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# Ranking of critical species to preserve the functionality of mutualistic networks using the k-core decomposition

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Mutualistic communities play an important role in biodiversity preservation. They are modeled as bipartite networks and measurements of centrality and degree help to order species and their relative importance for network robustness. Identifying the most endangered ones or those more prone to trigger cascade extinctions is essential to define conservation policies. In this work, we explain how a classical graph analysis tool, the k-core decomposition, provides new ranking magnitudes that reach outstanding performance for these purposes.

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# Ranking of critical species to preserve the functionality of mutualistic networks using the k-core decomposition

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## ABSTRACT

Mutualistic communities play an important role in biodiversity preservation. They are modeled as bipartite networks and measurements of centrality and degree help to order species and their relative importance for network robustness. Identifying the most endangered ones or those more prone to trigger cascade extinctions is essential to define conservation policies. In this work, we explain how a classical graph analysis tool, the k-core decomposition, provides new ranking magnitudes that reach outstanding performance for these purposes.

## INTRODUCTION

Biotic interaction networks play an essential role in the stability of ecosystems (Tylianakis et al., 2010), as well as in the maintenance of biodiversity (Bascompte et al., 2006). Because community dynamics greatly depend on the way species interact, these networks have been described as the "biodiversity architecture" (Bascompte and Jordano, 2007). Network analysis has become an important approach to provide information on community organization and to predict dynamics and species extinctions in response to ecosystem disturbance (Tylianakis et al., 2010; Thébault and Fontaine, 2010; Traveset and Richardson, 2014). Among other assessments, these studies can point out key species, whose stability would prevent cascading extinctions, and the consequent loss of biodiversity (Sole and Montoya, 2001; Suweis et al., 2013; Dakos et al., 2014; Santamaría et al., 2015). Research on cascading species extinctions as a result of perturbations in biotic interactions has tackled two main issues: the different ways to rank a hypothetical extinction sequence and the robustness and fragility measures (Pocock et al., 2012). There are different strategies both to sort species according to their importance and to measure their influence on extinction. For instance, in early studies on the resilience of food webs Dunne et al. ranked species by degree (i.e., the number of interactions) using three different scenarios of removal: a) from the species with the highest degree to the species with the lowest degree; b) from the lowest to the highest; c) species selected in a random way(Dunne et al., 2002). Memmott et al. worked the same idea to assess the robustness of mutualistic communities, removing active species and measuring the fraction of remaining passive species (Memmott et al., 2004).

An observed property of mutualistic interactions is the existence of generalists, highly interconnected, and specialists, with few interactions linked to the generalists, but rarely among them. The nucleus of interactions among generalists seems to be the foundation of resilience. This property has been traditionally identified with nestedness (Bascompte et al., 2003), although there are new approaches to describe it in a more general way as a core-periphery organization (Csermely et al., 2013; Rombach et al.,

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2014).

Identification of key nodes for community preservation is another active field of research. Besides classical measures of centrality, new rankings are available and provide efficient ways to find out them in bipartite networks (Tacchella et al., 2012; Domínguez-García and Muñoz, 2015).

In this paper, we aim to explain how the *k-core decomposition*, sheds light on the understanding of robustness in mutualism. The tool classifies the nodes of the network in shells, as in an onion-like structure with the most connected nodes in its center. Taking into account just the very basic topological properties, the decomposition helps to assess in detail the structure of mutualism and enlightens on the processes of species extinction cascades. Derived from the k-core decomposition we introduce three new magnitudes, hereafter called *k-magnitudes*, that describe network compactness (k-radius), combined quantity and quality of interactions (k-degree) and species vulnerability to trigger extinction cascades (k-risk). We assess the best criteria for identifying the species for which the networks are most vulnerable to cascade extinctions by comparing k-degree and k-risk ranking criteria with ranking by well-known indexes and applying them in two network destruction procedures. To conduct the test, we use one of the most complete available data sets (Fortuna et al., 2014).

# MATERIALS AND METHODS

## Data

We have analyzed the *Web of life* collection (Fortuna et al., 2014), comprised by 89 mutualistic networks, with 59 communities of plants and pollinators and 30 of seed dispersers (`http://www.web-of-life.es/`). There are 57 communities with binary adjacency matrix (i.e., the interaction between the two species is recorded but not its strength), and 32 with weighted matrix, where the strength is accounted for. Network sizes range from 6 to 997 species, the minimum number of links is 6 and the maximum is 2933.

## Decomposition and k-magnitudes

The idea of core decomposition was first described by Seidman to measure local density and cohesion in social graphs (Seidman, 1983). It has been successfully applied to visualize large systems and networks (Alvarez-Hamelin et al., 2005; Kitsak et al., 2010; Zhang et al., 2010; Barberá et al., 2015).

The *k-core* of a network is a maximal connected sub-network of degree greater or equal than $k$. That means that each node is tied to at least $k$ other nodes in the same sub-network.

A simple algorithm to perform the *k-core decomposition* prunes links of nodes of degree equal or less than $k$ (Batagelj and Zaversnik, 2003). The process starts removing links with one of their edges in a node of degree 1. This procedure is recursive and ends when all the remaining nodes have at least two links. The isolated nodes are the 1-*shell*. Then it continues with $k = 2$, and so on. After performing the *k-decomposition*, each species belongs to one of the *k-shells* (Fig. 1). The *m-core* includes all nodes of *m-shell*, $m+1$-*shell*...

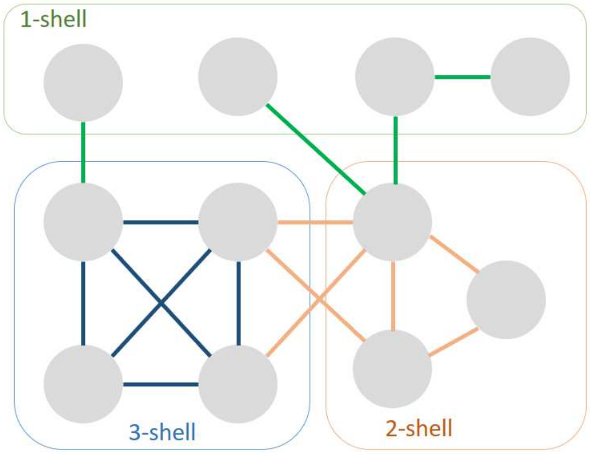

**Figure 1.** *k-core* decomposition of a fictional network. Green links are pruned during the first iteration, orange during the second and blue during the last one.

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Mutualistic networks are bipartite, with two guilds of species (plant-pollinator or plant-seed disperser in the studied collection). Links among nodes of the same class are forbidden. We will call these guilds $A$ and $B$.

Based on the k-core decomposition, we define three *k-magnitudes*. In order to quantify the distance from a node to the innermost shell of the partner guild, we define $k_{radius}$. The $k_{radius}$ of node $m$ of guild $A$ is the average distance to all species of the innermost shell of guild $B$. We call this set $N^B$.

$$k^A_{radius}(m) = \frac{1}{\mid N^B \mid} \sum_{j \in N^B} dist_{mj} \qquad m \in A \tag{1}$$

where $dist_{mj}$ is the shortest path from species $m$ to each of the $j$ species that belong to $N^B$. The minimum possible $k_{radius}$ value is 1 for one node of the innermost shell directly linked to each one of the innermost shell set of the opposite guild.

To obtain a measure of centrality in this *k-shell* based decomposition, we define $k_{degree}$ as

$$k^A_{degree}(m) = \sum_j \frac{a_{mj}}{k^B_{radius}(j)} \qquad m \in A, \forall j \in B \tag{2}$$

where $a_{mj}$ is the element of the interaction matrix that represents the link, considered as binary. If the network is weighted, $a_{mj}$ will count as 1 for this purpose if there is interaction, 0 otherwise. $k_{degree}(m)$ is a weighted *degree* where each node $i$ linked to node $m$ adds the inverse of its $k_{radius}(i)$. Generalists score high $k_{degree}$, whereas specialists, which have only one or two links, with similar $k_{radius}$, score lower $k_{degree}$. This magnitude reminds the definition of the *Harary index* (Plavšić et al., 1993) but only considering paths from the nodes tied from $m$ to the nodes of the innermost shell.

