



# On the relation between centralities and trophic positions in ecological networks

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## Abstract

In the last decades, many works investigated the trophic structure of communities, in particular, the position of species in food webs (e.g. their trophic position, and more recently, their centrality). Despite encouraging applications on binary food web data, and the acknowledged need of studying weighted webs, few advances have been realized for trophic networks.

Here we aim to contribute to the synthetic treatment of these complementary issues. We wish to unveil emerging patterns by analyzing the relationship between several indices of centrality and trophic position.

Studying 19 ecosystems, we ranked the nodes according to their positional importance values (based on various centrality indices) and we compared the rank order of coefficients with various measurements of trophic position. We aimed to reveal potential biases of finding high centrality nodes among basal, intermediate and top species. Finally, we discuss the consequences of observed features on ecosystem functioning.

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## 1. Introduction

The focus of conservation biology recently started to shift from identifying rarity of species to characterizing their relative importance (keystone species) and effects on ecosystem functioning.

In this context, studying the complexity of multi-species trophic interactions through the network approach looks like a helpful perspective to identify species roles and importance (e.g. centrality in the network, see Margalef, 1991).

Since Lindeman (1942) introduced the concept of trophic level, food webs have long interested ecologists. Trophic structure has been commonly studied as food chain length (Wulff & Ulanowicz, 1989; Bondavalli *et al.*, 2006) but other applications used effective trophic position to infer controlling factors at the whole system level (Christian & Luczkovich, 1999).

Beside trophic analysis, many recent investigations calculated local indices specific to a single species as a function of its topological position (Jordán *et al.*, 2006, 2007). However, emerging patterns are often related to binary data (e.g. link distribution, Montoya & Solé, 2002; Dunne *et al.*,

2002) and no relations between trophic structure and centralities have been detected.

In the present work we studied 19 ecosystem networks, calculating trophic positions and node centralities both in unweighted and weighted versions. We aimed to clarify the following questions: a) Are there general patterns linking species feeding behaviour and their relative importance estimated with centrality measures? b) How are distributed species densities of frequency as regards to centrality and trophic position values? (e.g. do prevail nodes with lowest centrality or are they normally distributed with highest frequencies corresponding to intermediate values?) c) Which are the effects of weighting on trophic positions and centrality indices?

Finally, we briefly sketched on consequences that centrality distribution along trophic chain may have on ecosystem functioning.

## 2. Methods

### 2.1. Data

We analyzed 19 ecological networks based on predator-prey interactions. Data are freely available at the CBL website ([www.cbl.umces.edu](http://www.cbl.umces.edu), collected mostly by R.E. Ulanowicz and colleagues).

In the studied webs, flow intensities are measured as energy (i.e. kcal m<sup>-2</sup> year<sup>-1</sup> or cal cm<sup>-2</sup> year<sup>-1</sup>) or matter (gC m<sup>-2</sup> year<sup>-1</sup> or mgC m<sup>-2</sup> summer<sup>-1</sup>). The number of compartments range from 21 (e.g. Charca de Maspalomas network) to 125 (e.g. wet version of the Florida Bay network). Table 1 provides detailed information on trophic networks.

### 2.2. Methods I – Trophic analysis

Ecological trophic networks describe ecosystems as boxes (species or trophospecies) connected by weighted arrows (quantity of nutrients or energy transferred by feeding relationships).

We applied Ecosystem Network Analysis (ENA, Ulanowicz, 1986), a collection of quantitative methods mapping the intricacy of energy flows. Within this framework we calculated trophic

positions (*TP*) by Canonical Trophic Aggregation (CTA, Ulanowicz & Kemp, 1979; Scotti *et al.*, 2006), a suite of matrix manipulations apportioning every species to a series of discrete trophic levels *sensu* Lindeman (1942). The effective trophic position is defined as the weighted average length of all the loopless pathways that originate from outside the system and reach a given living compartment (i.e. the average weighted distance between producers and a given node, plus one).

