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Published in:
Ecological Complexity : An International Journal on Biocomplexity in the Environment and Theoretical Ecology

DOI:
doi:10.1016/j.ecocom.2009.03.008

Publication date:
2010

Document Version
Early version, also known as pre-print

Citation for published version (APA):
Martín González, A. M., Dalsgaard, B., & Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity : An International Journal on Biocomplexity in the Environment and Theoretical Ecology, 7, 36-43. https://doi.org/doi:10.1016/j.ecocom.2009.03.008

Download date: 07. maj. 2019

Ecological Complexity 7 (2010) 36–43

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Centrality measures and the importance of generalist species in pollination networks

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ARTICLE INFO

Article history:
Received 30 July 2007
Received in revised form 9 March 2009
Accepted 10 March 2009
Available online 7 April 2009

Keywords:
Betweenness centrality
Closeness centrality
Generalization level
Pollination networks
Keystone species

ABSTRACT

Studies of complex networks show that nodes with high centrality scores are important to network structure and stability. Following this rationale, centrality measures can be used to (i) identify keystone species in ecological networks, a major issue in community ecology, and (ii) differentiate the keystone species concept, e.g. species may play a key role in a network for different topological reasons. In 34 pollination communities we examine the relationship between the generalization level of species (*ND*) and two complementary centrality indices: closeness (*CC*) and betweenness centrality (*BC*). *CC* measures the proximity of a species to all other species in the community, while *BC* describes the importance of a species as a connector. Most networks had a linear *ND*–*CC* relationship with a minimum *CC* value of 0.41. Hence, species were close to each and will be likely to be rapidly affected by disturbances. Contrarily, in most networks, the *ND*–*BC* relationships were power-law distributed with exponents larger than one. Only 59% of the species were connectors ($BC > 0$). In particular, there was a connector threshold value of $ND = 0.46$. Species above this threshold represent ~40%, almost all of which were connectors. These results indicate that in pollination systems the most generalized species are usually network keystone species, playing at least two roles: (i) interact closely with most other species (high *CC*) and (ii) connect otherwise unconnected subnetworks (high *BC*). We discuss the implications of centrality measures to community-based conservation ecology.

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1. Introduction

The topological structure of complex networks strongly determines their dynamics and stability (Strogatz, 2001; Kolasa, 2005, 2006; Namba et al., 2008). However, not all nodes are equally important for dynamics and stability of the system. The topological importance of nodes is commonly quantified using centrality indices (Freeman, 1979; Wasserman and Faust, 1994; de Nooy et al., 2005; Estrada and Bodin, 2008). The higher importance of these central nodes is illustrated by a faster breakdown of the network structure when they are selectively removed than when nodes are removed at random (e.g. Albert et al., 2000; Jeong et al., 2000; Memmott et al., 2004). Different centrality indices measure different aspects related to the position of a node within its network. For example, closeness centrality (*CC*) measures the proximity of a node to all other nodes in the network (Freeman, 1979), i.e. nodes with high *CC* values can rapidly affect other nodes and *vice versa*. Alternatively, betweenness centrality (*BC*) describes the importance of a node as a connector between different parts of the network (Freeman, 1979). Nodes with $BC > 0$ connect areas of the network that would otherwise be sparsely or not connected at all (Newman, 2004).

The same concept of node centrality can be applied to ecological networks (Jordán et al., 2006; Estrada, 2007) to identify keystone species (*sensu* Paine, 1969). Species with the potential to affect many other species will have a high *CC*. Species which are important to the cohesiveness of the network will have a positive *BC*. A couple of studies have explored this topic in food webs (Jordán et al., 2006; Estrada, 2007). However, despite evidence of declining pollinator populations (Biesmeijer et al., 2006), possible linked plant extinctions and overall degradation of pollinator community biodiversity (Allen-Wardell et al., 1998; Kearns et al., 1998), node centrality has not been explored in pollination networks. Here we examine how these two common centrality indices, *CC* and *BC*, are distributed among species in pollination networks.

We expect a positive correlation between the generalization level of a species and its importance to network stability for two

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doi:10.1016/j.ecocom.2009.03.008

reasons: (i) nodes with many links (i.e. species with a high generalization level) have on average shorter distances to the rest of the nodes in the network, as shown in several ecological and non-ecological studies (Dunne et al., 2002; Goh et al., 2002; Guimerà and Amaral, 2004; Hahn and Kerns, 2004; Memmott et al., 2004; Jordán et al., 2006; Lee, 2006; Estrada, 2007); and (ii) nestedness, a dominant pattern widely observed in pollination networks. Nestedness implies a highly centralized structure composed of a periphery of specialist species attached to a densely connected core of generalists (Bascompte et al., 2003). This core of generalist species is suggested to play a key role in the evolution and persistence of pollination communities (Bascompte et al., 2003; Memmott et al., 2004).

