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Topological keystone species complexes in ecological interaction networks

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Abstract: Advanced techniques of network analysis allow the quantification of the indirect interactions and the topological importance of components in ecological interaction networks. In current conservation biology, considering indirect causal effects, identifying keystone species and outlining multispecies approaches begin to be high priority goals. We make an attempt to connect these issues within a network context. Our main interest is to determine the positionally most important set of n nodes in a network, to analyse whether a set of nodes for small n is a subset of another for larger n , and to quantify this nestedness. We apply the KeyPlayer software, a novel tool for network analysis in ecology, introduced originally in mathematical sociology. Topological keystone species complexes are defined, we illustrate the use of this method in a case study and analyse a database of 9 plant-pollinator interaction networks. Our main conclusion is that multispecies approaches may give results very different from single species analyses.

Abbreviation: KP – Key Player.

Introduction

Network analysis is a useful tool for better understanding relationships between subsystems of ecological systems, by quantifying indirect effects, positional importance and the part to whole relationship, in general. In fact, holistic approaches are probably more exact than ever before: we always knew that everything is connected to everything else but recently we have begun to understand exactly how and to what extent (Patten 1991, 1995, Jordán et al. 2003a, Fath 2004, Gattie et al. 2006). Also, beyond local and global analyses, there are a variety of “mesoscale” approaches to topological problems (Patten 1981, Jordán 2001, Jordán and Scheuring 2002), considering neighbours of neighbours but not necessarily whole systems. Quantification of the key elements of ecological networks (defined as topological keystone species, Jordán et al. 1999, 2006, Libralato et al. 2006) could provide objective basis for setting conservation priorities. Key network components are more important to be protected since their deletion would cause a larger damage to the

evolutionary coadjusted, reliable functioning of the interaction network (Jordán et al. 2002, 2003b, Allesina et al. 2006). Nevertheless, beyond characterising the positional importance of single nodes in networks, it can also be of interest how important is a given set of nodes, or exactly which set of n nodes is the most important in maintaining network integrity (by quantifying the structural effect of their deletion). The problem seems to be of ecological relevance, especially since recognising keystone species complexes (Daily et al. 1993).

Pollinators provide services to both natural and agricultural ecosystems, and are important components of biological diversity (Waser and Ollerton 2006). There are many observations about pollinators decline worldwide, partly because of landscape ecological processes (habitat fragmentation, Crooks and Soulé 1999), causing the so-called pollination crisis (Kearns et al. 1998, Vamosi et al. 2006, but see Ghazoul 2005). The loss of pollinators results in decline of plants and associated invertebrates through indirect interactions (Daily 1997), therefore, the

conservation of plant-pollinator interactions is of community-wide importance (Jordano 1987, Memmott 1999, Bascompte et al. 2003). We are increasingly aware of the fact that plant-pollinator interactions are by far not typically pairwise interactions but involve a number of species on both sides (Bronstein 2001). Thus, classical models and experiments are of little use in understanding these extremely complicated systems. We present a topological analysis of 9 plant-pollinator networks and explore what topology can add to our understanding about these systems. We acknowledge that a relatively simple and general topological approach is surely not suitable for understanding every fine detail of these communities but also think that the most basic architecture of interaction networks does have a large effect on their dynamics (see e.g., Fussmann and Heber 2002, Jordán et al. 2002). Also, our approach is better as the involved interactions really function and the interacting plant and pollinator partners significantly affect each other. To our knowledge, this is not a quite realistic assumption.

Our aims are (1) to demonstrate the use of graph theory in defining and quantifying keystone species complexes, (2) quantifying the nestedness of these complexes, (3) to present a case study illustrating the difference between single-species and multispecies approaches.

Materials and methods

The database

We used the web-based database of NCEAS, University of Santa Barbara, California (ref.: NCEAS), containing 88 interaction webs, including 31 plant-pollinator webs. Out of these 31 webs we used only 9 (Table 1: our codes reflect the names of original authors of each web - references are given in NCEAS), since (1) we did not want to decide how to aggregate several web variants coded by "vaz", (2) we had to exclude "dup" for technical reasons to be explained later and (3) we could use webs with binary data. These 9 webs are fairly comparable in a methodical sense and large enough for illustrating this technique.