Following this approach, primary producers (autotrophs) receiving energy from outside the system are set to *TP* equal to 1, herbivores to 2 and so forth. If we consider an omnivorous species with a fractionary diet based for 10% on a primary producer and for 90% on a herbivore, its *TP* gives rise from the composition of two pathways: a) external source → primary producer → omnivore (0.1 × 2 steps = 0.2); b) external source → primary producer → herbivore → omnivore (0.9 × 3 steps = 2.7). The final *TP* of the omnivore equals 2.9 (0.2 + 2.7 = 2.9).

Alternative version of the *TP* is the unweighted counterpart (*unwTP*), estimated using only topological information, without considering weights on trophic links. In this case, total inputs to a node are equally distributed between entering flows (in the previous example, *TP* = 2.5 for the omnivore).

Theoretically, also the shortest (*unwTPmin*) and longest (*unwTPmax*) energy pathways can be computed but here we have not used these indices. Details on the four measures of trophic position are described in Figure 1 and Table 2.

### 2.3. Methods II – Centrality indices

Although trophic position is a property of a species in a directed trophic network (representing flow of energy from producers to consumers), in order to better understand the ecological role a species plays in a community we may be interested also in the undirected network of interactions. Doing so, we can evaluate the top-down and horizontal interaction structure of species (e.g. trophic cascade and apparent competition, respectively). Shortly, energy flows are represented by a digraph, while interspecific interactions must be represented by an undirected graph (alternatively, by a digraph where there are two arrows of different direction between



each pair of nodes). There is a wealth of topological indices for characterizing the centrality of nodes in networks. Recently, these have been applied in ecological literature, in order to outline a quantitative context for identifying keystone species (Jordán *et al.*, 1999, 2006, 2007; Estrada, 2007).

Different centrality indices characterize different aspects of node centrality, depending on the nature of the network (Vasas & Jordán, 2006). Key nodes can be identified in both directed and undirected, both weighted and unweighted, both signed and unsigned networks, as well as either considering or not indirect effects. Here we used 13 measures of centrality as follows: degree centrality ( $D$ , Wassermann & Faust,

1994), weighted degree centrality ( $wD$ , Wassermann & Faust, 1994), betweenness centrality ( $BC$ , Wassermann & Faust, 1994), undirected betweenness centrality ( $undBC$ , Wassermann & Faust, 1994), topological importance index for  $n = 1, 2, 3$  and  $8$  steps ( $TI^n$ , Jordán *et al.*, 2003) and its weighted version for the same  $n$  values ( $WI^n$ , Jordán *et al.*, 2003). Weight of links is considered by  $wD$  and  $WI^n$ , direction of links is considered by  $BC$  and indirect effects are considered by all except for  $D$  and  $wD$ . For technical details, see also Jordán and Scheuring (2004). Centrality values were normalized setting the maximal value to 1.

Table 1

For each trophic network we present the number of nodes ( $n$ ), the number of nodes representing living compartments ( $nl$ ); the number of links ( $l$ ); directed connectivity ( $C = l/n^2$ ) and currency used to quantify flow intensities.