In this paper, we use a database of 34 pollination networks to investigate the topological importance of plant and pollinator species in relation to their generalization level. Our objectives are: (i) to examine the relationship between generalization level and closeness (*CC*) and betweenness centrality (*BC*) scores; (ii) search for phase transitional phenomena in the relations between generalization and *CC* and *BC*; and (iii) discuss the potential use of *CC* and *BC* as indicators of keystone species in pollination networks.

2. Data

We analyzed 34 well-resolved pollination networks from a variety of climatic regions, altitudes and levels of insularity (see Appendix A for references). For each data set, we made a 2-mode plant–pollinator interaction network in which a plant and an animal species are connected if flower visitation is observed. We then transformed each 2-mode network into two 1-mode network: (1) a 1-mode plant network where nodes are plant species and a link between two plants represents that they share at least a common pollinator species, and (2) a 1-mode pollinator network where nodes are pollinator species and a link between two pollinators represents that they visit at least one common plant species.

3. Data analysis

For each species we measured the level of generalization and the closeness and betweenness centrality. We define the generalization level of a species as the proportion of species it interacts with out of the total possible in the network (normalised degree, *ND*). As mentioned, *CC* measures how close a focal species *i* is to all other species in the network (Freeman, 1979; de Nooy et al., 2005). *CC* of *i* is

$$CC_i = \sum_{j=1;i\neq j}^{n} \frac{d_{ij}}{n-1}$$

where n is number of species, and d_{ij} is the shortest distance between species i and j measured in number of links. Effects of species upon each other become weaker with increasing link distance. Therefore, in systems where distances are great, global measures of importance such as CC may be inappropriate (Estrada, 2007). However, pollination networks are small worlds, i.e. all species are close to each other (Olesen et al., 2006). Therefore, *CC* stills gives important information about direct and indirect effects among species in pollination networks.

BC of a species *i* is the fraction of shortest paths between all pairs of species in the network, which pass through *i* (Freeman, 1979; de Nooy et al., 2005). *BC* of *i* is

$$BC_i = 2 \sum_{j<k;i\neq j} \frac{g_{jk}(i)/g_{jk}}{(n-1)(n-2)}$$

where n is number of species in the network, g_{jk} is number of shortest paths linking any two species, and $g_{jk}(i)$ is the number of those shortest paths among g_{jk}, that pass through i (Wasserman and Faust, 1994). Species with a $BC > 0$ are termed connectors.

We tested for linear correlations between *ND–CC* and *ND–BC*, respectively, using Spearman rank correlation analysis. We then inspected the *ND–CC* and *ND–BC* relationships in more detail, testing to which of two simple models they had the best fit: linear (centrality = $aND + b$) and power-law (centrality = cND^d), where a, b, c, and d are constants. For *ND–BC* relationships following a power-law, we identified a "connector threshold value" in *ND* above which the relationship increased rapidly, i.e. a kind of phase transition. We did this by locating the best fit line to the scores within the predicted confidence limits of the tail of the power-law. We defined this connector threshold value where the best fit line intersected with the *ND*-axis (where $BC = 0$). We compared this value in the different networks and estimated the proportion of species below and above this threshold value and how many of these species were connectors. We used Pajek *v* 1.15 to calculate centrality scores, and JMP for statistical analyses.

4. Results

All *ND–CC* and *ND–BC* correlations were significant. *ND* and *CC* were strongly correlated (Table 1). When analyzing the *ND–CC* relationships in more detail most networks had a linear relationship but some had a best fit to a power-law model (Fig. 1 and Table 1; Appendix A). In the latter cases the exponents varied between zero and one, i.e. there was a rapid increase in *CC* values for low *ND* values and a stabilisation of *CC* at higher *ND* values (Fig. 1D). The interception of the *ND–CC* correlation averaged a *CC* of 0.41. Hence, only the most specialized species had a small *CC* (Table 1; Appendix A).

On the other hand *ND–BC* correlations were weaker. The *ND–BC* relationship followed, with very few exceptions, a power-law model with an exponent larger than one (Table 1; Appendix A), i.e. there was a slow increase in *BC* at low *ND* and a fast increase at higher *ND* values (Fig. 2). The interception of the *ND–BC* correlation

Table 1
Spearman rank correlations of *ND–CC* and *ND–BC* for plant and animal species. The number of networks for which the best fit is a linear or a power-law relationship is given. The average power-law exponent is based on those networks for which the best fit is a power-law. The interception with the centrality axis is based on the best fit line. All means followed by SD.