Figure 2 shows how $k_{degree}$ works for one particular network. There are many nodes with the same *degree* value, such as specialists with just one or two links, that from a ranking point of view are equivalent. On the contrary $k_{degree}$, maps the degree distribution onto a more continuous one, because of the weight of the inverse of $k_{radius}$. In Fig. 2C the cumulative distributions of both indexes are overimposed over the *degree* scale.

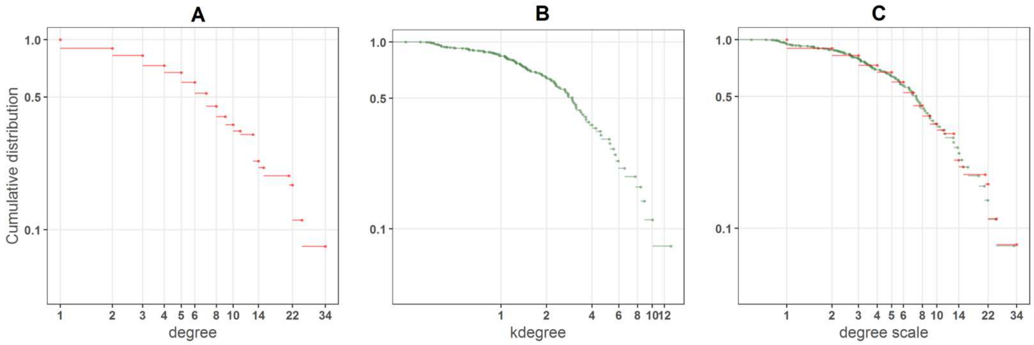

**Figure 2.** (A)- Degree, (B)- $k_{degree}$ and (C) combined degree and $k_{degree}$ distributions of a big plant pollinator community in Central Los Andes, Chile Arroyo et al. (1982).

Finally, we introduce $k_{risk}$ as a way to measure how vulnerable is a network to the loss of a particular species:

$$k^A_{risk}(m) = \sum_i a_{mi} \left(k^A_{shell}(m) - k^B_{shell}(i)\right) + \varepsilon k^A_{shell}(m) \qquad m \in A, \forall i \; in \; B, \; k^B_{shell}(i) < k^A_{shell}(m) \tag{3}$$

The $k_{risk}$ of one species is the sum of the nodes of lower *k-shells* that are tied to it. Each one is weighted by the difference of the $k$ indexes. The second element of equation 3 is meant to solve ties among species when they belong to different *k-shells*, and is a very small quantity (in our implementation we use 0.01, two orders of magnitude lesser than the sum).

In an intuitive way, if we remove one node strongly connected to others of lower *k-shells*, these species are in high risk of being dragged by the primary extinction. On the other hand, the extinction is much less dangerous for the species of higher *k-shells* linked to the same node, because they enjoy more redundant paths towards the network nucleus.

## Applying the $k$-magnitudes to a network

Fig. 3 is an small seed disperser network with five species of plants, four species of thrushes and eleven links. We call, by convention, *guild A* the set of plants, and *guild B* the set of birds. The *k-core* decomposition was performed with the `R igraph` package (Csardi and Nepusz, 2006) . The maximum *k* index is 2. The four bird species belong to *2-shell*; there are three plant species in *1-shell* and two in *2-shell*. In this example each species of *2-shell* is directly tied to all species of the opposite guild *2-shell*, but this is not a general rule.

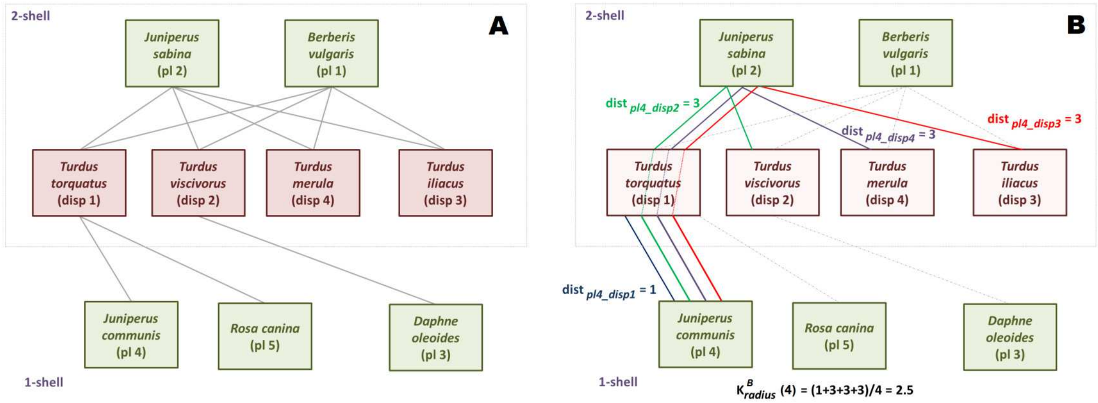

**Figure 3. Computation of the *k-magnitudes*.** Seed disperser network in Santa Bárbara, Sierra de Baza (Spain) (Jordano, 1993). A: Decomposed network. B: Computing $k^B_{radius}(4)$.

The shortest path from plant species 2 to each of the four bird species of *2-shell* is 1, because of the direct links. So, $k^A_{radius}(2)$ is 1. The same reasoning is valid for plant species 1. The reader may check that the $k_{radius}$ of bird species of *2-shell* is 1 as well, measuring their shortest paths to plants species 1 and 2.

Computation of this magnitude is simple although a bit more laborious for *1-shell* plant species. We work plant species 4 as an example. First, we find the shortest paths to each bird species of *2-shell*. Shortest paths are depicted with different colors. Plant species 4 is tied to seed disperser species 1, so distance is 1. On the other hand, there is no direct link with bird species 2. Shortest path is $pl4$-$disp1$-$pl2$-$disp2$, and distance is 3. It is easy to check that distances from plant species 4 to bird species 3 and 4 are also 3. Once we have found the four distances, we compute $k^B_{radius}(4)$ as the average of 1, 3, 3 and 3, that is 2.5.

The values of $k_{degree}$ are straightforward to compute. For instance, the $k_{degree}$ of disperser species 1 is:

$$k^B_{degree}(1) = \frac{1}{k^A_{radius}(1)} + \frac{1}{k^A_{radius}(2)} + \frac{1}{k^A_{radius}(4)} + \frac{1}{k^A_{radius}(5)} = 2.8 \quad (4)$$

The last *k-magnitude* we defined was $k_{risk}$. We use again the disperser species 1 as example. Links to species of the same or upper *k-shells* are irrelevant to compute $k_{risk}$, so only bird species 4 and 5 are taken into account.

$$k^B_{risk}(1) = k^B_{shell}(1) - k^A_{shell}(4) + k^B_{shell}(1) - k^A_{shell}(5) + \varepsilon k^B_{shell}(1) = (2-1) + (2-1) + 0.01x2 = 2.02 \quad (5)$$

This magnitude may seem counter-intuitive, because the $k_{risk}$ of a highly connected species like plant 1 is 0.02, almost the same of that of peripheral plant 3. This is because plant 1 has no ties with lower *k-shell* animal species. The $k_{risk}$ ranks species to assess resilience, it has not an absolute meaning. It just tells us that it is more dangerous for the network to remove the disperser 1 than plant 1, and plant 1 than plant 3.

The *k-magnitudes* of the example network are shown in table 1.

| *Species* | $k_{shell}$ | $k_{radius}$ | $k_{degree}$ | $k_{risk}$ |
|---:|---:|---:|---:|---:|
| pl1 | 2 | 1 | 4 | 0.02 |
| pl2 | 2 | 1 | 4 | 0.02 |
| pl3 | 1 | 2.5 | 1 | 0.01 |
| pl4 | 1 | 2.5 | 1 | 0.01 |
| pl5 | 1 | 2.5 | 1 | 0.01 |
| disp1 | 2 | 1 | 2.8 | 2.02 |
| disp2 | 2 | 1 | 2.4 | 1.02 |
| disp3 | 2 | 1 | 2 | 0.02 |
| disp4 | 2 | 1 | 2 | 0.02 |

**Table 1.** *K-magnitudes* of the network of Fig. 3.

### Extinction procedures

We carried out two static extinction procedures. Static assumption implies that there is not rewiring (e.g., plants that have lost their pollinators are not pollinated by other insects) , despite this kind of network reorganization is observed in nature (Ramos-Jiliberto et al., 2012; Goldstein and Zych, 2016; Timóteo et al., 2016). Nodes are ranked once, before the procedure starts.