Trophic network	n	nl	l	C	currency
Charca de Maspalomas	21	18	55	0.125	mgC m <sup>-2</sup> day <sup>-1</sup>
Chesapeake Mesohaline Network	36	33	122	0.094	mgC m <sup>-2</sup> summer <sup>-1</sup>
Crystal River Creek (control)	21	20	82	0.186	mgC m <sup>-2</sup> day <sup>-1</sup>
Crystal River Creek (delta temp.)	21	20	61	0.138	mgC m <sup>-2</sup> day <sup>-1</sup>
Lower Chesapeake Bay in Summer	34	31	115	0.099	mgC m <sup>-2</sup> summer <sup>-1</sup>
St. Marks River (Florida) Flow Network	51	48	270	0.104	mgC m <sup>-2</sup> day <sup>-1</sup>
Lake Michigan Control Network	36	35	172	0.133	gC m <sup>-2</sup> year <sup>-1</sup>
Middle Chesapeake Bay in Summer	34	31	149	0.129	mgC m <sup>-2</sup> summer <sup>-1</sup>
Mondego Estuary	43	42	348	0.188	gAFDW m <sup>-2</sup> year <sup>-1</sup>
Final Narragansett Bay Model	32	31	158	0.154	mgC m <sup>-2</sup> year <sup>-1</sup>
Upper Chesapeake Bay in Summer	34	31	158	0.137	mgC m <sup>-2</sup> summer <sup>-1</sup>
Cypress, Dry Season	68	65	554	0.120	gC m <sup>-2</sup> year <sup>-1</sup>
Cypress, Wet Season	68	65	545	0.118	gC m <sup>-2</sup> year <sup>-1</sup>
Everglades Graminoids, Dry Season	66	63	793	0.182	gC m <sup>-2</sup> year <sup>-1</sup>
Everglades Graminoids, Wet Season	66	63	793	0.182	gC m <sup>-2</sup> year <sup>-1</sup>
Florida Bay, Dry Season	125	122	1969	0.126	gC m <sup>-2</sup> year <sup>-1</sup>
Florida Bay, Wet Season	125	122	1938	0.124	gC m <sup>-2</sup> year <sup>-1</sup>
Mangrove Estuary, Dry Season	94	91	1339	0.152	gC m <sup>-2</sup> year <sup>-1</sup>
Mangrove Estuary, Wet Season	94	91	1340	0.152	gC m <sup>-2</sup> year <sup>-1</sup>

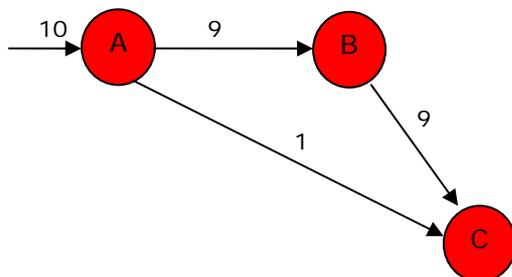


Figure 1

Illustration of four different trophic positions of a node in a hypothetical three-compartment network. Compartment A, receiving exclusively energy from outside, is a primary producer ( $TP = 1$ ), while B, feeding only on A, is a herbivore ( $TP = 2$ ). Node C, feeding both on A (10%) and B (90%), have a  $TP$  equal to  $2.9 = 0.1 \times 2 + 0.9 \times 3$  (as a primary carnivore in 90%). In the unweighted form of  $TP$  ( $unwTP$ ), C receives 50% of energy from A and 50% from B, and its  $unwTP$  is  $2.5 (0.5 \times 2 + 0.5 \times 3)$ . Shortest pathway to C is 2 steps (outside  $\rightarrow$  A  $\rightarrow$  C) while longest is 3 steps (outside  $\rightarrow$  A  $\rightarrow$  B  $\rightarrow$  C):  $unwTP_{min} = 2$ ,  $unwTP_{max} = 3$ .

Table 2

Here we summarize, for the node C depicted in Figure 1, pathways (Path) and calculations (Calculus) giving rise to different trophic positions (Value), depending on the form of trophic position considered (Trophic position).

Trophic position	Path	Calculus	Value
<i>TP</i>	(9/10) outside → A → B → C (is 90% a primary consumer)	$0.9 \times 3 = 2.7$	2.9
	(1/10) outside → A → C (is 10% a herbivore)	$0.1 \times 2 = 0.2$	
<i>unwTP</i>	(1/2) outside → A → B → C (is 50% a primary consumer)	$0.5 \times 3 = 1.5$	2.5
	(1/2) outside → A → C (is 50% a herbivore)	$0.5 \times 2 = 1$	
<i>unwTPmin</i>	outside → A → C	2 steps	2
<i>unwTPmax</i>	outside → A → B → C	3 steps	3

#### 2.4. Methods III – Comparison of indices

First we plotted each centrality index against the two definitions of trophic position adopted (*TP* and *unwTP*), both for pooled data and single systems. In this first step we investigated if centrality patterns are associated to particular feeding activities (e.g. are top predators more specialist than other species? Are primary producers more central than omnivores?).