Centrality measure	Network	Spearman rank r_s[a]	Linear	Power-law	Power-law exponent	Interception with *CC*/*BC*
CC	Plants	0.99 ± 0.01	33	1	0.36 ± 0.00	0.40 ± 0.06
	Animals	0.97 ± 0.03	27	7	0.22 ± 0.15	0.42 ± 0.04
	Total	0.98 ± 0.03	60	8	0.24 ± 0.15	0.41 ± 0.05
BC	Plants	0.84 ± 0.11	3	31	6.45 ± 5.72	−0.03 ± 0.04
	Animals	0.74 ± 0.14	0	34	4.38 ± 2.05	−0.03 ± 0.04
	Total	0.79 ± 0.14	3	65	5.37 ± 4.31	−0.03 ± 0.04

[a] All significant at $p < 0.01$ or $p < 0.05$.

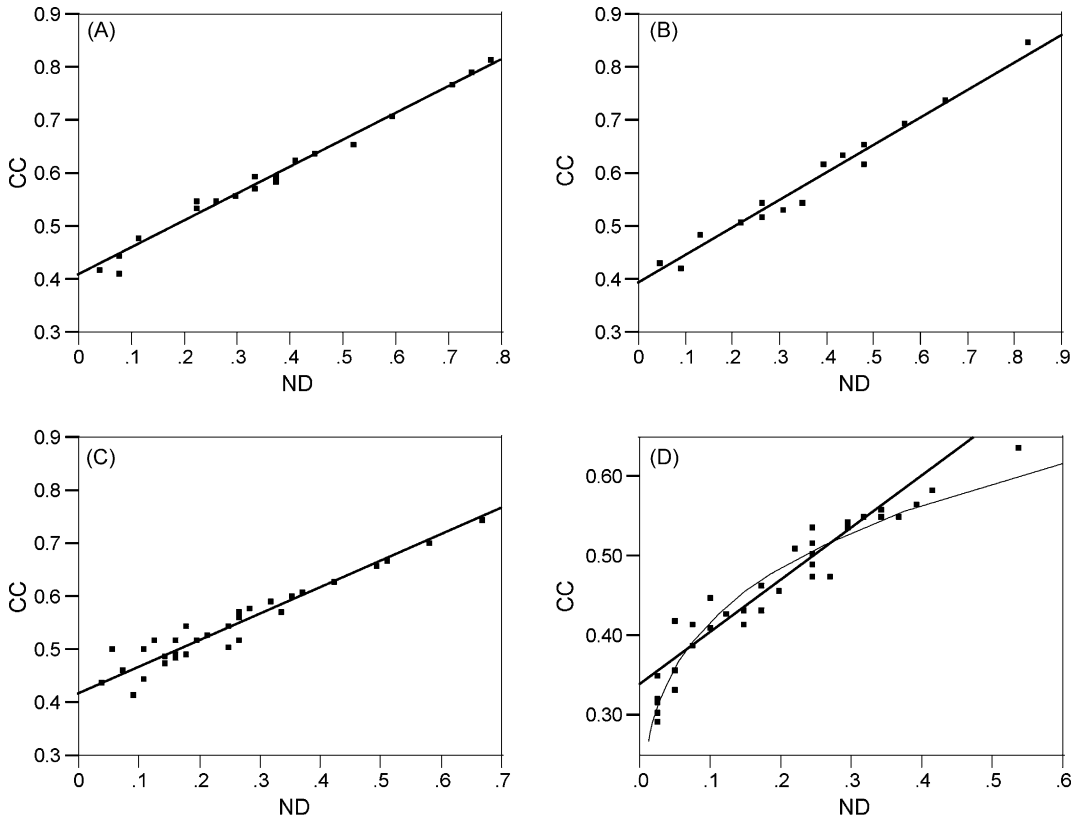

Fig. 1. Example networks to illustrate *ND–CC* relationship: (A) Arctic plants, Northern Canada (Hocking, 1968); (B) Caribbean lowland plants, Dominica (Martín González, A.M., et al., unpublished); (C) Oceania animals, New Zealand (Primack, 1983; Arthur's Pass study site); (D) South America animals, Venezuela (Ramírez, 1989). Best fit for graphs (A)–(C) is a linear model, whereas for graph d is a power-law. For each graph, the line of best fit and its interception with the *CC*-axis is shown. Dots may represent several species.

