4
6 Kakutani et al. (1990)	314	113	427	774	0.14	6762	43.1	0.23	1443	25.5	0.86	0.73	2.00	4	1.84	5
7 Yamazaki and Kato (2003)	295	99	394	599	0.08	3502	23.7	0.16	784	15.8	0.86	0.72	2.31	4	2.02	5
8 Kato and Miura (1996)	187	64	251	430	0.15	2586	27.7	0.26	528	16.5	0.81	0.74	2.01	4	1.87	4
9 Herrera (1988)	179	26	205	412	0.34	5434	60.7	0.74	241	18.5	0.87	0.88	1.67	3	1.26	2
10 Arroyo et al. (1982) low	101	84	185	361	0.19	947	18.8	0.35	1217	29.0	0.83	0.79	1.90	4	1.66	3
11 Primack (1983) Cass	139	41	180	374	0.25	2416	34.8	0.48	394	19.2	0.81	0.79	1.84	4	1.55	3
12 Primack (1983) Craigieburn	118	49	167	346	0.25	1703	28.9	0.63	735	30.0	0.83	0.84	1.79	3	1.41	4
13 Elberling and Olesen (1999)	118	24	142	242	0.22	1547	26.2	0.59	164	13.7	0.86	0.80	1.86	3	1.46	3
14 Inouye and Pyke (1988)	81	36	117	253	0.28	900	22.2	0.60	381	21.2	0.82	0.86	1.75	3	1.36	3
15 Kevan (1970)	91	20	111	190	0.56	2273	50.0	0.43	81	8.1	0.91	0.81	1.44	3	1.53	2
16 Hocking (1968)	81	29	110	179	0.43	1377	34.0	0.32	130	9.0	0.85	0.79	1.59	4	1.75	3
17 Olesen et al. (submitted for publication) wastegr. DK	82	26	108	249	0.34	1116	27.2	0.75	245	18.8	0.81	0.85	1.69	3	1.25	2
18 Olesen et al. (submitted for publication) Greenland	76	31	107	456	0.57	1613	42.4	0.94	437	28.2	0.83	0.95	1.43	3	1.06	2
19 Arroyo et al. (1982) mid	64	43	107	196	0.24	479	15.0	0.36	328	15.3	0.78	0.80	1.91	4	1.65	4
20 Percival (1974)	36	61	97	178	0.40	250	13.9	0.41	752	24.7	0.80	0.87	1.74	4	1.76	4
21 Ramirez (1989)	46	47	93	151	0.16	162	7.0	0.28	303	12.9	0.75	0.77	2.27	5	1.95	4
22 Olesen et al. (submitted for publication) Gomera	55	29	84	145	0.40	588	21.4	0.54	218	15.0	0.87	0.87	1.61	3	1.48	3
23 Primack (1983) Arthur's Pass	60	18	78	120	0.21	364	12.1	0.54	83	9.2	0.80	0.76	1.91	3	1.40	3
24 L. Stald et al. (unpubl.) gorge Tenerife	51	17	68	130	0.33	417	16.4	0.85	116	13.6	0.85	0.94	1.72	3	1.15	2
25 Arroyo et al. (1982) high	25	36	61	81	0.28	83	6.6	0.35	221	12.3	0.80	0.83	1.94	3	1.73	3
26 M. Bundgaard & J. M. Olesen (unpubl.) DK	44	16	60	278	0.81	770	35.0	1.00	120	15.0	0.90	1.00	1.19	2	1.00	1
27 P. Witt & J. M. Olesen (unpubl.) Greenland	39	15	54	92	0.42	314	16.1	0.71	75	10.0	0.86	0.88	1.56	3	1.18	2
28 Olesen et al. (submitted for publication) Bog DK	40	10	50	72	0.33	260	13.0	0.64	29	5.8	0.87	0.87	1.74	3	1.36	2
29 Olesen et al. (submitted for publication) Forest DK	42	8	50	79	0.41	357	17.0	0.82	23	5.8	0.84	0.83	1.59	2	1.18	2
30 Dupont et al. (2003), Tenerife	38	11	49	108	0.57	402	21.2	0.87	48	8.7	0.80	0.92	1.43	3	1.13	2
31 L. Stald et al. (unpubl.) mountain slope Tenerife	35	14	49	86	0.46	273	15.6	0.68	62	8.9	0.85	0.83	1.54	2	1.32	2
32 Lundgren and Olesen (in press) Greenland	26	17	43	63	0.43	139	10.7	0.48	65	7.6	0.87	0.84	1.56	3	1.46	2
33 Schemske et al. (1978)	33	7	40	65	0.74	392	23.8	0.86	18	5.1	0.91	0.91	1.26	2	1.43	2
34 McMullen (1993)	22	10	32	27	0.18	41	3.7	0.18	8	1.6	0.94	0.87	1.47	2	1.20	2
35 Mosquin and Martin (1967)	18	11	29	27	0.39	59	6.6	0.49	27	4.9	0.89	0.94	1.37	2	1.07	2
36 Olesen et al. (2002), Mauritius	13	14	27	52	0.72	56	8.6	0.89	81	11.6	0.87	0.93	1.28	2	1.11	2
37 Olesen et al. (2002), Azores	12	10	22	30	0.56	37	6.2	0.58	26	5.2	0.88	0.81	1.45	3	1.42	2
Mean	155	42	197	401	0.34	4450	29.4	0.54	610	18.3	0.85	0.84	1.73	3.2	1.47	2.8
Standard deviation	211.4	36.0	242.5	578.1	0.191	9662	24.46	0.237	1179	17.21	0.042	0.070	0.279	0.82	0.286	1.00
Minimum	12	7	22	27	0.08	37	3.7	0.16	8	1.6	0.75	0.72	1.19	2	1	1
Maximum	840	131	952	2933	0.81	38687	106.1	1.00	6748	103.0	0.94	1.00	2.31	5	2.02	5
Median	64	29	107	190	0.33	770	22.2	0.54	221	15.0	0.85	0.83	1.74	3	1.43	3

