



Relationships between centrality indices and trophic levels in food webs

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Abstract: In the last decades, many works investigated the trophic structure of communities stressing, in particular, the role played by species in food webs (e.g., their trophic level and, more recently, their centrality). There exist some encouraging applications, but few details are known about the relationships between centrality measurements and trophic levels. In addition, these studies almost refer to unweighted trophic networks, despite the acknowledged need of investigating weighted webs. Here we aim to contribute to the synthetic treatment of these complementary issues by analyzing several indices of centrality and trophic level. 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 unweighted or weighted trophic levels. Our goal was revealing potential biases in finding high centrality nodes among basal, intermediate and top species. We found that key species occupy intermediate positions of the trophic hierarchy. In case of unweighted data, trophic levels of key nodes do not deviate from trends displayed by the whole dataset. Significant differences were observed when using weighted data. These results contradict the common belief of many ecologists that identified top-predators and charismatic megafauna as main targets of conservation policies. We discuss the potential consequences of the observed features on ecosystem dynamics.

Abbreviation: TL—Trophic Level.

Introduction

The focus of conservation biology recently started to shift from identifying rarity of species to characterizing their relative importance and effects on ecosystem functioning (Jordán 2009). This perspective is challenging the aesthetic principles that have often inspired ecologists in the past, by targeting charismatic megafauna, endemic species and top-predators as the main objectives of conservation policies (Simberloff 1998, Dale and Beyeler 2001). Currently, biodiversity preservation aims at maintaining ecosystem structure and a reliable supply of ecosystem services, with key species defined on the basis of the functional role they play in the dynamics of ecological communities (Jones and Lawton 1995, Kareiva and Levin 2003). In this context, studying the complexity of multi-species trophic interactions through the network approach helps to identify species roles and importance, by defining their centrality (Margalef 1991), examining effects on secondary extinctions (Dunne et al. 2002a, 2002b, 2004, Allesina et al. 2006) and suggesting managing strategies for ecosystems (Bodini 2000).

Since Lindeman (1942) introduced the concept of trophic level (TL), food webs have long interested ecologists (Post 2002). Although TLs are discrete integers, individual consumers and their populations or guilds often feed across sev-

eral TLs (Odum and Heald 1975). Thus, network nodes representing species or trophospecies may have fractional “effective trophic levels” (Odum and Heald 1975, Levine 1980). The trophic structure has been commonly studied in terms of food chain length, in order to compare ecosystems (Wulff and Ulanowicz 1989), evaluate fishery trends (Pauly et al. 1998) examine theoretical issues of energy flow (Burns 1989) and detect ecosystem stress (Bondavalli et al. 2006). Other applications used trophic level to infer controlling factors and fishing impacts at the whole system level (Christian and Luczkovich 1999, Coll et al. 2006).

Beside trophic analysis, that accounts for the number of feeding steps experienced by energy reaching species in ecosystems, many recent investigations calculated local and “meso-scale” indices specific to a single node as a function of its topological position (Estrada 2007, Jordán et al. 2006a, 2007). These centrality indices provide complementary information to trophic levels, describing how species are related to their community. The most widely applied index is the degree centrality (D). It quantifies the local topology of each species, by summing up the total number of prey and predators that are directly connected (Dunne et al. 2002a). An alternative is to derive the link distribution that illustrates the spectrum of individual degrees in the whole ecosystem (Solé and Montoya 2001). This approach is often adopted to

infer whether the network under investigation is small-world (Watts and Strogatz 1998) or scale-free, with few hubs (strongly connected nodes) responsible for the majority of the topology (Albert et al. 2000). However, analyses based on local and global viewpoints do not inform about the relative position of species within the network, failing to capture the indirect effects due to more distant connections. Jordán and Scheuring (2002) argued that an intermediate “meso-scale”, between the local and the global, is the most relevant to understand relations in ecological communities. This framework includes top-down and bottom-up processes (Abrams et al. 1996), apparent competition (Holt and Lawton 1994), trophic cascades (Menge 1995), and more complex interactions across multiple trophic levels (Bodini 2000). Betweenness centrality (BC - Wasserman and Faust 1994) and topological importance (TI^m - Jordán et al. 2003) are commonly used metrics to assess the indirect influence of a species on other members of the community. The first index quantifies how frequently a node is in the shortest path between other nodes, while the latter gives clues on the indirect chain effects.