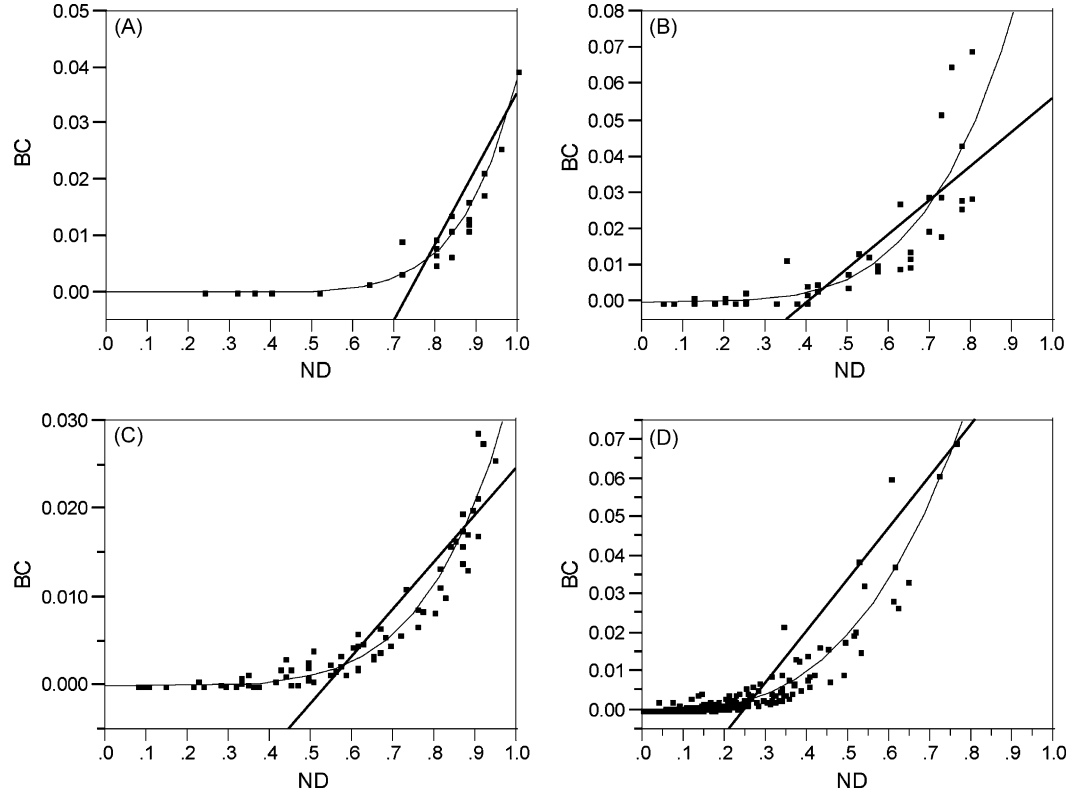

Fig. 2. Example networks to illustrate *ND–BC* relationship: (A) Mediterranean plants, Southern Spain (Herrera, 1988); (B) Oceanian plants, New Zealand (Primack, 1983; Cass study site); (C) Arctic animals, Greenland (Olesen, J.M., Elberling, H., unpublished); (D) Asian forest animals, Japan (Inoue et al., 1990). All graphs follow a power-law model. The best fit lines of the scores within the predicted confidence limits of the tail of the power-law are shown. The connector threshold is the interception with the *ND*-axis (when *BC* = 0). Dots may represent several species.

Table 2
Proportional number of connector species, connector threshold values and distribution of connector species below and above the connector threshold value are given. The values are averaged for all networks with a power-law relation between *ND*–*BC*. All means followed by SD.

Network	% connector species	Connector threshold value (*ND*)	% species below threshold	% species above threshold	% connector species below threshold	% connector species above threshold
Plants	72 ± 15	0.55 ± 0.20	46 ± 21	54 ± 21	43 ± 25	97 ± 8
Animals	47 ± 15	0.38 ± 0.16	71 ± 17	29 ± 17	28 ± 16	94 ± 13
Total	59 ± 20	0.46 ± 0.20	59 ± 23	41 ± 23	35 ± 22	96 ± 11

was approximately zero (Table 1; Appendix A). In general, *BC* was zero for species with low *ND*, up to a "connector threshold value" (*ND* = 0.46) above which *BC* of species increased rapidly (Fig. 2). Interestingly, this value was quite constant across networks. Overall, 59% of the species had an *ND* below the threshold value, of which only 35% were connectors. On the other hand, 41% of the species had *ND* greater than the threshold value, of which 96% were connectors (Table 2). Plant networks had a higher threshold value, a higher proportion of connectors and a higher proportion of species above the threshold than animal networks (Appendix B). This difference is, at least partially, due to a sampling artefact. Sampling methods used in pollination network studies are plant-centered, that is the plant species are those being systematically observed, whereas the pollinators are only recorded when visiting flowers. This methodology boosts the connectivity of the plant species, and the difference between plants and animals will therefore not be discussed further.