Then, for every network, we ranked nodes and extracted 3 species showing highest values (doing so, we collected the *TP* values of 57 nodes for each index). With *TPs* of selected compartments we constructed histograms of density, estimating their functions of distribution along the trophic chain. Fitting goodness were measured by Shapiro-Francia test (*W* index; Shapiro & Francia, 1972), in case of normal distribution, or by  $\chi^2$  otherwise (with  $H_0$ : the data follow a specified distribution;  $H_A$ : the data do not follow the specified distribution). In this way, we checked if more central nodes, for different definitions of centrality: a) are associated to basal, intermediate or top species; b) correspond to a well defined range of *TP*; c) display a trend caused by trophic and energetic constraints.

Finally, using pooled data, we depicted histograms of density for all the centralities and trophic positions. In particular, we used histogram of *TPs*, in comparison to density patterns showed by more central nodes, to test if there are significative differences between the distribution of whole database *TPs* and that displayed by the 57 nodes with higher centralities. With pooled data we also showed densities of nodes respect to each centrality index, studying their relative distribution in ecosystems (e.g. are more central species rare? Are nodes normally

distributed between the whole range of normalized centrality values exhibited?).

### 3. Results

When centrality pooled data were studied respect to trophic positions, no trends were identified. However, dealing with keystone species means be focused on nodes with higher centralities and we decided to extract, for each ecosystem, subgroups of 3 most central nodes, identifying their *TPs*. In Table 3 and Figure 2 we illustrated this procedure applied to Crystal River Creek “control”.

Table 3

Normalized centralities (maximal value = 1) for 19 living nodes in Crystal River Creek “control” network and their *TP* values. We excluded one node (2 - Macrophytes) because it showed no connections with other living compartments. For each centrality index, the 3 nodes of highest values are highlighted: *D* in green, *undBC* in orange, *TI* in blue and *WI*<sup>8</sup> in yellow.

Species	<i>D</i>	<i>undBC</i>	<i>TI</i>	<i>WI</i> <sup>8</sup>	<i>TP</i>
1 - Microphytes	0.417	0.267	0.396	0.945	1.000
3 - Zooplankton	0.583	0.367	0.603	1.000	2.000
4 - Benthic invertebrates	1.000	1.000	1.000	0.677	2.000
5 - Blacktip shark	0.083	0.000	0.065	0.048	3.000
6 - Stingray	0.417	0.075	0.269	0.019	3.862
7 - Striped anchovy	0.167	0.006	0.074	0.002	2.667
8 - Bay anchovy	0.500	0.117	0.280	0.127	3.537
9 - Needlefish	0.583	0.304	0.399	0.051	4.329
10 - Sheepshead killifish	0.417	0.087	0.235	0.014	2.109
11 - Goldspotted killifish	0.500	0.130	0.282	0.035	2.446
12 - Gulf killifish	0.750	0.444	0.543	0.191	3.623
13 - Longnosed killifish	0.250	0.004	0.110	0.160	3.000
14 - Silverside	0.583	0.212	0.345	0.528	2.937
15 - Moharra	0.500	0.117	0.280	0.145	2.859
16 - Silver jenny	0.167	0.006	0.074	0.003	2.846
17 - Sheepshead	0.167	0.012	0.093	0.007	2.500
18 - Pinfish	0.667	0.186	0.432	0.077	4.052
19 - Mullet	0.417	0.512	0.541	0.204	2.000
20 - Gulf flounder	0.333	0.013	0.197	0.004	4.455

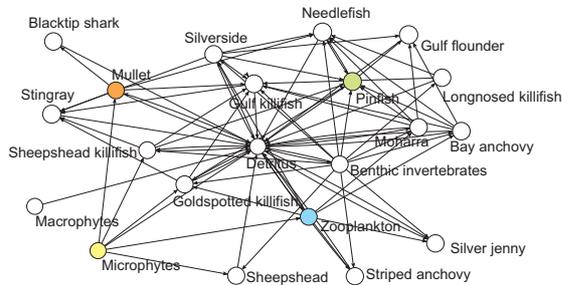


Figure 2

Crystal River Creek "control", 19 nodes. Nodes with a single color in Table 3 are colored; the figure helps understanding the indices:  $D$  in green (many neighbours) = 18 - Pinfish;  $undBC$  in orange (many exclusive shortest pathways crossing) = 19 - Mullet;  $TI^1$  in blue (many low-degree neighbours) = 3 - Zooplankton;  $WI^8$  in yellow (evidently big flows down there) = 1 - Macrophytes.