Topological centralities provide basic details, but they refer to a static network representation. To increase the reality of the topological considerations, these indices can be combined with suitable metrics (e.g., interaction strength) or population dynamical approaches. Both local (weighted node degree, wD - see Wasserman and Faust 1994) and “meso-scale” (weighted topological importance, WT^m - see Jordán et al. 2006a) centralities can be computed in weighted versions. Patterns of interaction strength may seriously change the predictions based on the topology, and they are of key importance to understand ecosystem dynamics (Jordán and Scheuring 2002). To address central ecological questions, data quantifying link-strength should be analyzed. Despite this need, high quality and species-rich food webs (based on adjacency matrix) prevail in comparison to weighted trophic networks. As a consequence, emerging patterns concerning link density (Montoya and Solé 2002, Dunne et al. 2002a, 2002b) and trophic level (Williams and Martinez 2004) are mainly related to unweighted data.

Although links in food webs are representations of who eats whom in ecosystems and their topology is unequivocally determined by the species feeding behavior, little efforts focused on the connections between trophic structure and centralities. In the present work we studied 19 predator-prey interaction networks, calculating trophic levels and node centralities both in unweighted and weighted versions. We aim to clarify (a) how species are distributed as regards to trophic levels (e.g., do prevail nodes with lowest values, throughout the continuum range of the trophic chain, or are they normally distributed with highest frequencies corresponding to intermediate values?), (b) whether there are general patterns linking species feeding behavior and their relative importance estimated with centrality measures, and (c) which are the effects of weighting on trophic levels and centrality indices. Finally, we briefly sketch on consequences

Table 1. For each of the trophic network we present the number of nodes (S); the number of living nodes (nl); the number of links (I); directed connectivity ($C = I/S^2$) and currency used to quantify flow intensities.

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

that centrality distributions along trophic chain may have on ecosystem functioning.

Methods

Data

We analyzed 19 ecological networks based on predator-prey interactions. Data are freely available at the CBL website (www.cbl.umces.edu, collected mostly by R.E. Ulanowicz and colleagues). Flow intensities are measured as energy (e.g., kcal m⁻² year⁻¹ or cal cm⁻² year⁻¹) or matter (g C m⁻² year⁻¹ or mg C m⁻² summer⁻¹). The number of nodes ranges 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.

Methods I – Trophic analysis

Ecological trophic networks describe ecosystems as nodes (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 weighted trophic levels (wTL) by Canonical Trophic Aggregation (CTA, Ulanowicz and 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 level is defined as the weighted average length of all the loopless pathways that originate from outside the system and reach a given living node (i.e., the average weighted distance between producers and a given node, plus one):

$$wTL_j = 1 + \sum_{i=1}^S wTL_i + p_{ij} \quad (1)$$

where wTL_j is the trophic level of species j , wTL_i is the trophic level of its i^{th} prey, p_{ij} the fraction that species i constitutes within the diet of species j and S the total number of species. Alternative version of the trophic level is the unweighted counterpart (TL), 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 (Williams and Martinez 2004):

$$TL_j = 1 + \sum_{i=1}^S \frac{TL_i}{n_j} \quad (2)$$

where n_j is the number of prey in the diet of species j , and TL_i the trophic level of its i^{th} prey. Also the shortest and longest energy pathways can be computed (Pimm 1980, 1982) but here we have not used these indices. In our work, flow-based and prey-averaged trophic levels (wTL and TL , respectively) were analyzed as raw and normalized data, with the latter measured by the ratio:

$$nTL_j = \frac{TL_j - 1}{mTL - 1} \quad (3)$$

where mTL is the maximum trophic level in each ecosystem, TL_j is the trophic level of species j and nTL_j its normalized version.

Methods II – Centrality indices

Although trophic level is a property of species in directed food webs (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 key species (Jordán et al. 1999, 2006a, 2007, Estrada 2007).

Different centrality indices characterize different aspects of node centrality, depending on the nature of the network (Vasas and 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 12 measures of centrality as follows: degree centrality (D , Wasserman and Faust 1994), weighted degree centrality (wD , Wasserman and Faust 1994), betweenness centrality (BC , Wasserman and Faust 1994), undirected betweenness centrality ($undBC$, Wasserman and Faust 1994), topological importance index for $m = 1, 2, 3$ and 8 steps (TI^m , Jordán et al. 2003) and its weighted version for the same m values (WT^m , Jordán et al. 2003). Weight of links is considered by wD and WT^m , indirect effects are considered by all except for D and wD , while the direction of links is considered by BC . For technical details,

see also Jordán and Scheuring (2004). Centrality values were normalized setting the maximal value to 1.

Unweighted centralities are based on the pure topology, while their weighted counterparts are calculated with the additional information of the link strength. Unweighted indices refer to the static network configuration, and a partial shift to ecosystem functioning may be achieved by extending the analysis to weighted data.