These interaction networks consist of two sets of species A and B, i.e., plants and pollinators, connected by links representing pollination, so the endpoints of each link connect one node from A and another from B. Thus, the graphs representing these systems are bipartite graphs. The links can be weighted, by the number of visits, the frequency of visits, or pollinator individuals caught. We have not used these weights but it is still possible in further analyses. Individual links represent mutually positive (+/+) interspecific interactions (pollinating and being pol-

linated) but recent results have shown frequent changes in signs of these interactions (Bronstein 2001). However, our analysis has not explicitly considered link signs, so the results are insensitive to such changes. Further, we have taken these links as undirected, which is reasonable in the case of symmetrical interactions (as for sign). By considering undirected, unweighted and unsigned graph links, we lose some reality but gain generality. It is a question of high interest, however, how these kinds of information affect our results (cf. Vasas and Jordán 2006).

Methods

Topological keystone species. Species are not of equal importance in natural communities. Several kinds of important species have been defined including flagships, umbrellas or keystone species (Simberloff 1998). The crucial problem of keystone research and, more generally, in understanding the importance of species is that we lack quantitative approaches providing objective measures of importance. It has recently been suggested many times that an aspect of important species is their exact positions in the topological space of interspecific interactions (Jordán et al. 1999, Solé and Montoya 2001, Dunne et al. 2002, Jordán and Scheuring 2002, Jordán et al. 2006). Different centrality indices and network analytical techniques reflect different aspects of positional importance and provide different importance ranks for the species of the same community (Jordán et al. 2006). Here, we focus on techniques based on multispecies approaches. The simplest single-species measure of topological importance is node degree (D), i.e., the number of links connecting a species to others. This simple measure is a good reference point for comparisons with other more complicated ones (for a couple of centrality indices, see Jordán et al. 2006).

Topological keystone species complexes. In an interesting case study, Daily et al. (1993) defined keystone species complexes and called again for attention focused on the multispecies context in conservation biology (cf. Simberloff 1998). Based on the above concept, we define topological keystone species complexes as solutions of the KeyPlayer (KP) problem (Borgatti 2003a), in ecological network analysis (we note that this technique was introduced in sociometry, just like many other network indices used later in ecology, e.g., Harary 1961, Jordán et al. 1999, Krause et al. 2003). The KeyPlayer 1.44 software (Borgatti 2003b) is used to compute the importance of species combinations in maintaining the integrity of a network. We consider the so-called KeyPlayer Problem 2. This is as follows: if we "spread information" from n nodes, which n nodes have to be selected in order to reach

the others in the fastest way in the intact network (fastest means minimal number of steps, so we suppose that effects spread uniformly). The optimal choice of n nodes is defined as a KP-set. There is a simple approach to the KP-2 problem: we simply count the number of nodes (R_l) reachable within a given distance of l -step from a given set of n nodes. We have chosen $l = 2$ steps and increased the size of the KP-set from $n = 1$ to 6 (three or more steps indirect effects and seven or more species keystone complexes were not considered, because it is meaningless to analyse longer pathways in these subnetworks). We applied 10000 runs in each simulation. The outcome was six sets of nodes for each network, containing species codes. For each n , the software presents the percentage of nodes outside the KP-set but reachable from it in l steps. If this percentage reaches 100%, then the whole network is reachable from the KP-set and there is no reason to look for better solutions. In this case, we cannot create larger KP-sets. We have to mention here that the “dup” web was excluded from our analysis since this was the only interaction network where the subsequent KP-sets could not provide six subsequent solutions: 100% was reached in two steps.

The nestedness of topological keystone species complexes. KP-sets of different size may perfectly or partly include the members of smaller KP-sets, i.e., they may be nested to some extent. We propose that the nestedness of these sets may have consequences on the efficiency and success of conservation efforts. If larger sets incorporate the smaller ones, i.e., nestedness is high, then saving the most important species can be extended to saving the second one as well, and, if further sources are also available, this can still be extended to further species later on. However, if nestedness is low, it means that saving the most important species is useless if sources are increasingly available, because the optimal solution for saving the most important combination of n species does not suggest to save the most important $n-k$ ($k < n$) species. Depending on available sources, the set of species to be protected always changes. In order to estimate the success of conservation, it could be of extreme importance to understand which properties of networks will cause stronger structural constraints on the efficiency of conservation efforts (i.e., decreasing nestedness of KP-sets).

