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.

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 ν 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 $p < 0.05$.