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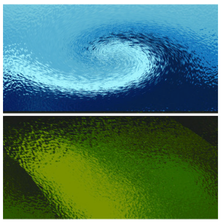

RESEARCH ARTICLE

Macroinvertebrates assembly in a patchy environment: centrality measures for the spatial network of detritus-based communities

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Abstract

1 - Spatial patterns influence the persistence of populations and communities, giving useful insights on the mechanisms that confer robustness to ecological networks.

2 - The mechanisms that regulate the spatial distribution of species are related to the ability of populations to respond to spatio-temporal variations of ecological conditions, contributing to network structure and dynamic of persisting communities.

3 - We applied the framework of complex network to study the colonization process of *Phragmites australis* leaf detritus in six different pools in the patchy aquatic environment of Tarquinia saltern (central Italy).

4 - We used the colonization data of macroinvertebrates on leaf detritus assigning a link between two taxa if they shared a common pool, and measured their positional importance within the network.

5 - We found high clustering and short path lenght among nodes that is representative of small-world pattern, showing the relationship between robustness and nodes synchronicity in network attachment dynamics.

6 - Here we show how the identification of local (individual use of substrates by macroinvertebrates) and global (network properties) patterns in community structure could be the key to better understand the ecology, evolution and management of complex ecological network.

Keywords: Tarquinia saltern, detritus, macroinvertebrates, colonization, network analysis, spatial network, robustness, perturbations

Introduction

Several studies have shown how the structural characteristics of many complex networks are related to their stability and dynamic (Albert *et al.*, 1999; Albert *et al.*, 2000), showing how some features in ecological networks and food webs followed well-defined patterns explained by network theory, as the degree distribution of links among species in food webs (Dunne *et al.* 2002), or nestedness and modularity in plants-pollinators networks (Bascompte *et al.*, 2003; Olesen *et al.*, 2007). Previous works suggest how the analysis of network topology can provide a new and straightforward way to quantify and identify keystone species (Jordán, 2009), or to improve the keystone concept by differentiating species on the basis of the role they play in a network (Gonzalez *et al.*, 2009). Network analysis also provides a robust way to study spatial networks (Urban and Keitt, 2001), describing any network where the links (or potential links) among nodes are constrained by their location in some kind of 'space'.

The topological structure of complex networks depends on the structural arrangement of nodes and links, thus, defining the importance of each node is crucial to determine the dynamic properties and stability of networks (Strogatz, 2001). In network analysis, the degree of importance of each node within a network is commonly quantified using the centrality indices (Freeman, 1979; Jordán *et al.*, 2006), where different indices measure different aspects of the positional importance of a node. The choice of using a particular index is a direct consequence of the type of information we want to extract from different types of networks (e.g., a spatial network of sites and plants, plants and their pollinators or species in food webs). Therefore, different indices reflect different aspects about the importance of a node within a network (Jordán, 2009).

For instance, a node with many interactions is important as it can affect many different nodes or serves as a bridge among nodes, influencing some important characteristics, as colonization and migration (Moilanen and Nieminen, 2002), cascading effect in food webs (Allesina *et al.*, 2006), the spread of parasites and disease (Fortuna *et al.*, 2009) or coevolutionary pattern in plants and their pollinators (Bastolla *et al.*, 2009).

Most ecological networks seem to have a well-defined pattern of interactions where several subwebs are attached to a 'network core', that acts as the 'glue providing cohesion' (Mélian and Bascompte, 2004; Bascompte and Stouffer, 2009), and this core of potentially interacting species is often composed by generalist species (Gonzalez *et al.*, 2009). Several studies suggest the importance of this cohesive pattern for robustness, making the networks less vulnerable against species deletion and slightly compromising their ability to provide essential ecosystem functions (e.g., nutrient recycling, decomposition) (Loreau *et al.*, 2001).

Here, we applied two of the most common measures of centrality, betweenness (*Bci*) and closeness (*Cci*), and the k-core partition, to uncover patterns in the colonization process of *Phragmites australis* (Cav.) Trin. ex Steud leaf detritus in artificial aquatic ecosystem. The main objectives are: I) to examine the relationship between the colonization ability of macroinvertebrates (e.g., abundances and frequencies of colonization) and their topological importance and II) to understand the effects of local changes in environmental conditions on network robustness and persistence.