5. Discussion

Our meta-analysis of centrality in pollination networks illustrates that most species are important to the overall connectance of the network (have high *CC*), whereas only the ~40% most generalized species play a key role as connectors ($BC > 0$). In general, for a species to be a connector it has to interact with almost half of the other species in the network. These generalized species connect subsets of the network, and their extinction may lead to community fragmentation (e.g. Jeong et al., 2000; Newman, 2004). This process makes generalist species vital to the overall network structure, functioning and resilience, playing a key role to the cohesiveness of pollination communities *beyond* what we would expect just by considering their number of interactions. These results are remarkably similar across networks from a variety of geographical and environmental settings.

Our study complements several previous studies that have shown that the structure of plant–pollinator assemblages are similar across communities, revealing the existence of universal rules and constraints in network development (e.g. Bascompte et al., 2003, 2006; Jordano et al., 2003; Olesen et al., 2006; Vázquez and Aizen, 2003, 2004). Hence, assembly processes are at least to some extent independent of abiotic factors and species taxonomy. Nestedness (Bascompte et al., 2003; Vázquez and Aizen, 2003, 2004), modularity (Dicks et al., 2002; Olesen et al., 2007), the small-world behaviour (Olesen et al., 2006), and the *ND*–*CC* and *ND*–*BC* relationships examined in this study seem to be universal features of the structure of pollination networks.

Knowledge about the structure of a network is fundamental to understand its functioning, stability and predict responses to disturbances (Strogatz, 2001; Bascompte et al., 2003; Newman, 2003; Kolasa, 2005, 2006; Jordán et al., 2006; Namba et al., 2008), hence the importance of identifying central nodes. In ecology, the use of centrality measures is a valuable methodological step towards a more precise and differentiated identification of keystone species, which might serve different topological roles. Recently, it was shown that species' morphology is an important factor structuring pollination networks (e.g. Stang et al., 2006; Dalsgaard et al., 2008). Thus future studies may look closer upon potential correlations between species' functional traits and centrality scores, ideally taking phylogeny into account (Rezende et al., 2007; Bersier and Kehrli, 2008). This would allow us to identify the importance of species traits and evolutionary history, beyond purely taxonomic status, for community stability and persistence. This approach should prove valuable to practical community-level conservation biology.

Acknowledgements

We are grateful to J. Bosch, A. Valido and two anonymous reviewers for comments greatly improving this manuscript. This research was supported by grants from the Faculty of Science at University of Aarhus (AMMG, BD), Svend G. Fiedler Foundation (AMMG), Augustinus Foundation (BD), Knud Højgaard Foundation (BD), and a Novozymes/World Wildlife-Denmark-grant (JMO).

Appendix A. Correlation coefficients, interception values and best fit models of the relationship between the normalised degree (*ND*), closeness (*CC*) and betweenness centrality (*BC*) of the various pollination communities studied

Region	Network	Size	*ND_CC*, r_s	*ND_BC*, r_s	*CC* intercept	*ND_CC* model	*BC* intercept	*ND_BC* model	Reference
Andes Low elevation	Plants	80	1.00**	0.81**	0.44	Linear	−0.01	Power-law (3.88)	Arroyo et al. (1982)
	Animals	97	0.98**	0.84**	0.44	Linear	−0.01	Power-law (3.59)	
Andes Mid elevation	Plants	40	1.00**	0.83**	0.42	Linear	−0.01	Power-law (3.97)	Arroyo et al. (1982)
	Animals	62	0.99**	0.88**	0.40	Linear	−0.02	Power-law (2.87)	
Andes High elevation	Plants	36	0.98**	0.59**	0.42	Linear	−0.06	Power-law (4.34)	Arroyo et al. (1982)
	Animals	25	0.95**	0.89**	0.38	Linear	−0.08	Power-law (2.79)	
Caribbean Highland	Plants	28	1.00**	0.58**	0.40	Linear	0.02	Linear	Dalsgaard, B., Martín González, A.M., Olesen, J.M. Puerto Rico, Caribbean. Unpublished data
	Animals	26	0.97**	0.55**	0.44	Linear	0.11	Power-law (2.69)	
Caribbean Lowland	Plants	26	0.95**	0.49*	0.37	Linear	0.00	Linear	Dalsgaard, B., Martín González, A.M., Olesen, J.M. Puerto Rico, Caribbean. Unpublished data
	Animals	30	0.86**	0.54**	0.35	Linear	−0.08	Power-law (6.21)	

Appendix A (*Continued*)

