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Succinctly assessing the topological importance of species in flower–pollinator networks

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ABSTRACT

The topological importance of species within networks is an important way of bringing a species-level consideration to the study of whole ecological networks. There are many different indices of topological importance, including centrality indices, but it is likely that a small number are sufficient to explain variation in topological importance. We used 14 indices to describe topological importance of plants and pollinators in 12 quantitative mutualistic (plant–pollinator) networks. The 14 indices varied in their consideration of interaction strength (weighted versus unweighted indices) and indirect interactions (from the local measure of degree to meso-scale indices). We use principal components approximation to assess how well every combination of 1–14 indices approximated to the results of principal components analysis (PCA). We found that one or two indices were sufficient to explain up to 90% of the variation in topological importance in both plants and pollinators. The choice of index was crucial because there was considerable variation between the best and the worst approximating subsets of indices. The best single indices were unweighted degree and unweighted topological importance (Jordán's TI index) with two steps (a measurement of apparent competition). The best pairs of indices consisted of a measure of a TI index and one of closeness centrality (weighted or unweighted) or d' (a standardised species-level measure of partner diversity). Although we have found indices that efficiently explain variation in topological importance, we recommend further research to discover the real-world relevance of different aspects of topological importance to species in ecological networks.

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1. Introduction

The application of complexity science to the study of food webs, in which species and their trophic interactions are represented by nodes and links, has recently led to a rich array of research (Bascompte et al., 2003; Montoya et al., 2006; Thébault and Fontaine, 2010). Much current research on ecological networks is concerned with the emergent properties of the whole network, e.g. how its connectance relates to ecosystem function (Dunne et al., 2002). However, the species (nodes in networks) are of interest in their own right, a fact which can be overlooked with analyses of the whole network. Considering the importance of the species within the structure of the network, i.e. its 'topological importance' or 'keystoneness' (Jordán, 2009), is one way of combining an interest in individual species and the holistic approach of the whole network (Jordán et al., 2008; Sazima et al., 2010).

There are many different ways of defining 'topological importance' and so there exist a large number of indices that assess this, including long-established centrality indices (Freeman, 1979; Bonacich, 1987) and indices recently developed specifically for ecological networks (Blüthgen et al., 2006; Estrada, 2007; Jordán et al., 2008, 2009); henceforth we term all of these "indices of topological importance". These indices are, to some degree, complementary in that they explain different aspects of topological importance (Friedkin, 1991), and so, by using more than one index, an overall understanding of the variation in the topological importance of nodes can be obtained (Sporns et al., 2007; Martín González et al., 2010). However, in practice, these indices are often highly correlated (Lee, 2006; Scotti et al., 2007; Jordán et al., 2008). It is therefore superfluous to consider many different indices of topological importance when seeking to describe the importance of each species in a food web. In the current study we address the question: how many indices, and which indices, should be selected

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in order to succinctly assess topological importance of nodes in food webs? Specifically we address this by considering 14 indices of topological importance in weighted plant–pollinator networks.

Much work considering the topological importance of species in food webs has been undertaken by F. Jordan and colleagues (e.g. Jordán et al., 1999, 2006, 2007, 2008, 2009; Benedek et al., 2007; Estrada, 2007). These food webs consist of trophic (feeding) links between species; the networks are multitrophic, i.e. consisting of several trophic levels of consumers and predators, and sometimes weighted, i.e. including information on interaction strengths.

A second type of 'food web' is the mutualistic bipartite network, exemplified by plant–pollinator networks. These bipartite networks have been widely studied to discover more about the assembly, structure and functioning of ecosystems (e.g. Memmott, 1999; Bascompte et al., 2003; Vazquez et al., 2009; Thébault and Fontaine, 2010). The best way of describing the topological importance of plant and pollinator species in mutualistic networks may be different to multitrophic food webs (Scotti et al., 2007). However, little work has been undertaken on the indices of topological importance of plant–pollinator networks, the exception being Martín González et al. (2010), who considered centrality indices in unweighted plant–pollinator networks. Our study therefore complements previous work by considering many different indices in weighted mutualistic networks.