In the first method, one species is removed each step, in decreasing order according to the chosen index, no matter to which guild it belongs. Four ranking indexes are compared: $k_{risk}$, $k_{degree}$, *degree* and *eigenvector centrality*. The $k$ indexes were computed with the `R` package `kcorebip`; *degree* and *eigenvector centrality* with the `degree` and `evcent` functions of the `igraph` package.

To estimate the damage caused to the network, the fraction of remaining giant component (i.e., the highest connected component of a given network) was used. The procedure stops when this ratio is equal or less than 0.5. To break ties, we ran 100 experiments for each network and index, shuffling species with the same ranking value. The percentage of removed species needed to get to 0.5 of the remaining giant component is used to measure the performance of the ranking. The lower the percentage of removed species, the more efficient the ranking is in destroying the network. The top performer scores the least average removal percentage. (Fig. 4).

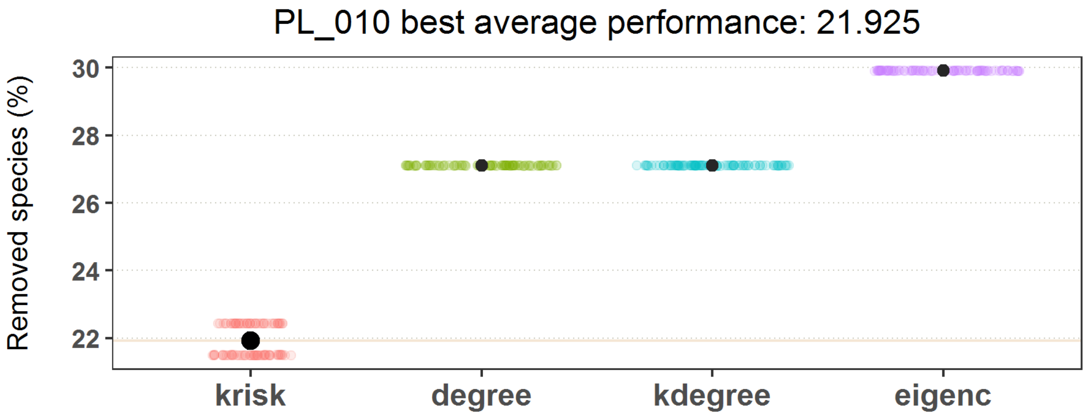

**Figure 4.** First extinction procedure. Performance of the four ranking indexes for a pollinator community described by Elberling and Olesen in Zackenberg Station (Greenland, unpublished). Individual dots are the results of each experiment while black dots are the average values
.

The second extinction procedure that we followed is more common in the literature. Only animal species are actively removed (primary extinctions); secondary extinctions happen when nodes become isolated (Memmott et al., 2004).

The fraction of surviving plant species is measured as a function of the removed fraction of animal species (Fig. 5A,C) and the area under the curve is the value to compare performance. We averaged the results of 100 repetitions.

In this case, in addition to the four indexes of the first experiment, we include *MusRank* a non-linear ranking algorithm for bipartite networks (Tacchella et al., 2012), inspired by *PageRank* (Allesina and Pascual, 2009). This algorithm is not valid for the first extinction method. Domínguez-García and Muñoz showed that *MusRank* achieves excellent performance for this extinction procedure (Domínguez-García and Muñoz, 2015).

In the second extinction procedure, we also measured the fraction of remaining giant component (Fig. 5B,D) . Extinction sequences are identical, the only difference is that both magnitudes are measured for each step.

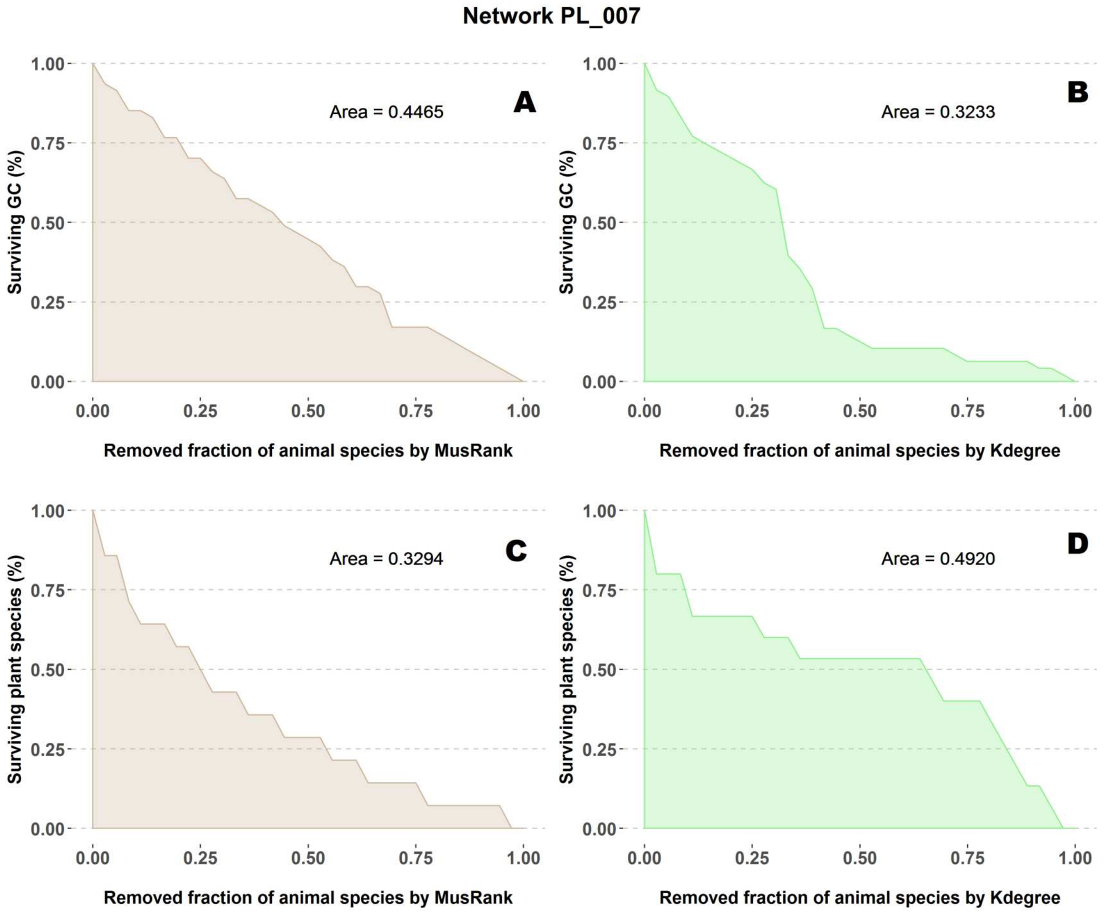

**Figure 5.** Extinction curves of the second algorithm for a pollination network in Suffolk, UK (Dicks et al., 2002). A,C: Percentage of surviving giant component and percentage of surviving plant species removing animal specied ranked by *MusRank*. B,D: Percentage of surviving giant component and percentage of surviving plant species removing animal specied ranked by $k_{degree}$.

# RESULTS

## First extinction method

$k_{risk}$ was the ranking method with the lowest average species removal percentage to destroy half of the Giant Component in most of the networks (67 out of 89 networks) (Table 2). Figure 6 shows the performance comparison of the four ranking criteria. There are some ties, more frequent when networks are small. Network size is the key factor to explain why the performance range is so wide.

As size increases, the removal percentage to break the giant component decreases. When the network is big, the primary extinction of key nodes triggers an important amount of secondary ones. If the

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community has 100 or more species, $k_{risk}$ is even a better predictor of the most damaging extinction sequence and outperforms the other indexes for 28 out of 32 networks.