Networks sorted according to descending S. A, no. pollinator spp.; P, no. plant spp.; S, species richness = A + P; I, no. links in 2-mode networks;  $d_A$ , density =  $\langle k_A \rangle / (A-1)$  or  $d_P = \langle k_P \rangle / (P-1)$ ; m, no. links observed;  $\langle k \rangle$ , average number of links per species;  $\langle c \rangle$ , average clustering coefficient, i.e. link density among neighbours to a species;  $\langle l \rangle$ , average shortest path length, i.e. average shortest distance among any pair of species; D, diameter, i.e. longest shortest path among any pair of species.

Table 2  
Parameters included in the analysis

Property		Definition
<i>2-Mode network</i>		
$A$	Pollinator community size	No. of pollinator species in the network
$P$	Plant community size	No. of plant species in the network
$S$	2-mode network size	$= A + P$
$I$	Link number	No. of links between $A$ and $P$
$C$	Connectance	$= I/(AP)$
$L_m$	Pollinator linkage level	No. of links between pollinator species $m$ and the plant community
$\langle L_m \rangle$	Average pollinator linkage level	$= I/A$
$L_n$	Plant linkage level	No. of links between plant species $n$ and the pollinator community
$\langle L_n \rangle$	Average plant linkage level	$= I/P$
<i>1-Mode network</i>		
$N$	Community size	$= A$ or $P$
$m$	Link number	No. of links between $N$
$d$	Link density	$= 2m/(N(N-1))$
$k_i$	Degree or linkage level of species $i$	No. of links between species $i$ and all other species in the network
$\langle k \rangle$	Average species degree or linkage level	$= 2m/N$
$\langle l \rangle$	Characteristic path length	No. of steps (i.e. links) along the shortest path between two species, averaged over all pairs of species
$D$	Network diameter	The longest of all shortest $l$ of any species pair in the network
$c_i$	Clustering coefficient of species $i$	Density of links within the neighbourhood of species $i$ . The neighbourhood of $i$ is the subgraph that consists of the $k_i$ species one step away from $i$ (excluding $i$ itself)

more or less extensive period, most often one season. All published networks are described in detail in their individual references (Table 1). The networks cover all latitudes and altitudes, and many habitat types. However, data from lowland rainforests are lacking. These habitats are with their high species richness and strong 3-dimensional structure extremely laborious to sample. In our analysis, we excluded any information about link strength, e.g. measured as number of flower visits or visitors per time unit per flower. Thus we only operated with presences or absences of links. Operationally, we define all flower visitors as pollinators.