In order to measure nestedness, we used the Nestedness Temperature Calculator software (NTC, Atmar and Patterson 1995), which is becoming more and more widespread in ecology (e.g., Báldi 2003, Bascompte et al. 2003) but has been used before for quite different purposes (for comparing the species composition of islands from a biogeographical perspective). Tables 2 and 3 help

to understand how to create a „presence-absence” matrix from KP data. In Tables 2b and 3b, the KP-sets of increasing size are shown (for $n = 1 \dots 6$). In Tables 2c and 3c, the rows of the matrix show the size of KP-sets and the columns correspond to species. In Table 3c, the first column is for species #25, because it appears first in the „KP-sets” (for $n = 1$). The tenth column is for species #4 appearing only in the KP-set for $n = 6$. Thus, a matrix entry shows whether the KP-set of species i contains the j^{th} species. The Nestedness Temperature Calculator software basically quantifies how ordered a matrix is (like the ones in Tables 2c and 3c). If larger KP-sets always contain smaller ones, the resulting matrix can be ordered according to an arrangement where all „1”-s are in one corner of the matrix, following the reordering of the rows and columns. The orderedness is expressed in percentages called the “temperature” of the matrix (where maximal nestedness is 0%) and Monte Carlo simulations provide a significance level determining the probability that a randomly generated matrix will be “colder” (more nested) than the actual one. We used the software by applying 500 runs for every simulation and taking the average significance value. We note that the matrices are much less nested than the ones typically studied in biogeography but no direct comparison is reasonable. However, we have perfectly nested matrices as well, like the one in Table 2.

Further network parameters. We look for correlations between some graph properties and nestedness to see which graph properties lead automatically to nestedness. We characterise whole networks by (1) the number of species ($N = N_r + N_c$, where N_r and N_c are the number of pollinator and plant species, respectively), (2) the number of links (L , all representing pollination interactions), (3) connectance ($bipC$, where „bip” stands for bipartite, according to a modified connectance measure for bipartite graphs, see Olesen et al. 2002):

$$bipC = \frac{L}{N_r * N_c},$$

and (4) the ratio of pollinator and plant species (N_r / N_c) as for asymmetry. The number of species and links as well as the connectance of the network are standard and widely used parameters for characterising the complexity of ecological networks, while asymmetry is used for characterising the topology of networks (of possibly similar complexity).

Results

We illustrate our methods by presenting the details of our analysis on two selected webs, coded by “med-2” and “ram”; the results calculated for other webs are given in

Table 1. Global characteristics of the studied interaction networks. Web codes follow that of the NCEAS database (NCEAS). N , N_r , N_c , N_r / N_c , L and $bipC$ correspond to the number of species, the number of pollinators, the number of plants, the ratio of pollinators to plants, the number of links and the connectivity of the graphs, respectively. P is a significance level which measures the „heat“ or nestedness of the matrix containing the ordered KP-sets. R is the reachability data for the final KP-sets: how much of the network would be conserved if we were able to maintain the KP-set of 6 species.

Web	N	Nr	Nc	Nr / Nc	L	bipC	P	R
arr_1	185	98	87	1.13	365	0.0428	0.034	93,5
arr_2	105	62	43	1.44	183	0.0686	0.028	96,1
arr_3	69	28	41	0.68	87	0.0758	0.161	97,1
cl	372	276	96	2.88	923	0.0348	0.042	93,0
hoc	127	86	41	2.10	184	0.0522	0.069	98,3
mcm	160	54	106	0.51	204	0.0356	0.036	96,2
med_1	88	46	42	1.10	83	0.0430	0.112	98,5
med_2	115	72	43	1.67	125	0.0404	0.017	97,9
ram	86	53	33	1.61	109	0.0623	0.366	85,2

Table 2. Local network indices for web “med_2”. **a:** species are ranked according to their degree (D , note that species only with $D > 3$ are presented). **b:** the KP-sets for $n = 1$ to 6 are presented. **c:** the resulting matrix whose nestedness is calculated by the Nestedness Temperature Calculator. For technical details and more explanation, see text.