Unweighted and weighted node degrees are local indices; they enumerate, for each species, the total number of neighbors (D , computed as the sum of direct links to prey and predators) and the intensity of the links connected to it (wD , obtained by summing up the strength of connections entering and exiting the target node). Topological importance, both in the unweighted and weighted forms (i.e., TI^m , WT^m), and betweenness centralities (i.e., BC , $undBC$) are “meso-scale” indices; they quantify the indirect consequences of each node on the other species of the network. Betweenness centralities are used to understand which focal nodes are responsible for maintaining the spread of top-down and bottom-up effects in the ecosystem. The topological importance estimates indirect chain effects.

Node degrees are computed without considering the energy flow direction; we did not distinguish between connections with prey (in-degree) and predators (out-degree). Also the topological importance investigates top-down and bottom-up effects using undirected graphs. The proportion of the shortest paths between pairs of nodes that are passing through the focal node may be constrained by flow direction (BC) or computed with undirected data ($undBC$).

Methods III – Comparison of indices

First, we plotted each centrality index against the unweighted or weighted version of trophic level (TL and wTL), both for pooled data and single systems. Specific combinations reflect the coherence in the way indices are computed (e.g., D vs. TL ; wD vs. wTL). The same approach was repeated using the normalized version of trophic level indices. Then, for every network, we ranked nodes according to centrality indices and extracted, for each of them, three species showing highest values (doing so we collected the trophic levels of 57 nodes for each centrality measurement). If there was a tie (e.g., third and fourth nodes in the ranking displayed the same centrality) we averaged the trophic levels. With selected nodes we constructed histograms of density, estimating the distributions of trophic levels along the trophic chain, or adopting a normalized scale. In particular, the raw scale is divided into 12 uniform classes (from $TL = 0$ to $TL = 6$) while the normalized is composed of 10 uniform classes ($0 \div 1$). In both cases, the lower limit of interval is excluded and the upper included. The first histogram class with normalized data is left-closed (i.e., $0.0 \leq nTL \leq 0.1$). We used Cramer-von Mises test for testing normality (W; Thode 2002, section 5.1.3), or Kolmogorov-Smirnov test (Chakravarti et al. 1967) otherwise ($Diff$; with H_0 : the data follow a specified distribution; H_A : the data do not follow the specified distribution).

Using pooled data, we depicted histograms of density for all the trophic levels. First, we applied the Cramer-von Mises test, with the null hypothesis that whole data form a Gaussian distribution. Then, we performed Mann-Whitney tests (Mann and Whitney 1948) to investigate whether there were significant differences between density patterns of trophic levels showed, for each centrality index, by the 57 nodes with higher values in comparison to what displayed by the whole database.

Results

When centrality pooled data were compared to trophic levels no trends were identified. However, dealing with key species means be focused on nodes with higher centralities and we decided to extract, for each ecosystem, subgroups of three “most central” nodes. Then, for each of the 12 centralities, we identified the trophic levels of these nodes. In Fig. 1 and Table 2 we illustrated this procedure applied to the Crystal River (control) Network.

Despite scattered points plotted with pooled data, densities of trophic levels corresponding to highly central nodes give rise to well defined trends (Fig. 2): (a) considering D , we identified a normal distribution for the trophic levels of key nodes (the intermediate interval between herbivores and primary carnivores is the higher frequency class, with $2.5 < TL \leq 3.0$); (b) in the case of wD , the number of nodes decreases along the trophic chain with an exponential function, and the mainly represented species are primary producers

Table 2. Centrality indices in Crystal River (control) Network. Normalized centralities (maximal value = 1) for 19 living nodes and their trophic positions. We excluded one node (2 - Macrophytes) because it showed no connections with other living nodes. For the first 3 indices we extracted the unweighted trophic positions (TP), while for the latter the weighted version (wTP).