Region	Network	Size	*ND_CC*, r_s	*ND_BC*, r_s	*CC* intercept	*ND_CC* model	*BC* intercept	*ND_BC* model	Reference
Canary Islands	Plants	11	1.00**	0.89**	0.30	Linear	−0.05	Power-law (13.22)	Dupont et al. (2003)
	Animals	38	1.00*	0.92**	0.43	Linear	−0.02	Power-law (3.55)	
Arctic	Plants	24	0.99**	0.74**	0.38	Linear	−0.01	Power-law (3.43)	Elberling and Olesen (1999)
	Animals	118	0.97**	0.73**	0.44	Linear	−0.01	Power-law (3.03)	
Mediterranean	Plants	26	1.00**	0.96**	0.40	Linear	−0.02	Power-law (7.62)	Herrera (1988)
	Animals	179	1.00**	0.60**	0.47	Linear	−0.01	Power-law (4.95)	
Arctic	Plants	28	0.99**	0.84**	0.41	Linear	−0.04	Power-law (2.97)	Hocking (1968)
	Animals	80	1.00**	0.75**	0.45	Linear	−0.01	Power-law (5.09)	
Japan	Plants	112	1.00**	0.92**	0.44	Linear	−0.01	Power-law (3.38)	Inoue et al. (1990)
	Animals	840	0.98**	0.69**	0.48	Linear	0.00	Power-law (3.01)	
Australian Mountains	Plants	35	1.00**	0.94**	0.42	Linear	−0.02	Power-law (5.47)	Inouye and Pyke (1988)
	Animals	79	0.99**	0.84**	0.45	Linear	−0.02	Power-law (3.88)	
Japan	Plants	106	1.00**	0.86**	0.44	Linear	−0.01	Power-law (3.81)	Kakutani et al. (1990)
	Animals	304	0.98**	0.59**	0.44	Power-law (0.12)	0.00	Power-law (3.31)	
Japan	Plants	62	0.99**	0.77**	0.42	Linear	−0.01	Power-law (3.38)	Kato and Miura (1996)
	Animals	186	0.95**	0.73**	0.43	Power-law (0.14)	−0.01	Power-law (3.14)	
Japan	Plants	103	0.98**	0.87**	0.40	Linear	−0.01	Power-law (3.52)	Kato (2000)
	Animals	615	0.94**	0.45**	0.41	Power-law (0.12)	0.00	Power-law (2.94)	
Japan	Plants	90	0.99**	0.87**	0.44	Linear	−0.01	Power-law (2.83)	Kato et al. (1990)
	Animals	678	0.97**	0.43**	0.46	Linear	0.00	Power-law (3.76)	
Japan	Plants	90	0.99**	0.89**	0.43	Linear	−0.02	Power-law (2.36)	Kato et al. (1993)
	Animals	356	0.92**	0.60**	0.43	Power-law (0.12)	0.00	Power-law (2.46)	
Arctic	Plants	19	1.00**	0.95**	0.44	Linear	−0.06	Power-law (6.42)	Kevan (1972)
	Animals	90	1.00**	0.77**	0.44	Linear	−0.01	Power-law (7.37)	
Arctic	Plants	16	1.00**	0.89**	0.42	Linear	−0.10	Power-law (5.60)	Lundgren and Olesen (2005)
	Animals	25	1.00**	0.80**	0.43	Linear	−0.06	Power-law (5.34)	
Caribbean Highland	Plants	17	0.99**	0.89**	0.40	Power-law (0.36)	−0.11	Power-law (3.79)	Martín González, A.M., Dalsgaard, B., Olesen, J.M. Dominica, Caribbean. Unpublished data
	Animals	15	0.97**	0.75**	0.35	Power-law (0.33)	−0.15	Power-law (2.84)	
Caribbean Lowland	Plants	24	0.98**	0.86**	0.40	Linear	−0.05	Power-law (3.71)	Martín González, A.M., Dalsgaard, B., Olesen, J.M. Dominica, Caribbean. Unpublished data
	Animals	67	0.96**	0.69**	0.40	Power-law (0.51)	−0.02	Power-law (11.51)	
Azores	Plants	10	1.00**	0.82**	0.41	Linear	−0.14	Power-law (6.58)	Olesen et al. (2002)
	Animals	12	1.00**	0.67*	0.43	Linear	−0.07	Power-law (9.91)	
Mascarene Islands	Plants	14	1.00**	0.92**	0.28	Linear	−0.03	Power-law (12.62)	Olesen et al. (2002)
	Animals	13	1.00**	0.93**	0.30	Linear	−0.10	Power-law (6.06)	
Arctic	Plants	31	1.00**	0.98**	0.17	Linear	−0.01	Power-law (7.20)	Olesen et al. (2008)
	Animals	76	1.00**	0.96**	0.43	Linear	−0.01	Power-law (5.05)	
Northern Europe	Plants	10	1.00**	0.93**	0.43	Linear	−0.08	Power-law (10.86)	Olesen, J.M. Denmark bog. Unpublished data
	Animals	40	0.98**	0.79**	0.43	Linear	−0.04	Power-law (3.73)	
Northern Europe	Plants	26	1.00**	0.91**	0.36	Linear		Power-law (5.68)	Olesen, J.M. Denmark wasteland. Unpublished data
	Animals	82	1.00**	0.88**	0.46	Linear	−0.01	Power-law (4.10)	
Canary Islands	Plants	29	1.00**	0.83**	0.43	Linear	−0.03	Power-law (6.61)	Olesen, J.M. Canary Islands. Unpublished data
	Animals	55	1.00**	0.82**	0.45	Linear	−0.03	Power-law (6.83)	
Caribbean Lowland	Plants	61	0.98**	0.69**	0.40	Linear	0.00	Power-law (3.12)	Percival (1974)
	Animals	36	0.98**	0.79**	0.40	Linear	−0.01	Power-law (4.53)	
Mediterranean	Plants	130	1.00**	0.91**	0.41	Linear	0.00	Power-law (13.18)	Petanidou, T., 1991. Pollination ecology in a phryganic ecosystem. Ph.D. Thesis. Aristotelian University, Thessaloniki
	Animals	663	0.99**	0.88**	0.48	Linear	0.00	Power-law (3.64)	
New Zealand Mountains	Plants	17	0.99**	0.81**	0.40	Linear	−0.04	Power-law (3.51)	Primack (1983); Arthur's Pass
	Animals	58	0.89**	0.85**	0.42	Linear	−0.04	Power-law (3.22)	
New Zealand Mountains	Plants	41	1.00**	0.92**	0.44	Linear	−0.01	Power-law (4.27)	Primack (1983); Cass
	Animals	139	0.99**	0.70**	0.44	Linear	−0.01	Power-law (3.22)	
New Zealand Mountains	Plants	49	1.00**	0.80**	0.41	Linear	0.00	Power-law (4.64)	Primack (1983); Cragieburn
	Animals	118	0.99**	0.47**	0.47	Linear	−0.01	Power-law (4.42)	