An adjacency matrix, whose elements consist of zeros and ones, describe a network. A “one” indicates presence of a link between two species, and a “zero” that no link was observed. A set of 2-mode pollination network properties were included in the analysis, see Table 2. As our network units, we used biological species and not trophic species because the taxonomic resolution was high in all networks. This is an advantage compared to traditional food web studies, which often use highly aggregated data. Each 2-mode network was transformed into two 1-mode networks by the use of a piece of software called Pajek (Version October 2003, freely available at <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>). One-mode networks consisting of  $N$  species ( $N = A$  or  $P$ ) have a set of properties, which govern their behaviour, see Table 2.

### 3. Results

#### 3.1. 2-mode networks

The 2-mode networks ranged tremendously in size,  $S$ , from just 22–952 taxonomic species (Table 1). Species

numbers of pollinators,  $A$ , and plants,  $P$ , from the same network were highly significantly correlated (1 Appendix). Average ratio between  $A$  and  $P$  was  $3.17 \pm 1.82$  (range 0.59–7.50, median 2.79).

#### 3.2. 1-mode networks

Each 2-mode network was transformed into a pair of 1-mode network relatives, one for the pollinators and one for the plants. This transformation, however, created small isolates of 1–2 species without link attachment to the main component of the network. These isolates were excluded from the calculations of  $\langle k \rangle$ ,  $\langle l \rangle$ ,  $\langle D \rangle$ , and  $\langle c \rangle$  (in 1-species isolates  $k = 0$ , and in 2-species isolates  $k = 1$ ). One reason for the existence of isolates may be the presence of specialized species groups; another may be an overall low link density,  $d$ , which may be either real or artificial, i.e. more sampling may have exposed links between isolates and the main component of the network. This seems likely because our data demonstrated a negative relationship between  $d$  and number of 1–2 species isolates per network (2 Appendix).

Total number of links in a pollinator network,  $m_A$ , and in a plant network,  $m_P$ , were highly significantly positively correlated (3 Appendix), and both increased significantly with  $A$  and  $P$ , respectively (4 Appendix). The latter two relationships were similar (5 Appendix).  $m_A$  and  $m_P$  were also highly significantly dependent upon total no. of links,  $I$ , in their 2-mode network relative (6 Appendix).

Link density in pollinator network,  $d_A$ , and plant network,  $d_P$ , were highly significantly positively correlated (7 Appendix), and both decreased significantly with  $A$  and  $P$ , respectively (8 Appendix). The latter two relationships

were statistically similar (9 Appendix).  $d_A$  and  $d_P$  also increased significantly with connectance,  $C$ , in the 2-mode network relative (10 Appendix).

Average number of degrees or links per pollinator species,  $\langle k_A \rangle$ , and per plant species,  $\langle k_P \rangle$ , in a pair of 1-mode networks were highly significantly positively correlated (11 Appendix), and both increased significantly with  $A$  and  $P$ , respectively (12 Appendix). The latter two relationships were similar (13 Appendix).  $\langle k_A \rangle$  and pollinator linkage level,  $\langle L_m \rangle$ , were uncorrelated (14 Appendix).  $\langle k_P \rangle$ , on the other hand, increased significantly with plant linkage level,  $\langle L_n \rangle$  (15 Appendix).

Average path length in a pollinator network,  $\langle l_A \rangle$ , and in a plant network,  $\langle l_P \rangle$ , were highly significantly positively correlated (16 Appendix), and both increased significantly with  $A$  and  $P$ , respectively (17 Appendix). The latter two relationships were similar (18 Appendix).  $\langle l_A \rangle$  and  $d_A$  were highly significantly negatively correlated (19 Appendix), and so were  $\langle l_P \rangle$  and  $d_P$  (20 Appendix).

Diameter in a pollinator network,  $D_A$ , and in a plant network,  $D_P$ , were highly significantly positively correlated (21 Appendix), and both parameters increased significantly with  $A$  and  $P$ , respectively (22 Appendix).