Species	D	$undBC$	TI^I	WT^R	TP	wTP
1 - Microphytes	0.417	0.267	0.396	0.945	1.000	1.000
3 - Zooplankton	0.583	0.367	0.603	1.000	2.000	2.000
4 - Benthic invertebrates	1.000	1.000	1.000	0.677	2.000	2.000
5 - Blacktip shark	0.083	0.000	0.065	0.048	3.000	3.000
6 - Stingray	0.417	0.075	0.269	0.019	3.660	3.862
7 - Striped anchovy	0.167	0.006	0.074	0.002	2.667	2.667
8 - Bay anchovy	0.500	0.117	0.280	0.127	3.115	3.537
9 - Needlefish	0.583	0.304	0.399	0.051	4.006	4.329
10 - Sheepshead killifish	0.417	0.087	0.235	0.014	2.333	2.109
11 - Goldspotted killifish	0.500	0.130	0.282	0.035	2.500	2.446
12 - Gulf killifish	0.750	0.444	0.543	0.191	3.661	3.623
13 - Longnosed killifish	0.250	0.004	0.110	0.160	3.000	3.000
14 - Silverside	0.583	0.212	0.345	0.528	2.667	2.937
15 - Moharra	0.500	0.117	0.280	0.145	2.667	2.859
16 - Silver jenny	0.167	0.006	0.074	0.003	2.667	2.846
17 - Sheepshead	0.167	0.012	0.093	0.007	2.500	2.500
18 - Pinfish	0.667	0.186	0.432	0.077	3.675	4.052
19 - Mullet	0.417	0.512	0.541	0.204	2.000	2.000
20 - Gulf flounder	0.333	0.013	0.197	0.004	4.138	4.455

($wTL = 1$); (c) normal distribution well fits densities for betweenness centralities computed with directed and undirected data; (d) species associated to higher TI^I are normally distributed and similarly happens for topological importance up to

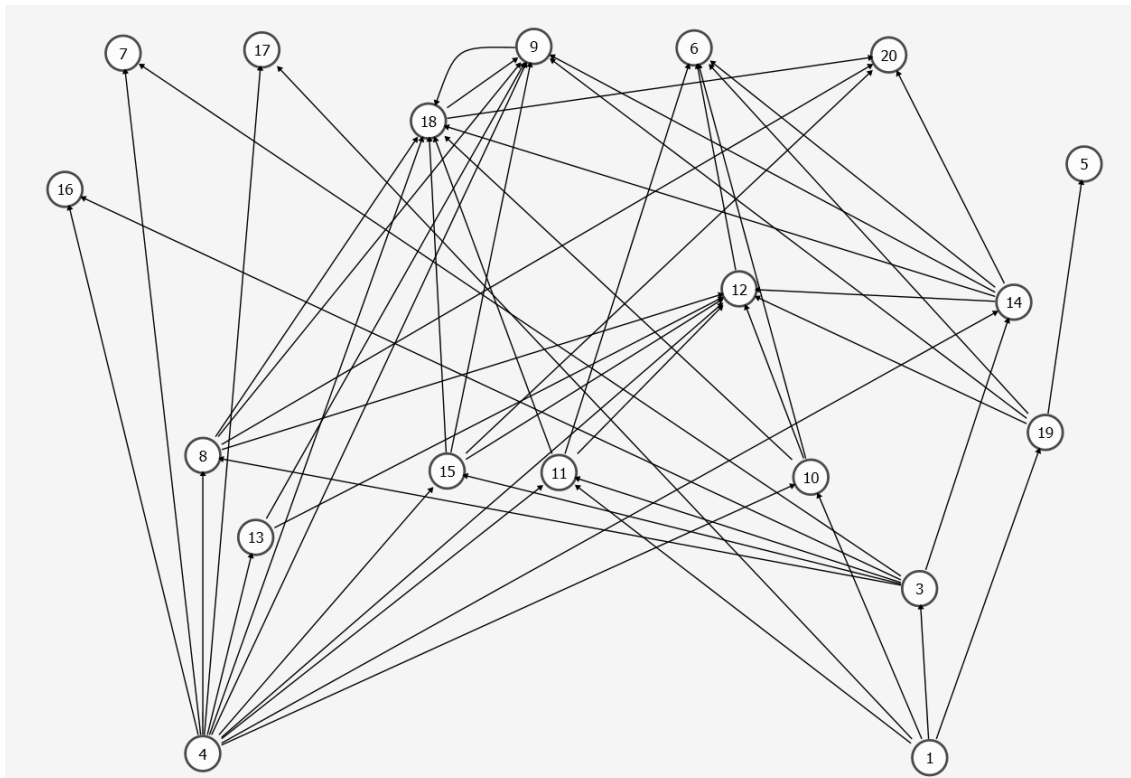


Figure 1. The food web of Crystal River (control) network (19 nodes, numbering corresponds to Table 2). Drawn by CoSbiLab Graph (Valentini and Jordán 2010).

more steps ($TI^2 \div TI^8$); (e) WI^m indices do not show any trend but the class corresponding to $2.0 < wTL \leq 2.5$ is always the most represented.