Appendix A (*Continued*)

Region	Network	Size	*ND_CC*, r_s	*ND_BC*, r_s	*CC* intercept	*ND_CC* model	*BC* intercept	*ND_BC* model	Reference
Northern South America	Plants		0.99**	0.73**	0.37	Linear	0.00	Linear	Ramírez (1989)
	Animals	42	0.97**	0.80**	0.34	Power-law (0.22)	−0.02	Power-law (2.26)	
Canary Islands	Plants	17	1.00**	0.85**	0.41	Linear	−0.01	Power-law (32.59)	Stadl et al., 2003. Tenerife, Gorge. Canary islands. Unpublished data
	Animals	51	0.95**	0.88**	0.44	Linear	−0.03	Power-law (3.39)	
Canary Islands	Plants	14	1.00**	0.98**	0.38	Linear	−0.07	Power-law (5.36)	Stadl et al., 2003. Tenerife, Slope. Canary Islands. Unpublished data
	Animals	35	1.00**	0.65**	0.43	Linear	−0.05	Power-law (4.32)	

* $p < 0.05$.
** $p < 0.01$.

Appendix B. The number of species, proportion of connector species, threshold value and distribution of species and connector species before and after the threshold for all networks with a ND–BC relation following a power-law

Region	Network	Size	%conn	Threshold	%spp before	%spp after	%conn before	%conn after	Reference
Andes Low elevation	Plants	80	68	0.49	61	39	47	100	Arroyo et al. (1982)
	Animals	97	53	0.32	77	23	39	100	
Andes Mid elevation	Plants	40	73	0.44	48	53	42	100	Arroyo et al. (1982)
	Animals	62	61	0.21	42	58	19	92	
Andes High elevation	Plants	36	44	0.50	89	11	38	100	Arroyo et al. (1982)
	Animals	25	52	0.21	36	64	11	75	
Caribbean Highland	Animals	26	19	0.21	92	8	13	100	Dalsgaard, B., Martín González, A.M., Olesen, J.M. Puerto Rico, Caribbean
Caribbean Lowland	Animals	30	23	0.30	83	17	8	100	Dalsgaard, B., Martín González, A.M., Olesen, J.M. Puerto Rico, Caribbean. Unpublished data
Canary Islands	Plants	11	73	0.80	9	91	0	80	Dupont et al. (2003)
	Animals	38	71	0.43	26	74	20	89	
Arctic	Plants	24	88	0.48	33	67	63	100	Elberling and Olesen (1999)
	Animals	118	35	0.30	80	20	18	100	
Mediterranean	Plants	26	77	0.74	35	65	33	100	Herrera (1988)
	Animals	179	53	0.54	84	16	34	100	
Arctic	Plants	28	57	0.36	57	43	25	100	Hocking (1968)
	Animals	80	56	0.53	61	39	12	100	
Japan	Plants	112	78	0.37	49	51	55	100	Inoue et al. (1990)
	Animals	840	33	0.24	92.5	7.5	27	100	
Australian Mountains	Plants	35	83	0.64	34	66	50	100	Inouye and Pyke (1988)
	Animals	79	57	0.36	72	28	40	100	
Japan	Plants	106	75	0.33	69	31	64	100	Kakutani et al. (1990)
	Animals	304	38	0.19	60	40	30	52	
Japan	Plants	62	73	0.34	61	39	55	100	Kato and Miura (1996)
	Animals	186	46	0.19	69	31	29	83	
Japan	Plants	103	71	0.28	68	32	57	100	Kato (2000)
	Animals	615	29	0.18	91	10	21	100	