Average clustering coefficient in a pollinator network,  $\langle c_A \rangle$ , and in a plant network,  $\langle c_P \rangle$ , were uncorrelated (23 Appendix), and so were  $\langle c_A \rangle$  and  $A$  (24 Appendix).  $\langle c_P \rangle$ , on the other hand, decreased significantly with  $P$  (25 Appendix).  $\langle c_A \rangle$  and  $d_A$  were highly significantly positively correlated (26 Appendix), and so were  $\langle c_P \rangle$  and  $d_P$  (27 Appendix).  $d$  is equal to  $\langle c_{random} \rangle$  in a random network, i.e. a similar-sized network with links randomly distributed among species. For our total data set,  $\langle d \rangle$  ( $= \langle \langle c_{random} \rangle \rangle$ )  $= 0.44 \pm 0.24$  ( $n = 74$  one-mode networks) and  $\langle \langle c_{actual} \rangle \rangle = 0.84 \pm 0.058$  ( $n = 74$ ). Thus clustering of species was much higher in actual than in random networks (28 Appendix).  $\langle c_A \rangle$  and  $\langle l_A \rangle$  were significantly negatively correlated (29 Appendix), and so were  $\langle c_P \rangle$  and  $\langle l_P \rangle$  (30 Appendix).

## 4. Discussion

### 4.1. Answers to our first four questions

The three pairs of 1- and 2-mode network properties,  $m$  and  $I$ ,  $d$  and  $C$ , and  $\langle k \rangle$  and  $\langle L \rangle$ , respectively, were all correlated, except for  $\langle k_A \rangle$  and  $\langle L_A \rangle$ . Thus the structure of 2-mode networks and their 1-mode versions are closely related.

$m$ ,  $d$ ,  $\langle k \rangle$ ,  $\langle l \rangle$ , and  $\langle c_P \rangle$  were all scale-variant, i.e. they were dependent upon size of network ( $A$  or  $P$ ).  $m$ ,  $d$ ,  $\langle k \rangle$ , and  $\langle l \rangle$ , but not  $\langle c \rangle$ , for 1-mode plant and pollinator networks were highly correlated.

$\langle \langle l \rangle \rangle$  was 1.7 and 1.5, and  $\langle \langle c \rangle \rangle$  was 0.85 and 0.84 for pollinators and plants, respectively. Thus pollination networks have very strong small-world properties.

### 4.2. The 5th question: comparison between food webs and pollination networks

Dunne et al. (2002) made a broad network analysis of 16 food webs ( $\langle N \rangle = 85$  species, range 25–172), and Montoya and Solé (2002) analysed four larger food webs ( $\langle N \rangle = 141$  species, range 93–182). The four webs from the latter study are included in Dunne et al. (2002).

Density,  $d$ , of 1-mode pollinator and plant networks is conceptually similar to connectance,  $C$ , of their 2-mode relatives and they were also found to be significantly related. However, in the 74 one-mode pollination networks,  $\langle d \rangle = 0.44 \pm 0.24$  and thus much larger than the  $\langle C \rangle = 0.12 \pm 0.09$  of the 37 two-mode networks.  $\langle d_{food\ webs} \rangle = 0.11 \pm 0.09$  for the 16 food webs studied by Dunne et al. (2002) (calculated from their Table 1, using the formula  $\langle d \rangle = \langle 2m/N^2 \rangle$ . We used  $\langle d \rangle = \langle 2m/(N(N-1)) \rangle$ ). If we use our formula on the data in Dunne et al. (2002), we get  $\langle d_{food\ webs} \rangle = 0.12 \pm 0.09$ ). Thus 1-mode pollination networks are much more densely linked than food webs.

In 1-mode pollination networks,  $\langle k \rangle$  increased significantly with number of species,  $N$ . However, linkage level of species in the 2-mode pollination networks was independent upon  $A$  and  $P$  (31 Appendix). Food web linkage level increased (marginally) significantly with  $N$  (32 Appendix) (Dunne et al., 2002).