Here we show how the spatial network of detritus colonizers in a patchy environment reveals a well-defined core of potentially interacting taxa and small-world properties, giving useful insight on network stability and functioning.

Materials and methods

Field experiment

Given their network-like properties, a spatial network can be analysed by network analysis, used in many different fields of ecology (Jordán et al., 2006; Fortuna *et al.*, 2006, 2009; Olesen et al., 2007; Jordán 2009). We studied the spatial assembly of macroinvertebrates on leaf detritus in the patchy aquatic environment of Tarquinia saltern, where a strong component of temporal dynamics was expected, i.e., with a marked turnover of taxa given by the fluctuating levels of salinity conditions. The spatial network is composed by 36 active pools characterized by a wide salinity gradient, from hyposaline (mean annual salinity 8.5 gL^{-1}) to hyperaline waters (mean annual salinity up to 100 gL^{-1}). The pools are shallow basins, whose connectivity is given by the inflow of seawater or by accidental events like flooding or heavy rains. The input of seawater occurs through a single opening, which connects the saltern with the sea, located north of the area (Figure 1).

To measure the colonization process of leaf detritus, we placed 48 mesh bags in six sampling sites, covering the full spectrum of salinity variation (Figure 1). Mesh bags were filled with *P. australis* leaf fragments weighed to the nearest mg after drying at

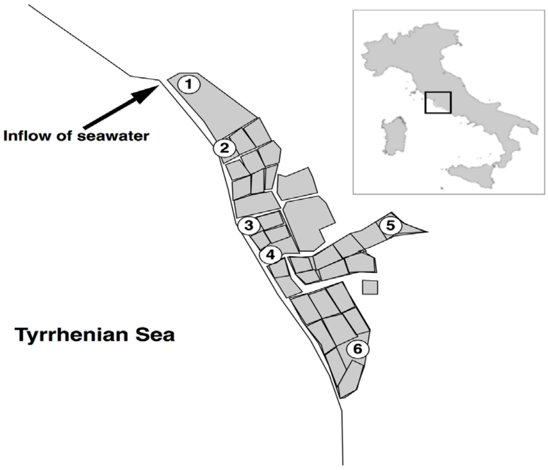

Figure 1. Study area and location of sampling sites. Mean annual salinity values: 1 = 44.8 ± 2.63 gL^{-1}; 2 = 50 ± 2.84 gL^{-1}; 3 = 88 ± 5.60 gL^{-1}; 4 = 100 ± 7.09 gL^{-1}; 5 = 8.5 ± 2.45 gL^{-1}; 6 = 115 ± 16.62 gL^{-1}.

60°C for at least 72 h (leaf pack: 2.000 ± 0.0004 g dry mass) having dimension of 10 x 10 cm with a coarse mesh of 5 x 5 mm. Mesh bags were recovered with a number of r = 4 replicates for each site, with a time step t of one month for a total of twelve months. We measured: I) the number of taxa that colonized the detrital substrates in different pools and II) the number of individuals for each sampled taxon, averaged over the r replicates.

Network analysis

In network analysis there are three main measures of centrality of a node: degree, closeness, and betweenness centrality. Degree centrality (Dc') refers to the number of links each node has, and characterizes the centrality of a node in the network based on its number of neighbours. Closeness centrality (Cc') is based on the distance of node i from every other nodes and is a measure of how closely a node is connected to other nodes in the network, based on the shortest paths between them. Betweenness centrality (Bc') is the proportion of paths between any combinations of two nodes in the network that pass through that particular node and measures how crucial a node is for the exchange of 'information' within a network.

There are significant differences in the centrality measures, produced by different scales used in their definition. Betweenness and closeness characterize the positional importance of a node at different scales, at local (i.e., the degree of influence a node has between pairs) and global (i.e., the sum of all distances separating a node from the rest), respectively. Since the use of a global measure, such as the Cc', is inappropriate in networks where distances are great (Estrada, 2007), it must account the distance among nodes, that is, measure the small-world properties of the network. A small-world network has a short path length l (i.e., average node-to-node distance) and high clustering coefficient (CC), where nodes being tightly linked together and the network has a high CC/l ratio than that observed in a random network (Wasserman and Faust, 1998).