Despite scattered points plotted with pooled data, densities of  $TPs$  corresponding to highly central nodes give rise to well defined trends (Figure 3): a) considering  $wD$  and  $D$ ,  $TPs$  decrease with a negative power function but highly represented species are at  $1 < TP \leq 2$  in case of  $wD$ , while central nodes are at  $2 < TP \leq 3$  with the unweighted version; b) normal distribution well fit  $TP$  densities for  $BC$  computed with directed and undirected data; c)  $TPs$  associated to higher  $TIs$  are normally distributed and similarly happens for topological importance up to more steps ( $TI^2 - TI^8$ ); d)  $WI$  does not show any trend of  $TPs$  when indirect effects are computed up to shorter pathways ( $WI^1$  and  $WI^2$ ), approaching the  $D$  distribution as indirect effects become longer.

We have also analyzed farness centrality in undirected networks but no clear density distribution of  $TPs$  were detected. In particular, negative power functions used with  $TP$  densities for more central nodes, in case of  $wD$  (density =  $TP^{-2.505} + 0.25$ ) and  $D$  (density =  $(TP-1.25)^{-1.830}$ ), are significant: a)  $wD$ ,  $\chi^2 = 4$  with  $p = 0.26$ ; b)  $D$ ,  $\chi^2 = 6.7$  with  $p = 0.35$ .

Normal distributions observed for  $TP$  histograms of nodes with highest betweenness and topological importance centralities, were always significant:  $BC$  (0.963,  $p = 0.08$ ),  $undBC$  ( $W = 0.960$ ,  $p = 0.06$ ) and  $TI^1$  ( $W = 0.960$ ,  $p = 0.06$ ),  $TI^2$  ( $W = 0.961$ ,  $p = 0.06$ ) and  $TI^8$  ( $W = 0.960$ ,  $p = 0.06$ ). It is interesting to notice how central nodes do not go with the mass,

showing different relative densities along the trophic chain, respect to the whole number of species (Figure 4).

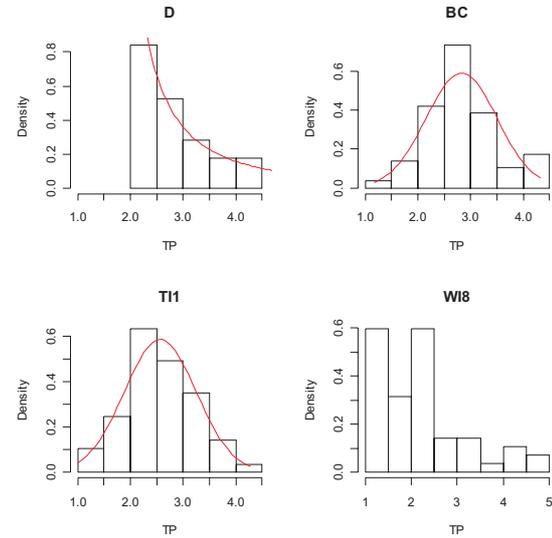


Figure 3

Distribution of densities for the trophic positions (TP) associated to the 57 nodes with the 3 highest centralities in the studied 19 ecosystems. Here we illustrated trends for unweighted degree centrality ( $D$ ), betweenness centrality computed with directed links ( $BC$ ), topological importance index up to 1 step ( $TI1$ ) and weighted topological importance up to 8 steps ( $WI8$ ). Negative power function for  $D$  and Gaussian curve describing  $BC$  and  $TI^1$  were added in red to histograms.