$\langle l \rangle$  was not significantly dependent upon  $N$  in the set of non-ecological webs analysed in Albert and Barabási (2001) (the two ecological webs excluded). However, Albert et al. (1999) and Barabási et al. (2000) demonstrated that the World-Wide Web grows according to  $\langle l \rangle = 0.35 + 2.06 \log N$ , where  $N$  is number of homepages. This is much faster than what we see in 1-mode pollination networks ( $n = 74$  (plants and pollinators pooled),  $\langle l \rangle = 0.82 + 0.46 \log N$ , and Table 3). The reason for this slower increase is that pollination networks are much more clustered than the World-Wide Web. This logarithmic scaling of  $\langle l \rangle$  is often termed the “small-world effect” (e.g. Hastings, 2003). In fact,  $\langle l \rangle$  of a network is of the order of the logarithm of its size (Watts and Strogatz, 1998) ( $\langle \langle l_{pollinators} \rangle \rangle = 1.7$  and  $\log \langle A \rangle = 1.9$ ;  $\langle \langle l_{plants} \rangle \rangle = 1.5$  and  $\log \langle P \rangle = 1.5$ ). In evolving standardized random networks,  $\langle l \rangle$  grows approximately as  $\ln \langle k \rangle / \ln N$  (Jung et al., 2002; Newman, 2001). The average of the latter expression was 1.4 for both pollinators and plants. In the small food webs analysed by Dunne et al. (2002),  $\langle l \rangle$  also increases with  $N$ . However, the relationship appears negative for the larger food webs (Table 3). In Williams et al. (2002)  $\langle l \rangle$  does not increase with  $N$  ( $F = 0.212$ ,  $p < 0.66$ ). The latter two results may be an artifact of small sample sizes.

In Dunne et al. (2002),  $\langle \langle l \rangle \rangle = 2.18$ , and in Williams et al. (2002),  $\langle \langle l \rangle \rangle = 1.93$ , which is considerably longer than in 1-mode pollination networks (1.60). However, Williams et al. (2002) also stress that “the two degrees of separation” may overestimate distances, because food webs

Table 3  
Comparisons of pollination and food webs

	Average path length ( $\langle l \rangle$ )		Clustering coefficient ( $\langle c \rangle$ )	
	This study ( $n = 74$ )	Dunne et al. (2002) ( $n = 16$ )	This study ( $n = 74$ )	Dunne et al. (2002) ( $n = 16$ )
Total no. species ( $N$ )	$\ln \langle l \rangle = 0.127 \ln N - 0.0427$ , $R^2 = 0.49$ , $F = 71.8$ , $p < 0.0001$	$\ln \langle l \rangle = -0.764$ $(\ln N)^2 + 0.947 \ln N$ , $R^2 = 0.33$ , $F = 4.73$ , $p < 0.03$	$\arcsin(c^{0.5}) = -0.0225$ $\ln N + 1.257$ , $R^2 = 0.06$ , $F = 5.92$ , $p < 0.02$	$\arcsin(c^{0.5}) = -0.0919$ $\ln N + 0.781$ , $R^2 = 0.14$ , $F = 3.53$ , $p < 0.08$
Link density ( $d$ )	$\ln \langle l \rangle = -0.649 \arcsin$ $(d^{0.5}) + 0.918$ , $R^2 = 0.79$ , $F = 272$ , $p < 0.0001$	$\ln \langle l \rangle = -1.841 \arcsin$ $(d^{0.5}) + 1.345$ , $R^2 = 0.81$ , $F = 66.8$ , $p < 0.0001$	$\arcsin(c^{0.5}) = 0.193 \arcsin$ $(d^{0.5}) + 1.030$ , $R^2 = 0.33$ , $F = 36.8$ , $p < 0.001$	$\arcsin(c^{0.5}) = 0.791 \arcsin$ $(d^{0.5}) + 0.134$ , $R^2 = 0.50$ , $F = 15.9$ , $p < 0.001$
Average no. links per species ( $\langle k \rangle$ )	$\ln \langle l \rangle = 0.0822 \ln$ $\langle k \rangle + 0.214$ , $R^2 = 0.10$ , $F = 8.99$ , $p < 0.004$	$\ln \langle l \rangle = -0.239 \ln$ $\langle k \rangle + 1.179$ , $R^2 = 0.44$ , $F = 12.6$ , $p < 0.003$	$\arcsin(c^{0.5}) = -0.00882 \ln$ $\langle k \rangle + 1.195$ , $R^2 = 0.00$ , $F = 0.446$ , $p < 0.51$	$\arcsin(c^{0.5}) = 0.0384 \ln$ $\langle k \rangle + 0.322$ , $R^2 = 0.00$ , $F = 0.622$ , $p < 0.44$

only take trophic interactions into account. One of the 1-mode pollination network (M. Bundgaard unpublished), was even fully connected, i.e.  $\langle l_{plants} \rangle = 1.00$ . Average diameter,  $D$ , in 1-mode pollination networks was  $3.0 \pm 0.9$  (Table 1, data for pollinators and plants were pooled). Thus even in large pollination networks, important species interaction dynamics is global and almost all species exert direct or strong indirect effects upon each other, i.e. local becomes global. Short  $\langle l \rangle$  and  $D$  corroborate the findings of Williams et al. (2002) that in ecological webs “everything is connected to everything”. Short species distance may also indicate that none of our pollination networks spanned over strong habitat boundaries, i.e. that the networks were not compartmentalized. The reasons for the prevalence of short  $\langle l \rangle$  and  $D$  in pollination networks have to be found in an exploration of their nested structure (Bascompte et al., 2003).