a.	species	D	b.	n
	77	34	KP-sets	1 1
	76	28		2 1 44
	75	11		3 1 44 81
	1	9		4 1 44 81 77
	7	6		5 1 44 81 77 85
	80	6		6 1 44 81 77 85 88
	94	5		
	78	5		
	92	5	c.	n
	72	4	KP-matrix	1 1 0 0 0 0 0
	30	4		2 1 1 0 0 0 0
	86	4		3 1 1 1 0 0 0
	49	4		4 1 1 1 1 0 0
				5 1 1 1 1 1 0
				6 1 1 1 1 1 1

Table 1. The “med_2” plant-pollinator web has been described in Argentina and contains binary links connecting 72 pollinator and 43 plant species. We refer to the species by codes from #1 to #115 (pollinators from #1 to #72 and plants from #73 to #115); species names are given in the original source (NCEAS). Individual species of “med_2” are characterised by their degree (D) and the presence or absence in the first six KP-sets ($n = 1$ to 6, Table 2). Key species is *Copestylum aricia* (#1), the two most important species are #1 and #44 (coded as *Dialictus sp1*) and the KP-set for $n=3$ contains species #1, #44 and #81 (*Lathyrus* sp.). Up to $n=6$, larger KP-sets always contain the smaller ones. In this case, network position may help in efficiently setting conservation priorities. Note however, that the most important species in maintaining the integrity of the network (the KP for $n=1$) has only nine

neighbours ($D=9$), while the species of highest degree (#77, $D=34$) appears only in the KP-set for $n=4$. Very interestingly, species #44 is a member of all but the first KP-sets but has only three neighbours ($D=3$). Two out of the three neighbours of species #44 are species #77 ($D=34$) and #75 ($D=11$), thus #44 bridges hubs of the network (the third neighbour is #86). The key role of species #44 in maintaining the integrity of this interaction network is clear only after calculating the KP indices reflecting indirect effects.

In some other webs, the KP-sets for more species do not contain KP-sets for fewer species. In “ram” (Table 3 and Fig. 1), the mostly connected species (#76, a plant, *Ludwigia nervosa*, $D = 16$) does not appear in any of the first six KP-sets. Instead, the single species KP-set ($n = 1$) contains species #25, which is only fourth in the D -based

Table 3. Local network indices for web “ram”, similarly to Table 2.

a.	species	D	b.	n
	76	16	KP-sets	1 25
	62	10		2 18 62
	18	8		3 25 26 56
	25	7		4 18 26 49 71
	12	6		5 18 26 49 71 1
	66	6		6 18 26 49 71 2 4
	69	6		
	61	5		
	71	5		
	11	4		
	26	4		
	45	4		
	50	4		
	56	4		
	64	4		
	74	4		
	78	4		
	81	4		

c.	n
KP-matrix	1 1 0 0 0 0 0 0 0 0 0
	2 0 1 1 0 0 0 0 0 0 0
	3 1 0 0 1 1 0 0 0 0 0
	4 0 1 0 1 0 1 1 0 0 0
	5 0 1 0 1 0 1 1 1 0 0
	6 0 1 0 1 0 1 1 0 1 1