We estimated a normal distribution for TL densities, in case of D ($\mu = 3.117$, $sd = 0.679$ with $W = 0.147$ with $p = 0.025$). An exponential function was used to fit histograms of density for wTL extracted with wD (density = $0.263^{wTL} + 0.210$), and was significant ($Diff = 0.333$ with $p = 0.931$). Distributions observed for TL histograms of density for nodes with highest betweenness and topological importance centralities can be approximated by normal functions: BC ($\mu = 3.117$, $sd = 0.679$ with $W = 0.078$ and $p = 0.215$), $undBC$ ($\mu = 2.730$, $sd = 0.740$ with $W = 0.154$ and $p = 0.020$) and TI^1 ($\mu = 2.763$, $sd = 0.763$ with $W = 0.110$ and $p = 0.080$), TI^2 ($\mu = 2.850$, $sd = 0.747$ with $W = 0.093$ and $p = 0.137$), TI^3 ($\mu = 2.968$, $sd = 0.707$ with $W = 0.164$ and $p = 0.015$) and TI^8 ($\mu = 2.913$, $sd = 0.792$ with $W = 0.124$ and $p = 0.051$).

We also studied the distributions of frequency for the normalized trophic levels. In comparison to what observed with raw data, trends described by the Gaussian distribution are attenuated, while the exponential function found with wD vanished (Fig. 3). Normal distributions were determined for nTL extracted with key nodes in case of: (a) D ($\mu = 0.593$, $sd = 0.199$ with $W = 0.164$ and $p = 0.015$); (b) directed ($BC - \mu = 0.627$, $sd = 0.199$ with $W = 0.1392$ and $p = 0.032$) and undirected ($undBC - \mu = 0.515$, $sd = 0.227$ with $W = 0.230$ and $p = 0.002$) versions of betweenness centrality; (c) topological importance “up to” 1, 2, 3 and 8 steps ($TI^1 - \mu = 0.521$, $sd = 0.220$ with $W = 0.197$ and $p = 0.006$; $TI^2 - \mu = 0.549$, $sd = 0.214$ with $W = 0.121$ and $p = 0.057$; $TI^3 - \mu = 0.581$, $sd =$

0.197 with $W = 0.206$ and $p = 0.004$; $TI^8 - \mu = 0.568$, $sd = 0.226$ with $W = 0.135$, $p = 0.037$).

Absence of any pattern was observed for wTL in case of weighted topological importance. The most represented class is $0.3 < nwTL \leq 0.4$, when indirect effects are calculated for shorter chains (WI^m , with $m = 1, 2, 3$). Key nodes are mainly assigned to the class $0.0 \leq nwTL \leq 0.1$ if extracted for WI^8 ; an interesting peak is also observed for some nodes in the top-predator class ($0.9 < nwTL \leq 1.0$). Similar features are displayed by wD .

TI^m and WI^m approach D and wD , respectively, with increasing number of steps (m).

Then, we extracted histograms of density for trophic levels of the whole dataset (19 ecosystems - 1001 nodes). Normal functions were fitted to these distributions, except for normalized unweighted data (Fig. 4): We found the following results: $TL - \mu = 2.965$, $sd = 1.009$ ($W = 0.968$ and $p \ll 0.001$); $wTL - \mu = 2.689$, $sd = 0.924$ ($W = 0.868$ and $p \ll 0.001$); $nwTL - \mu = 0.498$, $sd = 0.264$ ($W = 1.092$ and $p \ll 0.001$).

Finally, for each centrality index, we compared trends observed for trophic level densities of the key nodes (weighted and unweighted; raw and normalized) with the distributions of the whole dataset. Results are summarized in Table 3. Trophic level distributions of key nodes extracted for the weighted centralities (wD and WI^m) always differ from the patterns displayed by whole data (both raw and normalized). With unweighted data, no significant differences were detected, except for $undBC$, TI^1 and D (only with nTL).