In both 1-mode pollination networks and food webs,  $\langle l \rangle$  and  $d$  were negatively correlated (Dunne et al., 2002, Williams et al., 2002, Table 3). However, in pollination networks  $\langle l \rangle$  increased with  $\langle k \rangle$ , whereas this relationship was negative in food webs (Table 3).

$\langle c \rangle$  was not significantly dependent upon  $N$  in the set of webs given in Albert and Barabási (2001) (the two ecological webs excluded).  $\langle c \rangle$  in pollinator network and in food webs was also independent of species number, whereas plants'  $\langle c \rangle$  in 1-mode pollination networks decreased slightly with increasing species number (Table 3).

Dunne et al. (2002) analysed the clustering coefficient ratio,  $\langle c \rangle / \langle c_{random} \rangle$  (where  $\langle c_{random} \rangle = d$ ). In the 16 food webs analysed, this ratio varied between 0.3 and 3.8. In pollination networks the range was 1.0–10.9. Thus compared to randomly constructed networks, links were more clustered in pollination networks than in food webs. Dunne et al. (2002) showed that the clustering coefficient ratio for 34 biological (including the ecological ones) and non-biological networks increased as a power-law function with number of species (clustering coefficient ratio =  $0.028N^{0.96}$ ). Consequently, Dunne et al. (2002) also found that  $\langle c \rangle$  scaled linearly with  $\langle k \rangle$ , if all 34 networks were included. This relationship between  $\langle c \rangle$  and  $\langle k \rangle$  was not present among the 16 food webs alone (Table 3). Clustering

coefficient ratio of pollination networks behaved as in food webs with regard to species number ( $S$ ) (33 Appendix), although the increase was slower. As in food webs,  $\langle c \rangle$  and  $\langle k \rangle$  were also uncorrelated in pollination networks ( $F = 0.36$ ,  $p < 0.55$ ).

Dunne et al. (2002) suggest that one cannot expect to find a high clustering of species in food webs because of their multi-trophic level structure. In accordance with that, we observed the opposite for pollination networks with their 1-level structure.

Thus, overall, average path length  $\langle l \rangle$  and average clustering coefficient  $\langle c \rangle$  scaled similarly with respect to  $N$  and  $d$  in food and pollination webs (Table 3).

Our analysis demonstrates that pollination networks have strong small-world properties, i.e. a very high clustering coefficient,  $c$ , as in regular networks and a very short characteristic path length,  $l$ , as in random networks (Watts and Strogatz, 1998). The overall average  $\langle \langle c \rangle \rangle = 0.84 \pm 0.058$  is close to its maximum value of 1, and  $\langle \langle l \rangle \rangle = 1.60 \pm 0.31$  is close to its minimum value of 1. Species were more tightly connected in pollination networks than in food webs (food webs: Dunne et al. (2002)  $N = 16$ ,  $\langle \langle l \rangle \rangle = 2.18 \pm 0.60$ ,  $\langle \langle c \rangle \rangle = 0.16 \pm 0.10$ ; Montoya and Solé (2002)  $N = 4$ ,  $\langle \langle l \rangle \rangle = 2.58 \pm 0.55$ ,  $\langle \langle c \rangle \rangle = 0.23 \pm 0.08$ ). In addition, Dunne et al. (2002) showed that the smallest food webs had the highest clustering. A similar trend was only seen in our plant networks. However, when pollinator and plant data were pooled  $\langle c \rangle$  also decreased with increasing  $N$  (Table 3). Dunne et al. (2002) explained the overall low  $\langle c \rangle$  in food webs by their small size,  $N (< 172)$ . Although the pollination networks ranged far higher in species number ( $< 952$ ), small  $N$  cannot in this case explain low  $\langle c \rangle$ . On the contrary, since the smallest networks had the highest  $\langle c \rangle$  (Table 3).