**Table 2.** Average number of removed species to destroy half the Giant Component, according to the different indexes: $k_{risk}$ is the top performer for 67 networks, *degree* for 48, $k_{degree}$ for 39 and *eigenvector centrality* for 28 networks.

| *Network* | *GCsize* | $k_{risk}$ | *degree* | $k_{degree}$ | *eigen* | *Network* | *GCsize* | $k_{risk}$ | *degree* | $k_{degree}$ | *eigen* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| PL_001 | 177 | 21.73 | 22.13 | 22 | 23 | PL_046 | 60 | 11 | 11.94 | 13 | 14 |
| PL_002 | 103 | 14.46 | 12.51 | 13 | 15 | PL_047 | 205 | 4 | 4 | 4 | 4 |
| PL_003 | 61 | 5 | 5.35 | 6 | 6 | PL_048 | 266 | 10 | 10 | 9 | 12 |
| PL_004 | 112 | 3 | 3 | 3 | 3 | PL_049 | 262 | 11 | 13 | 15 | 16 |
| PL_005 | 361 | 25 | 30.73 | 36 | 42 | PL_050 | 49 | 6 | 6.36 | 7 | 7 |
| PL_006 | 78 | 3 | 3 | 3 | 3 | PL_051 | 104 | 3 | 3 | 3 | 3 |
| PL_007 | 50 | 5 | 4 | 4 | 4 | PL_052 | 52 | 6 | 6 | 6 | 7 |
| PL_008 | 49 | 6 | 7 | 7 | 11 | PL_053 | 364 | 19 | 22.49 | 23 | 34 |
| PL_009 | 142 | 7 | 7.52 | 8 | 12 | PL_054 | 414 | 23 | 25.23 | 27 | 30 |
| PL_010 | 107 | 23.46 | 29 | 29 | 32 | PL_055 | 253 | 16.40 | 17 | 19 |  |
| PL_011 | 27 | 4 | 5.04 | 6 | 6 | PL_056 | 456 | 22 | 28.71 | 33 | 43 |
| PL_012 | 84 | 7 | 7 | 7 | 7 | PL_057 | 997 | 17 | 17 | 20 | 36 |
| PL_013 | 65 | 4 | 4 | 4 | 5 | PL_058 | 111 | 14 | 17.55 | 19 | 20 |
| PL_014 | 108 | 6 | 5 | 5 | 6 | PL_059 | 26 | 6 | 5 | 5 | 5 |
| PL_015 | 793 | 48 | 56 | 60 | 87 | SD_001 | 28 | 3 | 3 | 3 | 5 |
| PL_016 | 205 | 9 | 9 | 10 | 17 | SD_002 | 40 | 5 | 5 | 5 | 5 |
| PL_017 | 104 | 9 | 10.52 | 11 | 11 | SD_003 | 41 | 4 | 4 | 4 | 4 |
| PL_018 | 144 | 18 | 19 | 23 | 24 | SD_004 | 52 | 4 | 4 | 4 | 4 |
| PL_019 | 123 | 14 | 15.37 | 16 | 18 | SD_005 | 34 | 3 | 3 | 3 | 3 |
| PL_020 | 109 | 3 | 3 | 3 | 3 | SD_006 | 34 | 4 | 4.31 | 5 | 5 |
| PL_021 | 766 | 12 | 12 | 12 | 38 | SD_007 | 79 | 3 | 3 | 3 | 3 |
| PL_022 | 66 | 4 | 4 | 4 | 4 | SD_008 | 26 | 9.83 | 8.45 | 8 | 11 |
| PL_023 | 90 | 3 | 3 | 3 | 3 | SD_009 | 25 | 3 | 4 | 4 | 5 |
| PL_024 | 22 | 4 | 3.55 | 3 | 3.0 | SD_010 | 64 | 8 | 8 | 9 | 13 |
| PL_025 | 57 | 6 | 6 | 6 | 10 | SD_011 | 25 | 6 | 5.33 | 5 | 6 |
| PL_026 | 150 | 2 | 2 | 2 | 2 | SD_012 | 64 | 12.71 | 12.53 | 12 | 14 |
| PL_027 | 75 | 8.54 | 8 | 9 | 11 | SD_013 | 55 | 11 | 8 | 19 | 14 |
| PL_028 | 180 | 13 | 14 | 16 | 24 | SD_014 | 33 | 9 | 10 | 10 | 10 |
| PL_029 | 167 | 17 | 16.97 | 17 | 19 | SD_015 | 32 | 4 | 4 | 4 | 4 |
| PL_030 | 70 | 10.23 | 6.65 | 7 | 13 | SD_016 | 85 | 17 | 18 | 20 | 23 |
| PL_031 | 91 | 9.53 | 7.92 | 13 | 17 | SD_017 | 24 | 7.28 | 6.62 | 10 | 10 |
| PL_032 | 40 | 2 | 2 | 2 | 2 | SD_018 | 53 | 5 | 5 | 5 | 5 |
| PL_033 | 47 | 8.65 | 8 | 10 | 12 | SD_019 | 209 | 13 | 16.48 | 20 | 21 |
| PL_034 | 151 | 6 | 7.54 | 8 | 9 | SD_020 | 58 | 7.65 | 9.22 | 10 | 10 |
| PL_035 | 97 | 6 | 7.54 | 8 | 9 | SD_021 | 46 | 9 | 10 | 10 | 10 |
| PL_036 | 22 | 3.68 | 2 | 2 | 2 | SD_022 | 317 | 39 | 50.43 | 53 | 60 |
| PL_037 | 50 | 5 | 5 | 5 | 7 | SD_023 | 23 | 4 | 4 | 4 | 4 |
| PL_038 | 50 | 4 | 4 | 4 | 7 | SD_024 | 19 | 6 | 6 | 7 | 8 |
| PL_039 | 68 | 6 | 6.68 | 9 | 10 | SD_025 | 13 | 4.38 | 4.16 | 4.16 | 4 |
| PL_040 | 70 | 8.56 | 7 | 9 | 10 | SD_026 | 6 | 2 | 2 | 2 | 2 |
| PL_041 | 70 | 10 | 10 | 11 | 12 | SD_027 | 16 | 3 | 3 | 3 | 3 |
| PL_042 | 16 | 2 | 2 | 2 | 2 | SD_028 | 13 | 3 | 3 | 3 | 3 |
| PL_043 | 110 | 12 | 14 | 14 | 19 | SD_029 | 9 | 2 | 2 | 2 | 2 |
| PL_044 | 712 | 21 | 23 | 25 | 49 | SD_030 | 9 | 2 | 2.65 | 2 | 2 |
| PL_045 | 41 | 6 | 5.45 | 7 | 8 |  |  |  |  |  |  |

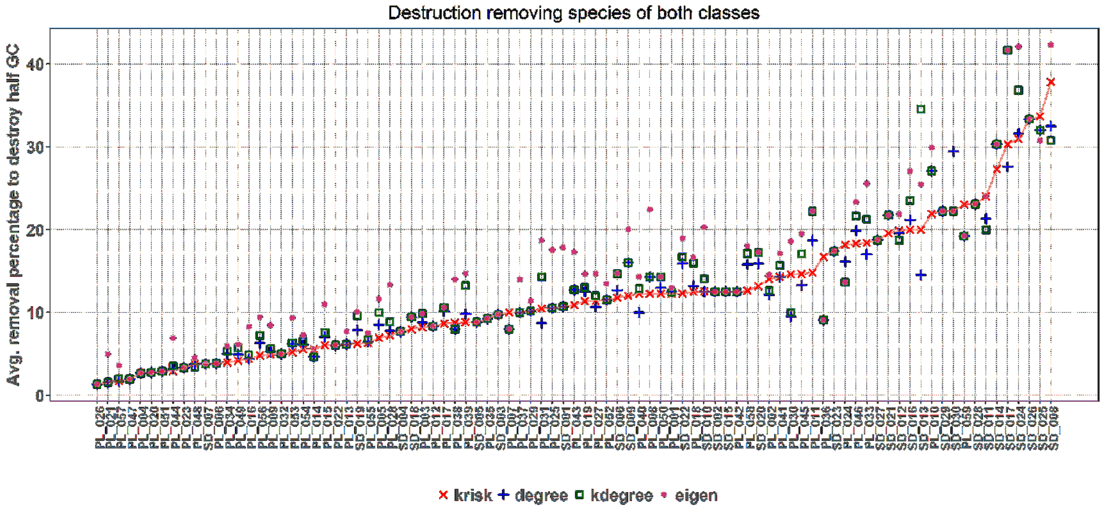

**Figure 6.** First extinction method. The average percentage of removed species to destroy the Giant Component is depicted for each network and ranking index. Under the $X$ axis, the name of each network as coded in the *web of life* database. The overall top performer is $k_{risk}$ (see Table 2). Species are ordered by the percentage of primary extinctions, ranked by $k_{risk}$ . The red line joins the $k_{risk}$ destruction percentage values as a visual reference to compare them with those of the other indexes.