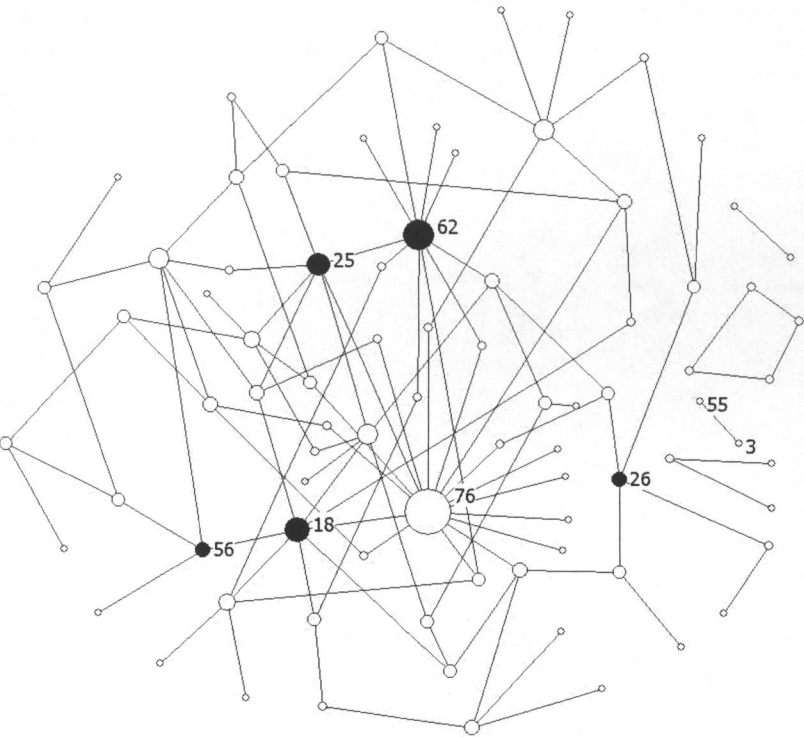


Figure 1. One of the 9 interaction networks analysed, the “ram” web describing a Venezuelan plant-pollinator community. The web was drawn by Net-DRAW, a subroutine of UCINET 6 (Borgatti et al. 2002). Size of nodes is proportional to degree (D). Note that the graph is not connected (e.g., nodes #3 and #55, on the right, form an isolated dyad). Members of the first three KP-sets are black (nodes #25, #18, #62, #26, #56, see Table 3b). Note that the node of highest degree (#76, see Table 3a) is white!

rank with $D = 7$ (a pollinator, *Helicobia morionella*). The KP-set for $n = 2$ contains the second and third species in the D -based rank (#62 is the plant *Hyptis dilatata* with $D = 10$, and #18 is the well known pollinator *Apis mellifera* with $D = 8$). Moreover, in the third KP-set two species appear with $D = 4$. Topological keystone species complexes of this network are highly unnested, suggesting that network topology has serious structural constraints on the efficiency of conservation efforts.

We characterise each network by several parameters (Table 1) and look for correlations but none of them changes significantly with nestedness.

Discussion

We applied a new technique in ecology for identifying the most important positions in interaction networks, also providing some assessment on the efficiency and success of conservation practices. The use of this approach was illustrated by an analysis of a database of plant-pollinator interactions, so our biological conclusions concern these systems. Because of the reticulate nature of plant-pollinator mutualisms, the importance of a single species cannot be assessed in isolation, but in a multispecies context. Facing the pollination crisis, and acknowledging that pol-

lination is a keystone interaction (Kearns et al. 1998), we need these network analytical techniques for better understanding the functioning of these systems. In the case of the studied networks, ecosystem functioning (defined as the integrity of the pollination network) depends more on system topology than on complexity or biodiversity (number of species or connectance, see also Quince et al. 2005).

We suggest that if the aim is to maintain the network architecture and functioning of this community, we should probably focus more on protecting KP species rather than those with the highest D values. The complexity of the system makes it impossible to guess these results at the first glance, and that is why network analytical techniques, especially multispecies approaches also considering indirect relationships, are needed in keystone research. These methods may reveal the hidden KPs in the background (cf. Paine 1969). Future conservation biology should work in a multispecies context, and focus on functionally important rather than on rare species (like less “sexy” invertebrates). An aim of network analysis is to find the reliable correlation between structural and functional importance (Jordán et al. 2002, 2003b, Libralato et al. 2006). Our result highlights that multispecies approaches may also have caveats. We showed that different multispecies approaches may give different key species, or groups of key species. The choice among key species depends on the exact conservation target. Thus, the problem- and context-dependence of conservation is of great importance, but also influenced by structural constraints.

As a very important future goal, we are now extending our analysis to “community food webs” representing entire ecosystems and will study whether the bipartite nature of our present networks caused any bias in results. Another important direction for future work is studying the sensitivity and robustness of the results. Finally, it would be interesting to know more about the possible reorganisation of links after damaging the network, i.e., network dynamics. Presently there is a massive lack of data on descriptive network dynamics in ecosystems (but see one example in Christian and Thomas 2003), so it is not easy to understand what kinds of changes to expect after disturbance. Our present study wants to be a first step towards these directions.

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