In conclusion, information about a few basic network parameters put us in a position from where we can achieve a fairly precise picture of the structure of both 1- and 2-mode networks. Although 1- and 2-mode networks structurally are fundamentally different, their properties are closely correlated. Thus link structure within and between trophic levels is correlated. This has important

implications to our general understanding of ecological web structure. 1-mode pollination networks are more tightly connected than food webs, maybe because they only consist of one trophic level. An analysis of each trophic level in food webs separately would be an interesting next step.

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### Appendix. (LR, least squares linear regression analysis)

(1) LR:  $N = 37$ ,  $\ln A = 1.073 \ln P + 0.728$ ,  $R_{adj}^2 = 0.67$ ,  $F = 74.4$ ,  $p < 0.0001$ .

(2) Pollinator networks: LR: no. isolates =  $0.79/d_A - 1.35$ ,  $R_{adj}^2 = 0.50$ ,  $F = 37.2$ ,  $p < 0.0001$ ; plant networks: no. isolates =  $1.99/d_P - 2.61$ ,  $R_{adj}^2 = 0.67$ ,  $F = 74.4$ ,  $p < 0.0001$ .

(3) LR:  $N = 37$ ,  $\ln m_A = 0.941 \ln m_P + 1.746$ ,  $R_{adj}^2 = 0.61$ ,  $F = 57.9$ ,  $p < 0.0001$ .

(4) LR:  $n = 37$ ,  $\ln m_A = 1.603 \ln A - 0.246$ ,  $R_{adj}^2 = 0.95$ ,  $F = 653$ ,  $p < 0.0001$ , and  $\ln m_P = 1.729 \ln P - 0.539$ ,  $R_{adj}^2 = 0.92$ ,  $F = 441$ ,  $p < 0.0001$ .

(5) *t*-test: slope:  $t = 1.21$ ,  $0.2 < p < 0.5$ ; intercept:  $t = 0.192$ ,  $p > 0.5$ .

(6) LR:  $\ln m_A = 1.531 \ln I - 1.388$ ,  $R_{adj}^2 = 0.91$ ,  $F = 363$ ,  $p < 0.0001$ , and  $\ln m_P = 1.232 \ln I - 1.230$ ,  $R_{adj}^2 = 0.84$ ,  $F = 183$ ,  $p < 0.0001$ .

(7) LR:  $N = 37$ ,  $\sin^{-1}(d_A^{0.5}) = 0.576 \sin^{-1}(d_P^{0.5}) + 0.121$ ,  $R_{adj}^2 = 0.55$ ,  $F = 44.6$ ,  $p < 0.0001$ .

(8) LR:  $\sin^{-1}(d_A^{0.5}) = -0.128 \ln A + 1.166$ ,  $R_{adj}^2 = 0.45$ ,  $F = 30.2$ ,  $p < 0.0001$ , and  $\sin^{-1}(d_P^{0.5}) = -0.167 \ln P + 1.410$ ,  $R_{adj}^2 = 0.26$ ,  $F = 13.4$ ,  $p < 0.001$ .

(9) *t*-test: slope:  $t = 0.963$ ,  $0.2 < p < 0.5$ ; intercept:  $t = 0.192$ ,  $p > 0.5$ .

(10) LR:  $\sin^{-1}(d_A^{0.5}) = 1.384 \sin^{-1}(C^{0.5}) + 0.149$ ,  $R_{adj}^2 = 0.81$ ,  $F = 155$ ,  $p < 0.0001$ , and  $\sin^{-1}(d_P^{0.5}) = 1.545 \sin^{-1}(C^{0.5}) + 0.332$ ,  $R_{adj}^2 = 0.59$ ,  $F = 53.3$ ,  $p < 0.0001$ .

(11) LR:  $N = 37$ ,  $\ln \langle k_A \rangle = 0.764 \ln \langle k_P \rangle + 1.077$ ,  $R_{adj}^2 = 0.51$ ,  $F = 39.1$ ,  $p < 0.0001$ .

(12) LR:  $\ln \langle k_A \rangle = 0.603 \ln A + 0.448$ ,  $R_{adj}^2 = 0.72$ ,  $F = 92.0$ ,  $p < 0.0001$ , and  $\ln \langle k_P \rangle = 0.729 \ln P + 0.153$ ,  $R_{adj}^2 = 0.68$ ,  $F = 78.4$ ,  $p < 0.0001$ .