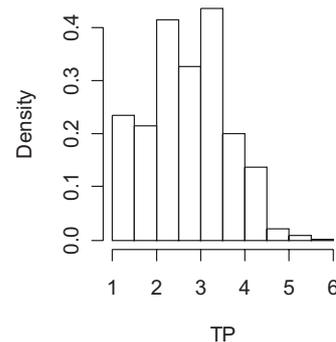


Figure 4

Relative distribution of all of the 1001 nodes in the 19 networks, in classes of trophic position.

We repeated the same studies, plotting centralities against the unweighted version of  $TP$  ( $unwTP$ ),

focusing on the importance of weighting link in trophic analysis. In Figure 5 histograms of  $unwTP$  are depicted for the same indices illustrated in Figure 3. In general, considering topology structure without information on link strength, we observed that: a) negative power function characterizing degree centralities is preserved with  $wD$ , becoming more confusing in  $D$ ; nonetheless, more representative trophic position intervals remain  $1 < unwTP \leq 2$  for the first and  $2 < unwTP \leq 3$  for the latter; b) normal distribution of  $TPs$  is maintained by  $undBC$  and lost in case of  $BC$ , with most central nodes confined to the interval  $2 < unwTP \leq 3.5$ ; c) with topological importance up to  $n$  steps ( $n=1, \dots, 8$ ),  $unwTP$  frequency distribution is normal, as with  $TP$ , suggesting scarce effects of weighting connections; d) weighted topological importance tends to be equally distributed when computed on few steps ( $WI^1 - WI^3$ ), while  $unwTPs \leq 2.5$  are more central in case of longer steps ( $WI^8$ ); also in this case, tendencies displayed by  $TPs$  are smoothed.

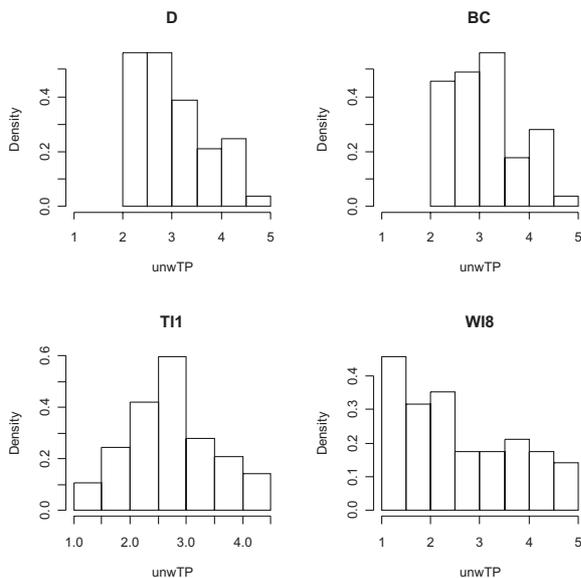


Figure 5

The same histograms as in Figure 3 but for unweighted trophic position ( $unwTP$ ). Trends are similar than in case of  $TP$  for  $TI$  ( $TI1$ ) and  $WI$  ( $WI8$ ), while the negative power function for  $D$  ( $D$ ) and the normal distribution for  $BC$  ( $BC$ ) disappeared.

Finally, we used normalized pooled data to highlight which are frequency distributions of nodes,

using different definitions of centrality: a) in case of  $D$ , intermediate centralities tend to prevail; b)  $wD$ ,  $BC$  and  $undBC$  showed a huge number of nodes with extremely low centralities and the few remaining compartments with higher values, suggesting that key nodes do not represent the total set of nodes; c) topological importance indices display a tendency of prevalence for nodes with low-intermediate values; when increasing steps of indirect effects (moving from  $TI^1$  to  $TI^8$ ), there is a shift, with intermediate and slightly higher centralities more represented; d) in the case of weighted version of  $TI$ , the number of nodes decrease with a negative power law with increasing centrality values. In Figure 6 frequency distributions for  $D$ ,  $BC$ ,  $TI^1$  and  $WI^8$  are showed.