## Second extinction method

*MusRank* ranking method had the lowest area under the extinction curve for 85 of the 89 studied networks (Figure 7), and in the other 4 the difference is so small that may be just an effect of the averaging procedure. So, *MusRank* is the optimal ranking index to destroy the network following this algorithm.

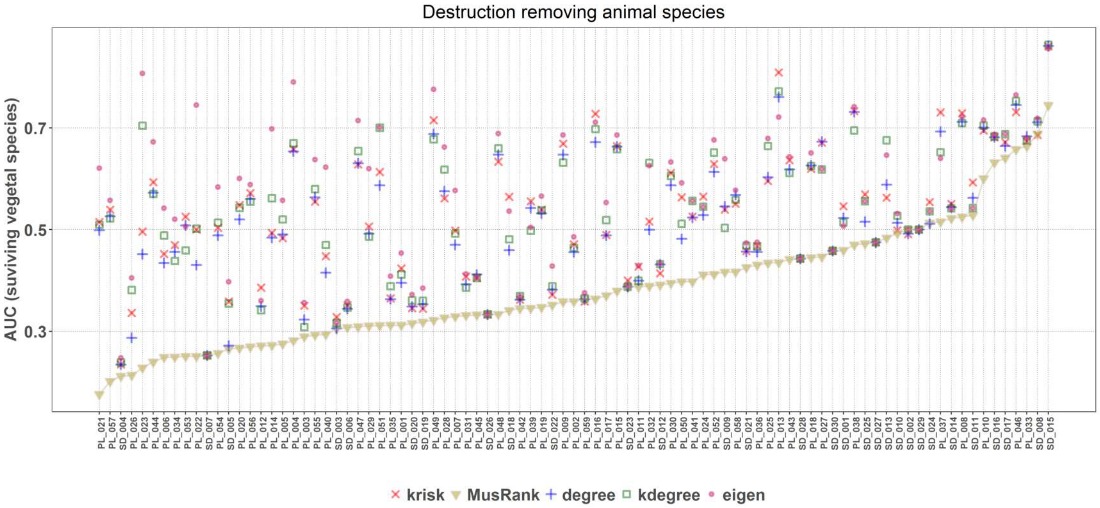

**Figure 7.** Second extinction procedure, measuring the surviving plant species fraction. The Area Under the extinction Curve is depicted for each network and index. The overall top performer is *MusRank* (see Table 3). The solid line joins the *MusRank* values. Species are ordered by the percentage of primary extinctions, ranked by *MusRank*.

On the contrary, when the efficiency of the network destruction was measured through the area under the curve of the surviving Giant Component fraction the *MusRank* index had the highest values, placing it as the least efficient ranking method according to this criterion (Figure 8). In this case, $k_{degree}$ is the most efficient index for 42 out of 89 networks. We must underline that the extinction sequences are the same, the only difference is the measured output.

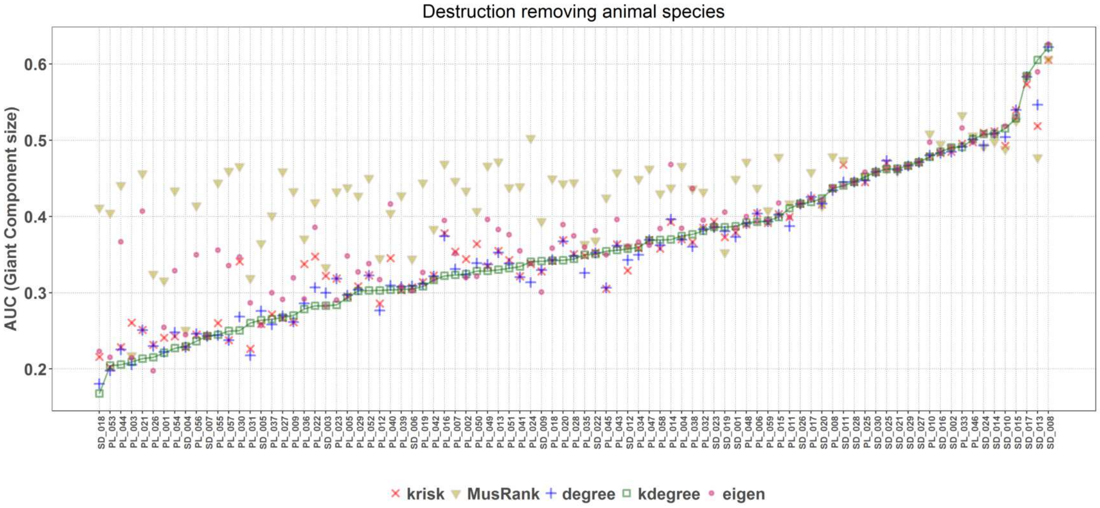

**Figure 8.** Second extinction procedure, measuring the surviving Giant Component fraction. The Area Under the extinction Curve is depicted for each network and index. The overall top performer is $k_{degree}$ (see Table 4). The solid line joins the $k_{degree}$ values. Species are ordered by the percentage of primary extinctions, ranked by $k_{degree}$.

Fig. 5 is an example of this counterintuitive response. On the upper row (subplots *A* and *B*), the difference for both ranking indexes when measuring the giant component. While this magnitude decreases at a constant pace for *MusRank*, there is a sharp reduction of the component size when one third of animal species are removed following the $k_{degree}$ ranking. On the lower row (subplots *C* and *D*), opposite results are obtained when accounting for the fraction of surviving plant species.

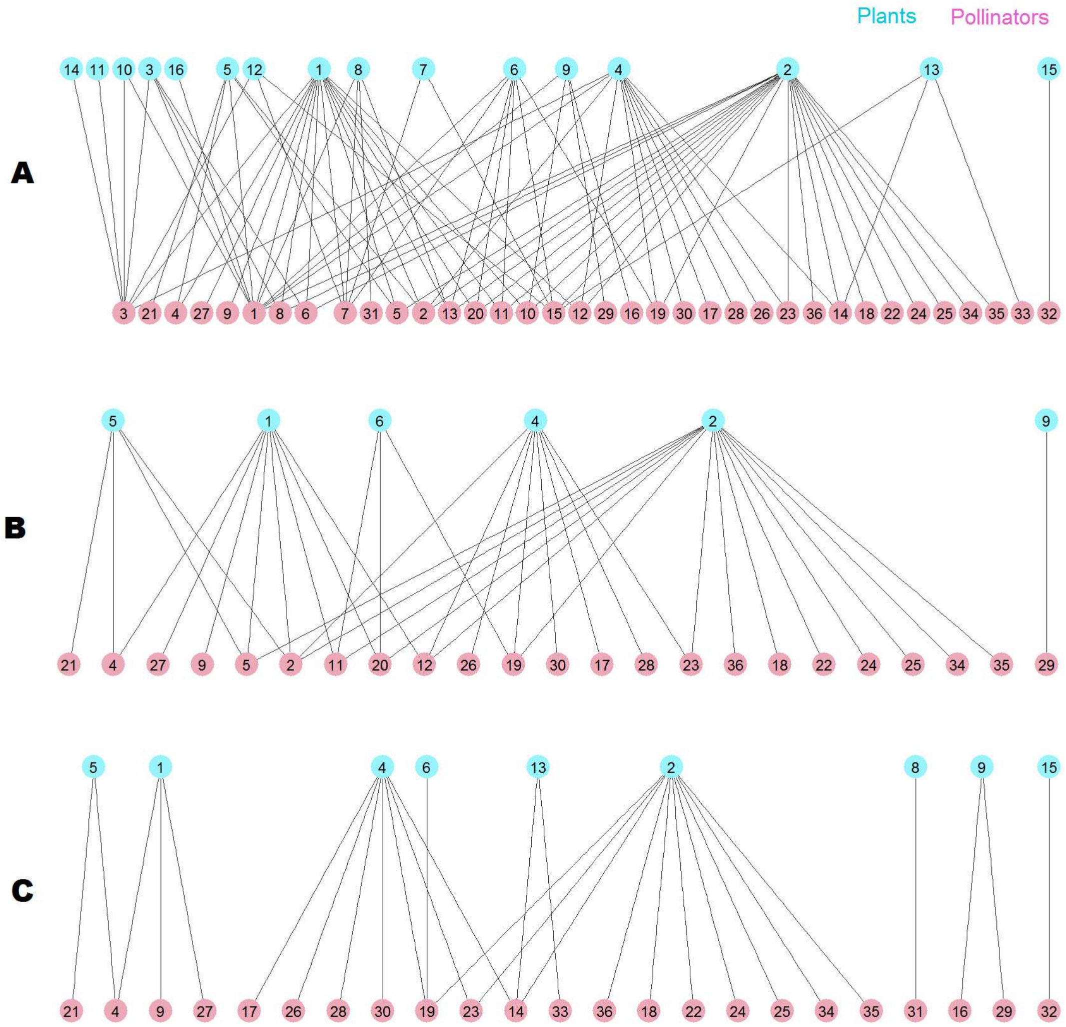

**Figure 9.** Pollinator network 007 (Dicks et al., 2002). A: Original configuration; B: Structure after the removal of the 13 top *MusRank*-ranked animal species. C: Structure after the removal of the 13 top $k_{degree}$-ranked animal species