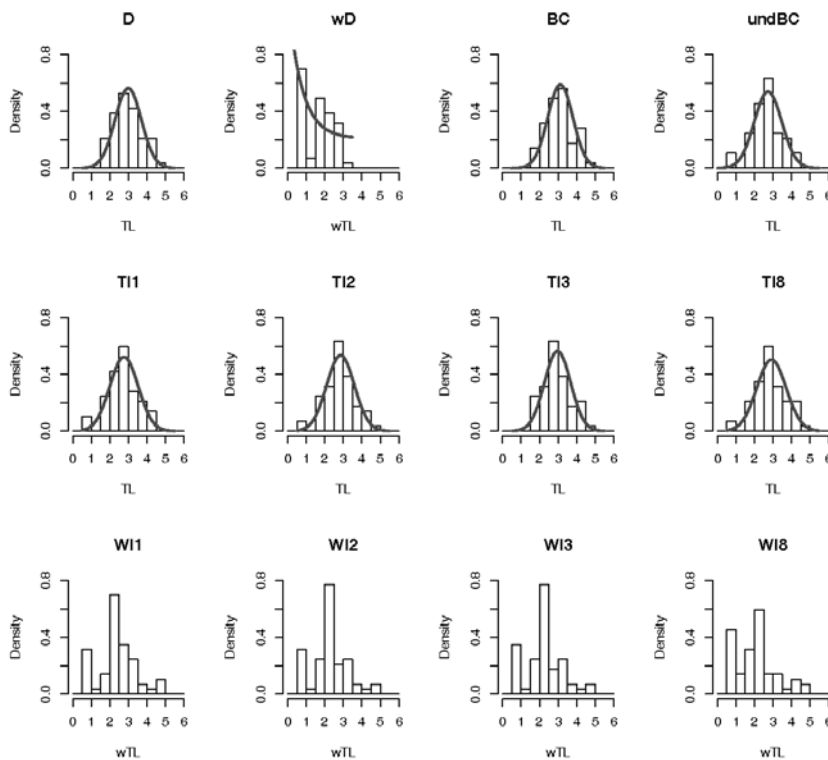


Figure 2. Histograms showing the density distributions of trophic levels associated to the species with highest centrality values. For each centrality index, the 3 species ranking higher in each ecosystem are extracted (19 ecosystems \cdot 3 species = 57 centrality values). Here we illustrate trends of unweighted trophic levels (TL), for nodes ranking higher in case of unweighted centralities (D , BC , $undBC$, TI^1 , TI^2 , TI^3 and TI^8). Distributions of weighted trophic levels (wTL) are showed when the weighted versions of centrality indices are considered (wD , WI^1 , WI^2 , WI^3 and WI^8). Exponential function for weighted degree centrality and Gaussian curves describing unweighted degree, betweenness and topological importance distributions are added to histograms.

Figure 3. Histograms of normalized trophic levels are depicted for degree centralities (unweighted and weighted), betweenness centralities (directed and undirected) and topological importance up to 1, 2, 3 and 8 steps (both in its unweighted and weighted version). Consistency between trophic level (nTL or $nwTL$) and centrality measurement (unweighted or weighted) is preserved. Gaussian curves estimated for unweighted degree, betweenness and topological importance centralities are depicted.