The consequences of a small-world pattern can be of great importance in recognizing evolutionary paths, the stability and the sensibility to perturbations in ecological networks. These findings suggest that such architecture would play a relevant role in enhancing nodes synchronization (Watts and Strogatz, 1998), strong robustness and fast responses to perturbations (Strogatz, 2001). In ecological networks, synchronization is often related to a correlation between changes in the abundances of different populations in different patches, documented with reference to many taxa (Leibold *et al.*, 2004). Synchronization may arise from migration (or dispersal) of populations among patches and from the dependence of all population dynamics on some common environmental noise (e.g., salinity, water temperature).

Therefore, in this work, synchronization among nodes might be given by the co-occurrence of macroinvertebrates (i.e., synchronicity in abundances and frequencies of colonization) in all the pools of the saltern. Since estuaries, salt marsh, and almost all natural habitats where environmental conditions are temporally variable (including solar salterns) are dynamical habitats in which the resident species are tolerant of a range of conditions, we would expect generalists to dominate (Teal, 1962; Day *et al.*, 1989) and the presence of a small-world pattern in network topology.

To find pattern in the spatial network of Tarquinia saltern, we first derived from the two-mode matrix, (i.e., a bipartite network, where links are established between two sets of nodes but not among nodes of the same set), a one-mode matrix (namely unipartite projection), establishing a link between two taxa if they share a common pool. Generally, from a bipartite network it is possible to derive a uni-modal network for each set of nodes, in this case taxa and pools. Since we were interested in the colonization process of macroinvertebrates on leaf detritus, in this work we do not consider the pools unipartite projection. We first measured the mean short-path length l and the clustering coefficient (CC) of observed network, comparing these measures with those of 1000 random networks with the same degree distribution as the empirical one (Bascompte *et al.*, 2003), and examined whether the empirical values of were significantly lower and CC significantly higher than the random ones. We then applied the *k*-core decomposition, to identify particular subsets of the graph, called *k*-cores, each one obtained by recursively removing all the vertices of degree smaller than k, until the degree of all remaining vertices is larger than or equal to k. Larger values of 'coreness' correspond to vertices with larger degree and more central position in the network structure.

Finally, we measured the centrality of nodes by using betweenness (Bc_i) and closeness centrality (Cc_i), following the rationale that: I) a taxon with $Bc_i > 0$ may be defined as a connector, linking areas of the network that would be not connected at all (Newman, 2003), since a large number of links passing through it and II) a taxon with high Cc_i is the one more closely related to each other and can quickly influence or be influenced by other taxa.

Betweenness centrality is defined as (Freeman, 1979):

$$Bc_i = \frac{1}{(S-1)(S-2)} \sum_{j,k \in V, j \neq k \neq i} l_{jk}(i)/l_{jk} \tag{1}$$

where S is the number of taxa, ljk is the number of shortest paths l connecting two taxa and ljk(*i*) is the number of shortest paths between taxa *i* and *j* that pass through *i*. Closeness centrality measure how close a taxon is to other taxa, and is defined as (Freeman, 1979):

$$Cc_i = \sum_{j=1; i \neq j} \frac{d_{ij}}{S-1} \tag{2}$$

where, S is the number of taxa and d_{ij} measure the shortest distance (i.e., the number of links) between *i* and *j*.

Centralities were compared among themselves and with the normalized abundances (n_i) and frequencies of colonization, defined as a proportion (f_i) of how many times a taxon colonized the detrital substrates in the pools during the field experiment:

$$f_i = \frac{\sum_{i=1}^{T} C_i}{T} \tag{3}$$

where c_i is the number of observed colonizations by taxon *i* and *T* the total time of experiment.

Here we discuss the network structure and topology of macroinvertebrates assembly on leaf detritus in a patchy environment, and their influence on the structure and robustness of the network.

Results

Table 1 - Mean shortest path length *l* and clustering coefficient (*CC*) showing the small-world properties of the network. *rN* corresponds to the values given by the null model with the same degree distribution of the original network (*N*).

	N	*rN*	*P*
$\langle l \rangle$	0.077	0.146 ± 0.002	< 0.001
CC	0.867	0.621 ± 0.025	< 0.001

We sampled a total of 2,406 individuals belonging to $S = 18$ taxa of macroinvertebrates on $P = 6$ pools, resulting in a total of $L = 38$ potential links in the two mode projection (Figure 2A) and $L = 95$ potential links among taxa in the unipartite projection (Figure 2B).