The destruction of this pollinator network sheds light on the root cause of the difference. The network has 36 pollinator and 16 plant species (Fig.9A), 2 of them are outside the giant component. When the 13 top animal species ranked by *MusRank* are removed (pollinators $3,1,7,15,32,6,14,33,13,31,8,16,10$), the community reaches the degraded structure of Fig.9B. The size of the giant component is 27 (54% of the original), and there are 23 pollinator and 6 plant species.

If we remove the 13 top animal species ranked by $k_{degree}$ (pollinators $1,3,7,13,15,2,11,20,12,8,6,5,10$) instead, the community structure is that of Fig.9C. Now, the size of the giant component is 19 (38% of the original), and there are 23 pollinator and 9 plant species. *MusRank* has killed more plant species, but the giant component is clearly smaller ranking by $k_{degree}$.

**Table 3.** Average area under the extinction curve, when the surviving fraction of plant species is measured. *MusRank* is the top performer for 85 networks , $k_{risk}$ for 9, *degree* for 8, $k_{degree}$ for 7 and *eigenvector centrality* for 7.

| *Network* | *MR* | $k_{risk}$ | $k_{degree}$ | *degree* | *eigenv* | *Network* | *MR* | $k_{risk}$ | $k_{degree}$ | *degree* | *eigenv* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| PL_001 | 0.3121 | 0.4236 | 0.4115 | 0.3956 | 0.4535 | PL_046 | 0.6577 | 0.7308 | 0.7528 | 0.7445 | 0.7642 |
| PL_002 | 0.3588 | 0.4710 | 0.4641 | 0.4555 | 0.4856 | PL_047 | 0.3091 | 0.6283 | 0.6541 | 0.6302 | 0.7143 |
| PL_003 | 0.2896 | 0.3505 | 0.3085 | 0.3232 | 0.3563 | PL_048 | 0.3336 | 0.6334 | 0.6594 | 0.6471 | 0.6887 |
| PL_004 | 0.2821 | 0.6579 | 0.6695 | 0.6536 | 0.7900 | PL_049 | 0.3220 | 0.7150 | 0.6773 | 0.6880 | 0.7757 |
| PL_005 | 0.2755 | 0.4836 | 0.5198 | 0.4906 | 0.5573 | PL_050 | 0.3976 | 0.5635 | 0.5114 | 0.4815 | 0.5918 |
| PL_006 | 0.2490 | 0.4520 | 0.4882 | 0.4344 | 0.5420 | PL_051 | 0.3115 | 0.6132 | 0.7000 | 0.5870 | 0.7008 |
| PL_007 | 0.3294 | 0.4982 | 0.4920 | 0.4702 | 0.5769 | PL_052 | 0.4121 | 0.6289 | 0.6514 | 0.6132 | 0.6761 |
| PL_008 | 0.5251 | 0.7287 | 0.7093 | 0.7117 | 0.7213 | PL_053 | 0.2510 | 0.5253 | 0.4590 | 0.5081 | 0.5058 |
| PL_009 | 0.3583 | 0.6689 | 0.6315 | 0.6473 | 0.6857 | PL_054 | 0.2568 | 0.5035 | 0.5136 | 0.4885 | 0.5835 |
| PL_010 | 0.6004 | 0.6948 | 0.7044 | 0.7003 | 0.7150 | PL_055 | 0.2929 | 0.5548 | 0.5795 | 0.5633 | 0.6378 |
| PL_011 | 0.3876 | 0.4272 | 0.3994 | 0.3999 | 0.4290 | PL_056 | 0.2696 | 0.5717 | 0.5545 | 0.5605 | 0.5885 |
| PL_012 | 0.2716 | 0.3860 | 0.3417 | 0.3494 | 0.3604 | PL_057 | 0.2019 | 0.5392 | 0.5217 | 0.5261 | 0.5576 |
| PL_013 | 0.4353 | 0.8088 | 0.7716 | 0.7606 | 0.7212 | PL_058 | 0.4168 | 0.5507 | 0.5585 | 0.5683 | 0.5773 |
| PL_014 | 0.2726 | 0.4935 | 0.5617 | 0.4840 | 0.6980 | PL_059 | 0.3639 | 0.3587 | 0.3649 | 0.3631 | 0.3757 |
| PL_015 | 0.3792 | 0.6637 | 0.6579 | 0.6633 | 0.6859 | SD_001 | 0.4592 | 0.5459 | 0.5141 | 0.5229 | 0.5068 |
| PL_016 | 0.3641 | 0.7275 | 0.6973 | 0.6719 | 0.7108 | SD_002 | 0.5000 | 0.4911 | 0.5000 | 0.4919 | 0.5000 |
| PL_017 | 0.3703 | 0.4895 | 0.5187 | 0.4886 | 0.5532 | SD_003 | 0.3051 | 0.3281 | 0.3166 | 0.3059 | 0.3166 |
| PL_018 | 0.4451 | 0.6194 | 0.6249 | 0.6259 | 0.6504 | SD_004 | 0.2121 | 0.2351 | 0.2389 | 0.2350 | 0.2476 |
| PL_019 | 0.3474 | 0.5391 | 0.5373 | 0.5320 | 0.5658 | SD_005 | 0.2656 | 0.3587 | 0.3546 | 0.2718 | 0.3974 |
| PL_020 | 0.2674 | 0.5480 | 0.5427 | 0.5199 | 0.6005 | SD_006 | 0.3078 | 0.3515 | 0.3471 | 0.3444 | 0.3588 |
| PL_021 | 0.1761 | 0.5147 | 0.5092 | 0.4985 | 0.6207 | SD_007 | 0.2528 | 0.2528 | 0.2528 | 0.2528 | 0.2528 |
| PL_022 | 0.2511 | 0.5003 | 0.5019 | 0.4304 | 0.7444 | SD_008 | 0.6875 | 0.6861 | 0.7125 | 0.7108 | 0.7188 |
| PL_023 | 0.2285 | 0.4959 | 0.7041 | 0.4517 | 0.8068 | SD_009 | 0.4167 | 0.5395 | 0.5033 | 0.5453 | 0.6389 |
| PL_024 | 0.4111 | 0.5650 | 0.5449 | 0.5283 | 0.5444 | SD_010 | 0.4929 | 0.4986 | 0.5271 | 0.5129 | 0.5314 |
| PL_025 | 0.4344 | 0.5956 | 0.6641 | 0.6030 | 0.6792 | SD_011 | 0.5286 | 0.5927 | 0.5422 | 0.5623 | 0.5422 |
| PL_026 | 0.2138 | 0.3362 | 0.3811 | 0.2874 | 0.4052 | SD_012 | 0.3912 | 0.4140 | 0.4321 | 0.4316 | 0.4332 |
| PL_027 | 0.4466 | 0.6711 | 0.6179 | 0.6728 | 0.6185 | SD_013 | 0.4835 | 0.5629 | 0.6754 | 0.5885 | 0.6462 |
| PL_028 | 0.3266 | 0.5613 | 0.6178 | 0.5754 | 0.6621 | SD_014 | 0.5221 | 0.5504 | 0.5415 | 0.5441 | 0.5404 |
| PL_029 | 0.3107 | 0.5061 | 0.4865 | 0.4919 | 0.6198 | SD_015 | 0.7444 | 0.8602 | 0.8633 | 0.8607 | 0.8556 |
| PL_030 | 0.3949 | 0.6113 | 0.6054 | 0.5870 | 0.6329 | SD_016 | 0.6318 | 0.6812 | 0.6830 | 0.6816 | 0.6872 |
| PL_031 | 0.3314 | 0.4078 | 0.3857 | 0.3926 | 0.4128 | SD_017 | 0.6406 | 0.6719 | 0.6875 | 0.6639 | 0.6875 |
| PL_032 | 0.3889 | 0.5157 | 0.6312 | 0.4995 | 0.6255 | SD_018 | 0.3413 | 0.5645 | 0.4809 | 0.4596 | 0.5361 |
| PL_033 | 0.6640 | 0.6732 | 0.6753 | 0.6832 | 0.6799 | SD_019 | 0.3185 | 0.3444 | 0.3602 | 0.3535 | 0.3849 |
| PL_034 | 0.2497 | 0.4697 | 0.4383 | 0.4563 | 0.5204 | SD_020 | 0.3155 | 0.3459 | 0.3608 | 0.3485 | 0.3722 |
| PL_035 | 0.3121 | 0.3648 | 0.3886 | 0.3633 | 0.4085 | SD_021 | 0.4254 | 0.4579 | 0.4682 | 0.4567 | 0.4737 |
| PL_036 | 0.4306 | 0.4677 | 0.4667 | 0.4560 | 0.4750 | SD_022 | 0.3517 | 0.3720 | 0.3886 | 0.3820 | 0.4284 |
| PL_037 | 0.5153 | 0.7303 | 0.6521 | 0.6924 | 0.6400 | SD_023 | 0.3875 | 0.4000 | 0.3875 | 0.3875 | 0.3875 |
| PL_038 | 0.4702 | 0.7328 | 0.6948 | 0.7310 | 0.7411 | SD_024 | 0.5130 | 0.5542 | 0.5357 | 0.5114 | 0.5357 |
| PL_039 | 0.3454 | 0.5556 | 0.4979 | 0.5425 | 0.5046 | SD_025 | 0.4722 | 0.5692 | 0.5556 | 0.5156 | 0.5556 |
| PL_040 | 0.2940 | 0.4478 | 0.4696 | 0.4153 | 0.6227 | SD_026 | 0.3333 | 0.3333 | 0.3333 | 0.3333 | 0.3333 |
| PL_041 | 0.3978 | 0.5253 | 0.5562 | 0.5238 | 0.5566 | SD_027 | 0.4750 | 0.4750 | 0.4750 | 0.4750 | 0.4750 |
| PL_042 | 0.3452 | 0.3621 | 0.3690 | 0.3621 | 0.3690 | SD_028 | 0.4429 | 0.4429 | 0.4429 | 0.4429 | 0.4429 |
| PL_043 | 0.4414 | 0.6364 | 0.6113 | 0.6183 | 0.6430 | SD_029 | 0.5000 | 0.5000 | 0.5000 | 0.5000 | 0.5000 |
| PL_044 | 0.2401 | 0.5932 | 0.5701 | 0.5723 | 0.6721 | SD_030 | 0.4583 | 0.4583 | 0.4583 | 0.4583 | 0.4583 |
| PL_045 | 0.3324 | 0.4052 | 0.4047 | 0.4116 | 0.4063 | | | | | | |