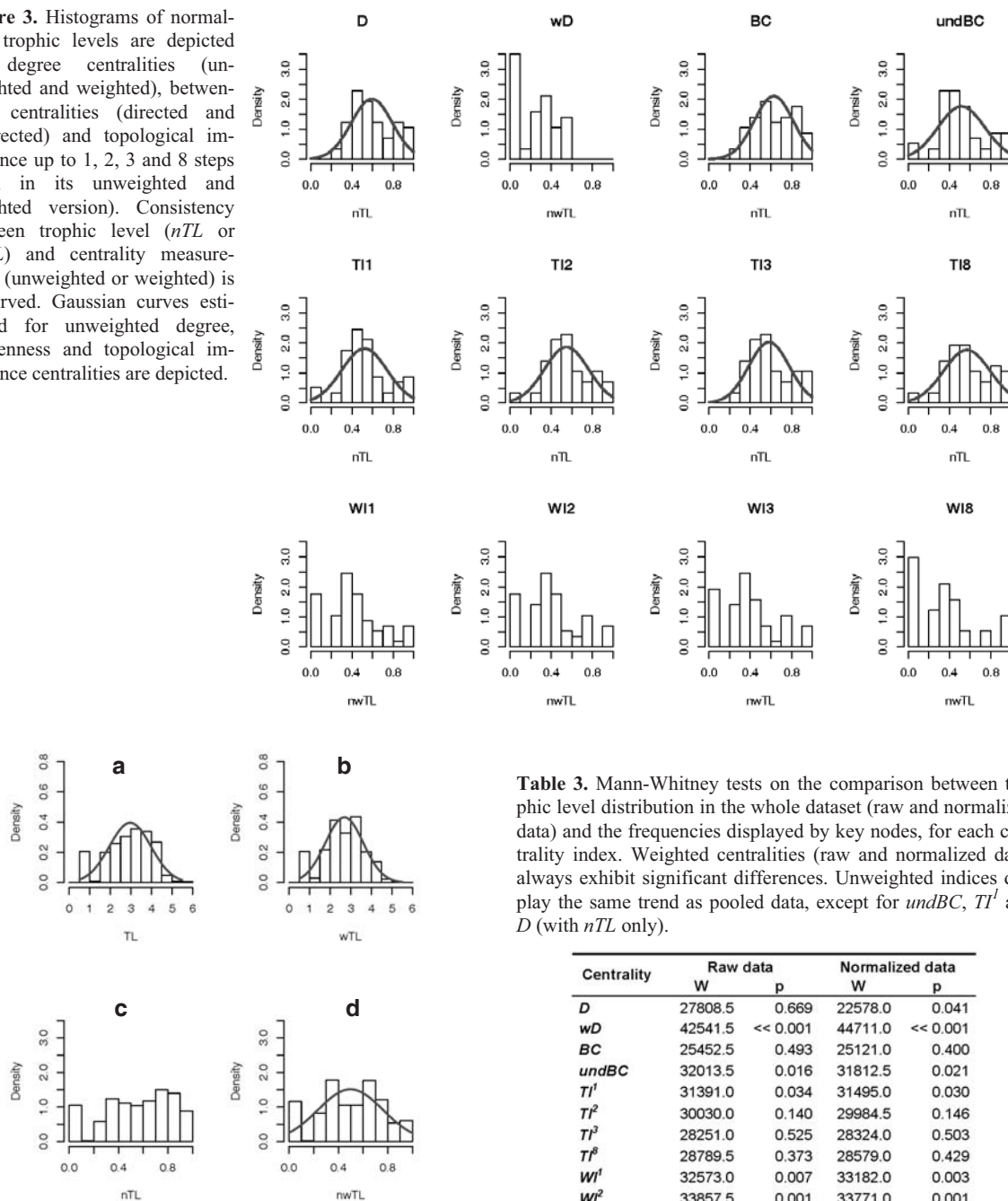


Figure 4. Histograms of trophic level densities for pooled data (1001 nodes, 19 trophic networks). In the first row we depicted charts of (a) unweighted (TL) and (b) weighted (wTL) trophic levels. Their normalized versions are illustrated below: (c) nTL ; (d) $nwTL$. The estimated Gaussian curves are depicted.

Discussion and conclusions

Recent studies characterized centrality index distributions (Solé and Montoya 2001, Jordán et al. 2006b, Bauer et al. 2009) and patterns of trophic levels in food webs (Wulff and Ulanowicz 1989, Bondavalli et al. 2006). In this manuscript we performed a comprehensive analysis to understand

Table 3. Mann-Whitney tests on the comparison between trophic level distribution in the whole dataset (raw and normalized data) and the frequencies displayed by key nodes, for each centrality index. Weighted centralities (raw and normalized data) always exhibit significant differences. Unweighted indices display the same trend as pooled data, except for $undBC$, TI^1 and D (with nTL only).

Centrality	Raw data		Normalized data	
	W	p	W	p
D	27808.5	0.669	22578.0	0.041
wD	42541.5	<< 0.001	44711.0	<< 0.001
BC	25452.5	0.493	25121.0	0.400
$undBC$	32013.5	0.016	31812.5	0.021
TI^1	31391.0	0.034	31495.0	0.030
TI^2	30030.0	0.140	29984.5	0.146
TI^3	28251.0	0.525	28324.0	0.503
TI^8	28789.5	0.373	28579.0	0.429
WI^1	32573.0	0.007	33182.0	0.003
WI^2	33857.5	0.001	33771.0	0.001
WI^3	34219.5	0.001	34250.0	0.001
WI^8	36420.0	<< 0.001	36065.0	<< 0.001

whether there exists a relationship connecting centrality indices to trophic levels.

We observed no regularities when centrality indices were studied, for the whole number of food web species, as a function of raw and normalized trophic levels. However, theoretical ecology and conservation biology aim to identify the most important species in ecosystems (Paine 1969, Mills et al. 1993), with Jordán et al. (1999) and Jordán (2001) that demonstrated how network perspective and centrality measurements can be fruitfully adopted in this sense. Inspired by the concept of keystone species (i.e., species with a dispro-