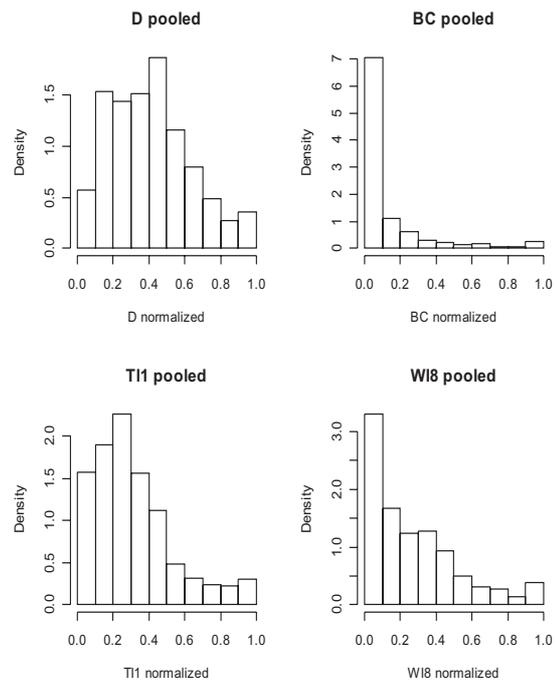


Figure 6

Relative distribution of densities when  $D$  ( $D$  pooled),  $BC$  ( $BC$  pooled),  $TI^1$  ( $TI1$  pooled) and  $WI^8$  ( $WI8$  pooled) are calculated for the 1001 living nodes included into the 19 studied ecosystems. While  $WI^8$  and  $BC$  are centralities with few extremely central nodes and many less important,  $D$  displays a prevalence of compartments with intermediate values and  $TI$  tends to a normal distribution with increasing number of steps up to which is measured.



#### 4. Conclusions

In general, we observed no regularities when centrality indices are studied as a function of trophic position (both *TP* and *unwTP*), for the whole number of food web species. However, theoretical ecology and conservation biology aim to identify the most important species in ecosystems (Paine, 1969; Mills *et al.*, 1993) and Jordán *et al.* (1999) and Jordán (2001) demonstrated how network perspective and centrality measures can be fruitfully adopted in this sense. Then, we analyzed *TP* trends associated to more central nodes, unveiling interesting features.

As suggested by Scotti *et al.* (2007), weighting links is particularly important in food webs for direct centrality indices, and this is confirmed by the present work: a) negative power distribution describing *TP* densities of more central nodes is preserved, switching from the weighted to unweighted version of trophic position, in presence of *wD* but not with *D*; b) the most representative *TP* classes of density are different using the nodes with highest degree centralities ( $1 < TP \leq 2$  in case of *wD* and  $2 < TP \leq 3$  with *D*), while they are the same with indirect indices; c) trends for histograms associated to *TI* are the same with *TPs* and *unwTPs*.

Still, at *TP*=1 there is a prominent number of central nodes for *wD* but none for *D*. This reflects a small number of huge flows resulted from aggregation. Moreover, higher species are not very central in the *D* case (for *wD* it is not surprising because of the small flows up there; see Hairston *et al.*, 1992), suggesting more constrained pathways characterizing top predators (they are more specialist than highly connected intermediate nodes). The majority of nodes with highest unweighted degree centralities have *TPs* included between 2 and 3 (both *TP* and *unwTP*) and this is consistent with trend of patterns exhibited by wasp-waist ecosystems (Jordán *et al.*, 2005).

Beside evidences on weighting, histograms estimated for *BC* and *undBC* display how direction is not so important when we use weighted data for trophic positions.

We also emphasized how topological importance tends to *D* with increasing number of steps up to which is estimated, while weighted importance approaches the *wD* distribution as indirect effects become longer (see Figure 6).

Our study contradicts the common idea identifying charismatic megafauna and top predators as the main objectives of conservation ecology, setting many basal and intermediate nodes as “keystone species” in natural systems. As a consequence, we propose that protection activities should focus their attention towards central rather than rare species, considering that *TP* distribution of key nodes do not follow trends exhibited by the whole food web species.

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