**Table 4.** Average area under the extinction curve, when the surviving fraction of the original giant component is measured. The top performer is $k_{degree}$ for 42 networks, *degree* for 24, $k_{risk}$ for 21, *eigenvector centrality* for 18 and *MusRank* for 16.

| *Network* | *MusRank* | $k_{risk}$ | $k_{degree}$ | *degree* | *eigenv* | *Network* | *MusRank* | $k_{risk}$ | $k_{degree}$ | *degree* | *eigenv* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| PL_001 | 0.3158 | 0.2410 | 0.2212 | 0.2224 | 0.2546 | PL_046 | 0.5060 | 0.4975 | 0.5013 | 0.5008 | 0.4987 |
| PL_002 | 0.4337 | 0.3441 | 0.3244 | 0.3237 | 0.3198 | PL_047 | 0.4626 | 0.3694 | 0.3686 | 0.3694 | 0.3622 |
| PL_003 | 0.2176 | 0.2607 | 0.2093 | 0.2056 | 0.2145 | PL_048 | 0.4715 | 0.3895 | 0.3920 | 0.3909 | 0.3998 |
| PL_004 | 0.4661 | 0.3700 | 0.3744 | 0.3697 | 0.3843 | PL_049 | 0.4662 | 0.3350 | 0.3286 | 0.3372 | 0.3960 |
| PL_005 | 0.4380 | 0.2954 | 0.2935 | 0.2968 | 0.3482 | PL_050 | 0.4068 | 0.3641 | 0.3285 | 0.3387 | 0.3214 |
| PL_006 | 0.4374 | 0.4044 | 0.3929 | 0.4038 | 0.3932 | PL_051 | 0.4380 | 0.3428 | 0.3322 | 0.3384 | 0.3762 |
| PL_007 | 0.4465 | 0.3539 | 0.3233 | 0.3310 | 0.3513 | PL_052 | 0.4502 | 0.3228 | 0.3029 | 0.3227 | 0.3381 |
| PL_008 | 0.4786 | 0.4363 | 0.4370 | 0.4344 | 0.4386 | PL_053 | 0.4046 | 0.2018 | 0.2045 | 0.1980 | 0.2153 |
| PL_009 | 0.4331 | 0.2613 | 0.2703 | 0.2617 | 0.3195 | PL_054 | 0.4337 | 0.2427 | 0.2273 | 0.2481 | 0.3287 |
| PL_010 | 0.5086 | 0.4789 | 0.4783 | 0.4802 | 0.4974 | PL_055 | 0.4443 | 0.2602 | 0.2449 | 0.2443 | 0.3557 |
| PL_011 | 0.4169 | 0.3994 | 0.4108 | 0.3874 | 0.3985 | PL_056 | 0.4142 | 0.2451 | 0.2364 | 0.2460 | 0.3498 |
| PL_012 | 0.3451 | 0.2859 | 0.3030 | 0.2768 | 0.3173 | PL_057 | 0.4597 | 0.2378 | 0.2498 | 0.2377 | 0.3355 |
| PL_013 | 0.4718 | 0.3548 | 0.3302 | 0.3527 | 0.3828 | PL_058 | 0.4301 | 0.3578 | 0.3694 | 0.3622 | 0.3840 |
| PL_014 | 0.4378 | 0.3928 | 0.3697 | 0.3965 | 0.4679 | PL_059 | 0.4077 | 0.3916 | 0.3944 | 0.3934 | 0.3954 |
| PL_015 | 0.4780 | 0.4030 | 0.3991 | 0.4025 | 0.4177 | SD_001 | 0.4489 | 0.3792 | 0.3871 | 0.3732 | 0.3854 |
| PL_016 | 0.4689 | 0.3781 | 0.3221 | 0.3743 | 0.3946 | SD_002 | 0.4905 | 0.4849 | 0.4905 | 0.4847 | 0.4905 |
| PL_017 | 0.4579 | 0.4240 | 0.4190 | 0.4257 | 0.4234 | SD_003 | 0.3333 | 0.3222 | 0.2829 | 0.2999 | 0.2829 |
| PL_018 | 0.4498 | 0.3419 | 0.3421 | 0.3432 | 0.3585 | SD_004 | 0.2510 | 0.2286 | 0.2298 | 0.2288 | 0.2448 |
| PL_019 | 0.4441 | 0.3138 | 0.3083 | 0.3118 | 0.3265 | SD_005 | 0.3646 | 0.2592 | 0.2640 | 0.2762 | 0.2569 |
| PL_020 | 0.4433 | 0.3688 | 0.3426 | 0.3674 | 0.3894 | SD_006 | 0.3444 | 0.3072 | 0.3049 | 0.3088 | 0.3025 |
| PL_021 | 0.4563 | 0.2512 | 0.2136 | 0.2510 | 0.4071 | SD_007 | 0.2433 | 0.2433 | 0.2433 | 0.2433 | 0.2433 |
| PL_022 | 0.4184 | 0.3475 | 0.2828 | 0.3068 | 0.3858 | SD_008 | 0.6060 | 0.6056 | 0.6220 | 0.6221 | 0.6260 |
| PL_023 | 0.4327 | 0.3187 | 0.2840 | 0.3185 | 0.2901 | SD_009 | 0.3935 | 0.3280 | 0.3415 | 0.3296 | 0.3009 |
| PL_024 | 0.5028 | 0.3380 | 0.3406 | 0.3135 | 0.3389 | SD_010 | 0.4881 | 0.4926 | 0.5153 | 0.5040 | 0.5187 |
| PL_025 | 0.4529 | 0.4451 | 0.4521 | 0.4472 | 0.4582 | SD_011 | 0.4736 | 0.4678 | 0.4405 | 0.4452 | 0.4405 |
| PL_026 | 0.3245 | 0.2316 | 0.2153 | 0.2300 | 0.1976 | SD_012 | 0.3603 | 0.3291 | 0.3575 | 0.3429 | 0.3609 |
| PL_027 | 0.4590 | 0.2669 | 0.2676 | 0.2698 | 0.2912 | SD_013 | 0.4772 | 0.5185 | 0.6053 | 0.5466 | 0.5897 |
| PL_028 | 0.4445 | 0.3505 | 0.3444 | 0.3483 | 0.3743 | SD_014 | 0.4982 | 0.5117 | 0.5081 | 0.5092 | 0.5074 |
| PL_029 | 0.4270 | 0.3084 | 0.3024 | 0.3040 | 0.3272 | SD_015 | 0.5251 | 0.5392 | 0.5288 | 0.5397 | 0.5299 |
| PL_030 | 0.4658 | 0.3410 | 0.2504 | 0.2685 | 0.3469 | SD_016 | 0.4949 | 0.4832 | 0.4849 | 0.4833 | 0.4852 |
| PL_031 | 0.3190 | 0.2263 | 0.2603 | 0.2178 | 0.2866 | SD_017 | 0.5842 | 0.5734 | 0.5842 | 0.5832 | 0.5842 |
| PL_032 | 0.4322 | 0.3853 | 0.3810 | 0.3831 | 0.3951 | SD_018 | 0.4112 | 0.2159 | 0.1678 | 0.1806 | 0.2231 |
| PL_033 | 0.5326 | 0.4953 | 0.4910 | 0.4914 | 0.5160 | SD_019 | 0.3528 | 0.3729 | 0.3861 | 0.3807 | 0.4058 |
| PL_034 | 0.4489 | 0.3585 | 0.3596 | 0.3497 | 0.3664 | SD_020 | 0.4135 | 0.4156 | 0.4236 | 0.4169 | 0.4229 |
| PL_035 | 0.3636 | 0.3488 | 0.3498 | 0.3259 | 0.3595 | SD_021 | 0.4594 | 0.4617 | 0.4627 | 0.4610 | 0.4627 |
| PL_036 | 0.3708 | 0.3377 | 0.2785 | 0.2859 | 0.2917 | SD_022 | 0.3681 | 0.3525 | 0.3508 | 0.3522 | 0.3814 |
| PL_037 | 0.4010 | 0.2716 | 0.2652 | 0.2585 | 0.2997 | SD_023 | 0.3860 | 0.3934 | 0.3860 | 0.3860 | 0.3860 |
| PL_038 | 0.4366 | 0.3665 | 0.3767 | 0.3605 | 0.4366 | SD_024 | 0.4916 | 0.5098 | 0.5079 | 0.4931 | 0.5079 |
| PL_039 | 0.4274 | 0.3036 | 0.3042 | 0.3080 | 0.3083 | SD_025 | 0.4621 | 0.4702 | 0.4621 | 0.4732 | 0.4621 |
| PL_040 | 0.4042 | 0.3454 | 0.3037 | 0.3096 | 0.4164 | SD_026 | 0.4167 | 0.4167 | 0.4167 | 0.4167 | 0.4167 |