portionate effect on the environment relative to their biomass), we discuss about key species by studying their structural importance (i.e., centrality indices). We compared distributions of trophic levels extracted from the most central nodes to that found with pooled data. Key nodes tend to occupy trophic levels in the range between herbivores and primary carnivores (Fig. 2), with a barycentric arrangement within the trophic chain (Fig. 3). However, trends for unweighted indices do not differ from the frequencies of the whole dataset, while weighted data display a significant deviation (Table 3). Our results are in accordance with Scotti et al. (2007) and Bauer et al. (2009) that demonstrated how weighting links is particularly important for food web centrality indices. In case of key nodes, the most representative wTL classes of density are primary producers (wD) and species within the interval $2.0 < wTL \leq 2.5$ (WT^m). A clear shift is exhibited by pooled data (Fig. 4) and key nodes under unweighted configurations (Fig. 2), with the majority of species falling within the interval of primary consumers ($2.5 < TL \leq 3.5$). Increasing the number of steps (m) up to which topological importance (IT^m) is estimated, nTL s of key nodes approximate the distribution of frequency exhibited by D ; the weighted importance (WT^m) tends to the wD distribution as indirect effects become longer (see Fig. 3). These results corroborate previous findings, showing that topological importance based on indirect effects produces a ranking of importance that is almost the same as degree (Jordán et al. 2003, 2006a). We argue that indirect effects tend to be weakened while spreading throughout biological networks, and only short step lengths are relevant.

A number of studies have examined link distribution (i.e., the statistical distribution of individual values of degree) in food webs to draw conclusions on community organization and dynamics (Montoya and Solé 2002, Dunne et al. 2002b, Jordán et al. 2006b). In this work, we illustrate that species with higher degree centrality values (D) are never associated to $TLs > 5.0$ (for wD it is not surprising because of the small flows up there; see Hairston and Hairston 1993). This would suggest the presence of more constrained pathways for species feeding at the higher levels of the trophic hierarchy (they are more specialist than highly connected intermediate nodes). However, when analyzing nTL we may appreciate how some of these species, despite having trophic levels lower than 5.0, are located at the top of the trophic chain, and they play the role of top-predator (e.g., mink, sargo and goldspotted killifish). In general, the majority of nodes with higher unweighted degree centralities have intermediate TL s (i.e., $2 < TL \leq 3.5$, and $0.3 < nTL \leq 0.6$), and this is consistent with patterns showed by wasp-waist ecosystems (Jordán et al. 2005). Still, at $wTL = 1$ there is a prominent number of central nodes for wD but none for D . This stands for a small number of huge flows resulted from aggregation.

Histograms we estimated for BC and $undBC$ illustrate how flow direction is of scarce interest to characterize the importance of key species in spreading indirect effects between other nodes. Normal distributions without significant differences from the whole data were observed.

For some species in the whole database, we calculated trophic levels higher than five (Fig. 4), but no key nodes stand at this level in the trophic hierarchy (Fig. 2). This trend is partially modified by including the normalized data, with top-predators defined in comparison to the trophic chain length of each ecosystem, rather than based on absolute values (i.e., species at $TL = 3.8$ are top-predators in ecosystems with no species feeding higher). Then, with all centrality indices but weighted degree, we found that some key nodes are top-predators (Fig. 3). In particular, the number of top-predators (i.e., $nwTL > 0.9$) increases when the weighted topological importance (WT^m) is computed on longer pathways ($m = 8$). These top-predators were extracted from two ecosystems (i.e., food webs of the Florida Bay, Wet and Dry seasons; Everglades Graminoids, Wet Season), and belong to three main taxonomic classes: birds (loon, predatory and omnivorous ducks), fish (demersal fishes) and mammals (mink).

Our study contradicts the misleading idea that charismatic megafauna, top-predators and endemic species should be the main objectives of conservation biology (Simberloff 1998, Dale and Beyeler 2001). We argue that assessing the state of biodiversity and developing strategies for halting its loss would receive a great benefit from the application of network analysis. The network perspective allows to forecast secondary effects (e.g., predicting the robustness of food webs to species extinction - see Dunne et al. 2004, Allesina et al. 2006), with key species defined on the basis of their structural importance (i.e., the ability in maintaining ecosystem functions - see Jones and Lawton 1995, Kareiva and Levin 2003). We found a wide range of variation in the trophic levels of key species, and they are often far from a top-predator behavior. If the goal is to preserve biodiversity and maintain a reliable supply of ecosystem services, we should identify key species considering their structural importance (Jordán 2009). We are not rejecting the importance of policies focusing on the conservation of species with high aesthetic and economic values, but considering their structural importance represents a long-term solution for managing diversity loss, while protecting the rarest or the more charismatic is only a symptomatic treatment (Jordán 2009).

By analyzing trophic patterns of functional key species we integrated previous information about the species with larger effects on others (Bauer et al. 2009, Jordán et al. 2006b). Many applications of network analysis are based on the unweighted degree centrality, but we emphasize that different indices (characterized by different patterns of trophic level) should be considered to describe the spread of indirect effects. Moreover, weighting links is of focal importance as a step towards stochastic dynamical modeling (Dematté et al. 2008, Priami 2009, Livi et al. submitted). We think that our study will provide useful hints of discussion for the development of objective and data-based conservation practices.

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