(13) *t*-test: slope:  $t = 1.21$ ,  $0.2 < p < 0.5$ ; intercept:  $t = 0.191$ ,  $p > 0.5$ .

(14)  $F = 0.78$ ,  $p < 0.38$ .

(15) LR:  $\ln \langle k_P \rangle = 0.668 \ln \langle L_n \rangle + 1.339$ ,  $R_{adj}^2 = 0.25$ ,  $F = 12.8$ ,  $p < 0.001$ .

(16) LR:  $N = 37$ ,  $\ln l_A = 0.647 \ln l_P + 0.297$ ,  $R_{adj}^2 = 0.58$ ,  $F = 50.4$ ,  $p < 0.0001$ .

(17) LR:  $\ln \langle l_A \rangle = 0.095 \ln A + 0.116$ ,  $R_{adj}^2 = 0.41$ ,  $F = 25.5$ ,  $p < 0.0001$ , and  $\ln \langle l_P \rangle = 0.149 \ln P - 0.142$ ,  $R_{adj}^2 = 0.42$ ,  $F = 26.7$ ,  $p < 0.0001$ .

(18) *t*-test: slope:  $t = 1.59$ ,  $0.2 < p < 0.5$ ; intercept:  $t = 0.182$ ,  $p > 0.5$ .

(19) LR:  $N = 37$ ,  $\ln \langle l_A \rangle = -0.713 \sin^{-1}(d_A^{0.5}) + 0.965$ ,  $R_{adj}^2 = 0.83$ ,  $F = 183$ ,  $p < 0.0001$ .

(20) LR:  $\ln \langle l_P \rangle = -0.591 \sin^{-1}(d_P^{0.5}) + 0.863$ ,  $R_{adj}^2 = 0.68$ ,  $F = 77.8$ ,  $p < 0.0001$ .

(21) LR:  $\ln D_A = 0.647 \ln D_P + 0.297$ ,  $R_{adj}^2 = 0.58$ ,  $F = 50.4$ ,  $p < 0.0001$ .

(22) LR:  $\ln D_A = 0.095 \ln A + 0.116$ ,  $R_{adj}^2 = 0.41$ ,  $F = 25.5$ ,  $p < 0.0001$ , and  $\ln D_P = 0.149 \ln P - 0.142$ ,  $R_{adj}^2 = 0.42$ ,  $F = 26.7$ ,  $p < 0.0001$ .

(23)  $F = 1.32$ ,  $p < 0.26$ .

(24)  $F = 1.32$ ,  $p < 0.26$ .

(25) LR:  $\ln \langle c_P \rangle = -0.055 \ln P + 0.005$ ,  $R_{adj}^2 = 0.30$ ,  $F = 16.2$ ,  $p < 0.001$ .

(26) LR:  $\ln \langle c_A \rangle = 0.240 \sin^{-1}(d_A^{0.5}) - 0.175$ ,  $R_{adj}^2 = 0.10$ ,  $F = 5.01$ ,  $p < 0.03$ .

(27) LR:  $\ln \langle c_P \rangle = 0.187 \sin^{-1}(d_P^{0.5}) - 0.215$ ,  $R_{adj}^2 = 0.47$ ,  $F = 32.7$ ,  $p < 0.0001$ .

(28) Paired *t*-test:  $t = 8.93$ ,  $p < 0.0001$ .

(29) LR:  $\ln \langle c_A \rangle = -0.149 \ln \langle l_A \rangle - 0.0887$ ,  $R_{adj}^2 = 0.22$ ,  $F = 11.0$ ,  $p < 0.002$ .

(30) LR:  $\ln \langle c_P \rangle = -0.368 \ln \langle l_P \rangle - 0.047$ ,  $R_{adj}^2 = 0.73$ ,  $F = 96.8$ ,  $p < 0.0001$ .

(31) LR: pollinators:  $F = 0.182$ ,  $p < 0.67$ , plants:  $F = 2.11$ ,  $p < 0.16$ .

(32) LR:  $\ln(\text{food web linkage level}) = 0.534 \ln N - 0.445$ ,  $R^2 = 0.18$ ,  $F = 4.32$ ,  $p < 0.057$ .

(33) LR on transformed values: clustering coefficient ratio =  $0.49 N^{0.39}$ ,  $R^2 = 0.53$ ,  $F = 83.7$ ,  $p < 0.0001$ .

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