Japan	Plants	90	69	0.33	52	48	40	100	Kato et al. (1990)
	Animals	678	26	0.28	90	10	18	100	
Japan	Plants	90	82	0.26	34	66	48	100	Kato et al. (1993)
	Animals	356	37	0.14	70	30	25	75	
Arctic	Plants	19	58	0.77	84	16	50	100	Kevan (1972)
	Animals	90	47	0.67	63	37	16	100	
Arctic	Plants	16	63	0.64	69	31	45	100	Lundgren and Olesen (2005)
	Animals	25	36	0.56	72	28	11	100	
Caribbean Highland	Plants	17	41	0.32	41	59	0	70	Martín González, A.M., Dalsgaard, B., Olesen, J.M. Dominica, Caribbean. Unpublished data
	Animals	15	27	0.22	53	47	0	57	
Caribbean Lowland	Plants	24	58	0.36	46	54	27	85	Martín González, A.M., Dalsgaard, B., Olesen, J.M. Dominica, Caribbean. Unpublished data
	Animals	67	42	0.52	91	9	36	100	
Azores	Plants	10	70	0.67	80	20	63	100	Olesen et al. (2002)
	Animals	12	33	0.64	75	25	11	100	

Appendix B (*Continued*)

Region	Network	Size	%conn	Threshold	%spp before	%spp after	%conn before	%conn after	Reference
Mascarene Islands	Plants	14	79	0.88	36	64	40	100	Olesen et al. (2002)
	Animals	13	69	0.58	54	46	53	100	
Arctic	Plants	31	100	0.79	6	94	100	100	Olesen et al. (2008)
	Animals	76	84	0.53	43	57	64	100	
Northern Europe	Plants	10	50	0.77	50	20	19	100	Olesen, J.M. Denmark bog.
	Animals	40	35	0.47	80	50	0	100	Unpublished data
Northern Europe	Plants	26	92	0.74	35	65	78	100	Olesen, J.M. Denmark wasteland.
	Animals	82	57	0.51	78	22	62	100	Unpublished data
Canary Islands	Plants	29	48	0.74	72	28	29	100	Olesen, J.M. Canary Islands.
	Animals	55	44	0.65	84	16	33	100	Unpublished data
Caribbean Lowland	Plants	61	52	0.34	41	59	16	78	Percival (1974)
	Animals	36	72	0.49	64	36	57	100	
Mediterranean	Plants	130	97	0.83	25	75	88	100	Petanidou, T. 1991. Pollination
	Animals	663	63	0.40	94	6	61	100	ecology in a phryganic ecosystem. Ph.D. Thesis. Aristotelian University, Thessaloniki
New Zealand Mountains	Plants	17	88	0.45	24	76	25	92	Primack (1983); Arthur's Pass
	Animals	58	48	0.21	62	38	17	100	
New Zealand Mountains	Plants	41	80	0.40	41	59	53	100	Primack (1983); Cass
	Animals	139	53	0.32	74	26	37	100	
New Zealand Mountains	Plants	49	90	0.54	27	73	62	100	Primack (1983); Cragieburn
	Animals	118	44	0.44	90	10	38	100	
Northern South America	Animals	42	52	0.20	60	40	24	94	Ramírez (1989)
Canary Islands	Plants	17	82	0.81	18	82	0	100	Stadl et al., 2003. Tenerife,
	Animals	51	45	0.36	65	35	15	100	Gorge. Canary Islands. Unpublished data
Canary Islands	Plants	14	71	0.62	43	57	33	100	Stadl et al., 2003. Tenerife,
	Animals	35	51	0.56	83	17	41	100	Slope. Canary Islands. Unpublished data

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