Among sampled taxa, 10 were classified as detritivores and 8 as predators (Table 2), according to the available literature (McCafferty 1983; Bramucci 2009).

The larvae of *Chironomus spp* (a genus well-suited and adapted to changing salinity conditions, Velasco *et al.*, 2006), were the most representative, increasing with the increase of salinity (Figure 3).

A different trend can be observed for the predator *Haliplus sp.*, which decreases with the increase of salinity, and for *Gammarus aequicauda*, and *Hydrobia acuta*, that show high abundances in pools with salinity near to seawater (Figure 3).

The spatial network of macroinvertebrates in Tarquinia saltern showed a small-world pattern, as revealed by the high clustering coefficient and the small mean-shortest path length among taxa (Table 1). The *CC/l* ratio was significantly higher (11.32) than that given by a random association between taxa and sites (4.25 ± 0.0002, $P < 0.001$).

The *k*-core partition of unipartite projection revealed $k = 3$ main subgraphs, observing how a large amount of predators (62.5%) was located in the most peripheral subgroup (black nodes in Figure 4A and Table 2), while 70% of detritivores in the main core of the network (white nodes in Figure 4A and Table 2). Only few taxa (the larvae of predator Coleoptera and the detritivores *Cerithium rupestre* and the larvae of dipterans) belong to an intermediate position between the central and peripheral taxa (gray nodes in Figure 4A and Table 2).

Results showed very similar values of closeness centrality (Cc_i) (Figure 4), while 50% of sampled taxa had a $Bc_i > 0$, with a