| PL_041 | 0.4394 | 0.3216 | 0.3344 | 0.3205 | 0.3550 | SD_027 | 0.4712 | 0.4712 | 0.4712 | 0.4712 | 0.4712 |
| PL_042 | 0.3833 | 0.3227 | 0.3167 | 0.3218 | 0.3167 | SD_028 | 0.4455 | 0.4455 | 0.4455 | 0.4455 | 0.4455 |
| PL_043 | 0.4577 | 0.3634 | 0.3558 | 0.3616 | 0.3959 | SD_029 | 0.4667 | 0.4667 | 0.4667 | 0.4667 | 0.4667 |
| PL_044 | 0.4410 | 0.2286 | 0.2058 | 0.2255 | 0.3669 | SD_030 | 0.4583 | 0.4583 | 0.4583 | 0.4583 | 0.4583 |
| PL_045 | 0.4246 | 0.3052 | 0.3544 | 0.3066 | 0.3496 | | | | | | |

# DISCUSSION

The *k-core decomposition* offers a new topological view of the structure of mutualistic networks. We have defined three new magnitudes to take advantage of their properties. Network compactness is described by $k_{radius}$, a measure of average proximity to top generalists of the partner guild. Second, $k_{degree}$ maps each node's degree onto a finer grain distribution. It has not only information on the number of neighbors but also on how they are connected to the innermost shell. Finally, $k_{risk}$ is set to identify species whose disappearance poses a greater risk to the entire network.

Comparing the *k-magnitudes* based extinction indexes ($k_{degree}$ and $k_{risk}$) with those routinely used when extinctions take place in both guilds, $k_{risk}$ is the best rank if the goal is to identify the key species to preserve most of the giant component. $k_{risk}$ identifies species linked to a high number of nodes of lower *k-shells*. These species provide vulnerability to the network because their extinction may drag many of the species with lower *k-shells* they are linked to, to extinction as well, as they do not enjoy redundant paths to the innermost shell.

Applying the well-known method of removing species of the primary class and measuring the extinctions in secondary class, the most effective extinction sequence, if the goal is to identify the key species to preserve most of the giant component, is $k_{degree}$. However, if the goal is to identify the key species to preserve the greatest species richness in the second class (e.g., plants in a plant-pollinator mutualistic network), the best criterion is *MusRank* as Fig. 7 makes clear . These results confirm those obtained by Domínguez-García and Muñoz (2015), over a larger network collection (89 in this work vs. 67 in the original paper).

The most striking result of the second method is how different performance is for a same ranking index, depending on the magnitude we measure. The root cause lies on the definitions of the indexes themselves. *MusRank* is optimal to destroy the plant guild. It identifies the most important active nodes of the bipartite network because of how they are linked to the most vulnerable passive ones. It was designed to excel with this extinction sequence and works with local properties. On the other hand, $k_{degree}$ is an excellent performer to destroy the giant component. It contains information on how nodes are connected to the innermost shell, and ranks higher those nodes strongly tied to that stable nucleus.

In summary, in this study, we show that the new *k-core* decomposition derived indexes, $k_{risk}$ and $k_{degree}$ provide a new insight into the structure of mutualistic networks. This insight is particularly useful because these indexes fair much better than other traditionally used ranking indexes, when the aim is to identify the species that are key to preserving the interactions and the functionality of the community. As complex network studies on mutualistic interactions are already being used to suggest conservation policies, it is of utmost importance to have a clear framework of what the conservation practitioners look for when implementing conservation and restoration plans. The static view of considering biodiversity conservation as the mere conservation of a list of species has long been substituted by a new paradigm which looks at conservation from a dynamic viewpoint in which species interactions and the functionality of the ecosystems play a major role (Heywood and Iriondo, 2003).

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## Competing Interests

The authors declare no competing interests.

## Author Contributions

J.G-A., J.M.P and J.G. developed the mathematical analysis. J.G-A. wrote the `R` code and J.M.P. the `Python` code and they both performed simulations. J.M.I. provided advice in the overall design of the work and ecological interpretation of results. All authors wrote the paper.

## Code

The R code for *k-core* decomposition and plotting has been published as a package at `https://www.github.com/jgalgarra/kcorebip`.
The rest of software is available at `https://github.com/jgalgarra/kcore_robustness`
Reproducibility instructions are detailed in the `README.md` file

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