One way of summarising the variation in indices of topological importance is to use multivariate statistics, e.g. principal components analysis (PCA) (Jolliffe, 2002). With PCA we can reduce the number of dimensions from many indices to a smaller number of principal components, each principal component being a linear combination of the original indices. This has proved successful in explaining topological importance in multi-trophic food webs (Estrada, 2007). However PCA has the disadvantage of relying on all the original variables, so all indices need to be calculated to describe the principal components for each new dataset. Also, the principal components are often not straightforward to interpret, especially where there are a large number of variables in the analysis (Cadima and Jolliffe, 2001). However, when considering a large number of indices, it is almost always the case that a small subset of the original indices can contain virtually all the information in the total number of indices (Jolliffe, 2002). So, if there was a small subset of the original indices that explained almost as much information, i.e. variation in the original data, as the principal components, then it would be more efficient to use these indices instead of the PCA. This approach is called principal components approximation (PCAp) (Cadima and Jolliffe, 2001) and we used this in the current study. Specifically, with PCAp, we assesses how well each subset of k indices approximates to the first k principal components, where k varies from one to the total number of indices (Cadima and Jolliffe, 2001).

In the current study we considered weighted plant–pollinator networks and our aims were: (1) to assess whether the best subsets of the original variables approximated well to the variance explained by the PCA; (2) to assess how many variables are required to adequately assess the total variation in the datasets; and (3) to identify which subsets of variables well explained the total variance. We wanted to be able to recommend specific indices that should be used to efficiently describe topological importance in quantitative bipartite ecological networks.

2. Datasets and indices of topological importance

We obtained twelve quantitative plant–pollinator networks from the Interaction Network database (http://www.nceas.ucsb.edu/interactionweb/). Currently, there are only a limited number of quantitative plant–pollinators in the public domain and we selected these twelve networks because they are widely and freely available and represent a wide range in the number of plant and animal species present (Appendix 1). For each plant and pollinator species in each network we calculated 14 indices of topological importance (Table 1). In most cases indices were calculated as part of existing packages within R (R Development Core Team, 2010). These indices included many of those previously considered for multitrophic food webs (Benedek et al., 2007; Jordán et al., 2007, 2009), including variation in their consideration of weighting and indirectedness (Scotti et al., 2007), and are described in the remainder of this section.

Degree is the most local measure of topological importance. It is identical to assessing feeding specialisation in terms of the number of species the focal species feed upon, thus taking no further account of the context of the node within the network.

Other indices are meso-scale indices (as per Jordán, 2009), since they consider indirect as well as direct links. The three centrality indices that we considered, namely closeness, eigenvector and betweenness centrality (Bonacich, 1972; Freeman, 1979), have been widely applied to many different type of networks. Closeness centrality is a measure of how close the focal species is to all others, thus how quickly it can influence many species (Martín González et al., 2010). Large values indicate species that are more hub-like and can rapidly affect many nodes within the network (Freeman, 1979). Eigenvector centrality is similar to the degree but takes account of the importance of those species with which the focal species interacts (Bonacich, 1972). A version of eigenvector centrality is used in the PageRank algorithm, and in multitrophic

Table 1
Indices of topological importance considered in this analysis and their calculation.

Abbreviation	Index	R package[a] and example code
uD	Unweighted degree	sna::degree(. . .,ignore.eval = TRUE)
wD	Weighted degree	sna::degree(. . .,ignore.eval = FALSE)
uCC	Unweighted closeness centrality	sna::closeness(. . ., cmode = "suminvundir", ignore.eval = TRUE)
wCC	Weighted closeness centrality	sna::closeness(. . ., cmode = "suminvundir", ignore.eval = FALSE)
uBC	Unweighted betweenness centrality	sna::betweenness(. . .,cmode = "undirected", ignore.eval = TRUE)
wBC	Weighted betweenness centrality	sna::betweenness(. . .,cmode = "undirected", ignore.eval = FALSE)
uEC	Unweighted eigenvector centrality	igraph::evcent(. . ., scale = FALSE, weights = NA)
wEC	Weighted eigenvector centrality	igraph::evcent(. . ., scale = FALSE, weights = NULL)
PP	Push–pull	bipartite::specieslevel(. . ., index = "interaction")
d′	*d′*	bipartite::specieslevel(. . ., index = "*d*")
uTI1	Unweighted topological importance with 1 step	Not currently implemented in an R package[b]
wTI1	Weighted topological importance with 1 step	Not currently implemented in an R package[b]
uTI2	Unweighted topological importance with 2 steps	Not currently implemented in an R package[b]
wTI2	Weighted topological importance with 2 steps	Not currently implemented in an R package[b]

[a] Packages are: sna 2.0 (Butts, 2009), bipartite 1.06 (Gruber et al., 2009), igraph 0.5.3(Csardi and Nepusz, 2006).
[b] TI indices can be calculated in CoSBiLab Graph (Valentini and Jordán, 2010).

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