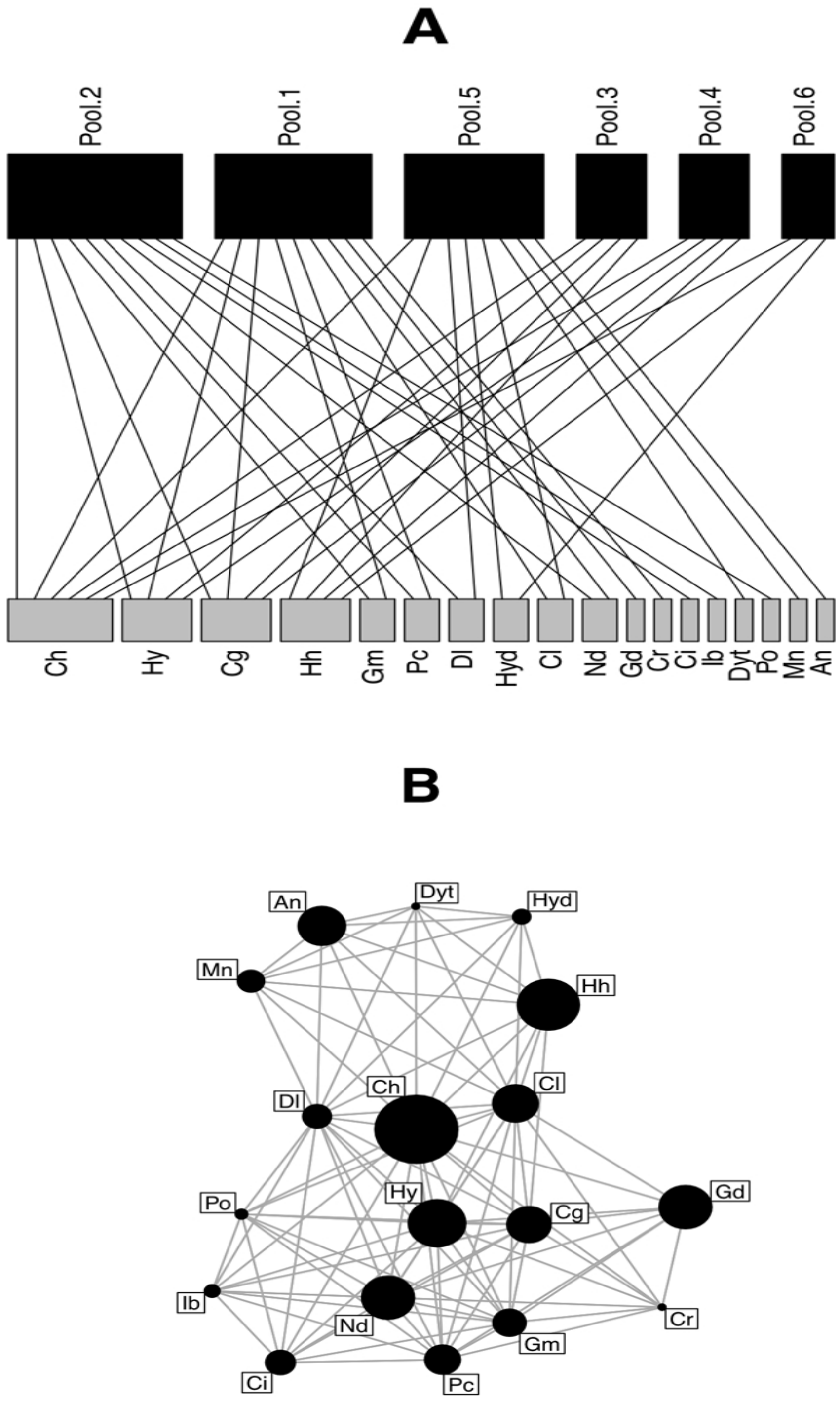

Figure 2. A bipartite network (A) where links are established between two different sets of nodes, taxa and pools, but not between nodes of the same set. Width of a box follows a decreasing order of colonization, from left to right. In the unipartite projection (B), the (potential) links are established between two taxa if they shared a common pool. Width of a node expresses the mean log-transformed abundances of sampled macroinvertebrates. Id for each taxon is given in Table 2.

Table 2 - Network parameters of each identified taxon. Bc_i is the betweenness centrality, Cc_i the closeness centrality and k the number of identified subgraphs, from the most peripheral (*1*) to the most central (3). Taxa legend: Ch = *Chironomus spp* (larvae); Gm = *Gammarus aequicauda*; Pc = *Perinereis cultrifera*; Gd = Gordiidae; Hy = *Hydrobia acuta*; Cg = *Cerastoderma glaucum*; Cr = *Cerithium rupestre*; Dl = (other) Diptera (larvae); Ci = *Corophium insidiosum*; Ib = *Idotea baltica*; Dyt = Dytiscidae (larvae); Hyd = Hydrophilidae; Cl = Coleoptera (larvae); Nd = Nereidae; Po = Polychaeta; Hh = *Haliplus* sp; Mn = *Micronecta* sp. (larvae); An = Anisoptera (nimphae).

	Detritivores				Predators		
	Bc_i	Cc_i	k		Bc_i	Cc_i	k
Cg	0.06	0.06	3	An	0	0.05	1
Ch	0.32	0.08	3	Cl	0.23	0.07	2
Ci	0	0.05	3	Dyt	0	0.05	1
Cr	0	0.05	2	Hh	0.03	0.05	1
Dl	0.22	0.07	3	Hyd	0	0.05	1
Gd	0	0.05	2	Mn	0	0.05	1
Gm	0.03	0.06	3	Nd	0.03	0.06	3
Hy	0.06	0.06	3	Po	0	0.05	3
Ib	0	0.05	3				
Pc	0.03	0.06	3				

high percentage of detritivores (60%) with a betweenness centrality higher than that of predators (37.5%) (Table 2 and Figure 4). Among detritivores, *Chironomus spp* showed the highest Bc_i (0.32), while the larvae of Coleoptera showed the highest betweenness centrality for predators (0.23).

The frequencies of colonization and the abundances of sampled macroinvertebrates showed a significant correlation (Spearman's ρ correlation) ($\rho = 0.77$, P < 0.001) (Figure 5), revealing how the most abundant taxa were also the most widespread. The frequencies of colonization showed a non-significant correlation neither with betweenness ($\rho = 0.29$, $P = 0.24$) nor with closeness centrality ($\rho = 0.22$, $P = 0.39$), while the abundances of sampled macroinvertebrates showed a significant correlation with Bc_i ($\rho = 0.57$, $P = 0.013$). Results also showed a significant correlation between Bci and Cc_i ($\rho = 1$, $P < 0.001$) revealing a general coincidence in the rankings produced by betweenness and closeness centrality, which in some way give certain regularity to the network.

This might indicate homogeneity in network topology related to nodes synchronicity in network attachment dynamics (e.g., a correlation between frequencies of colonization and abundances of

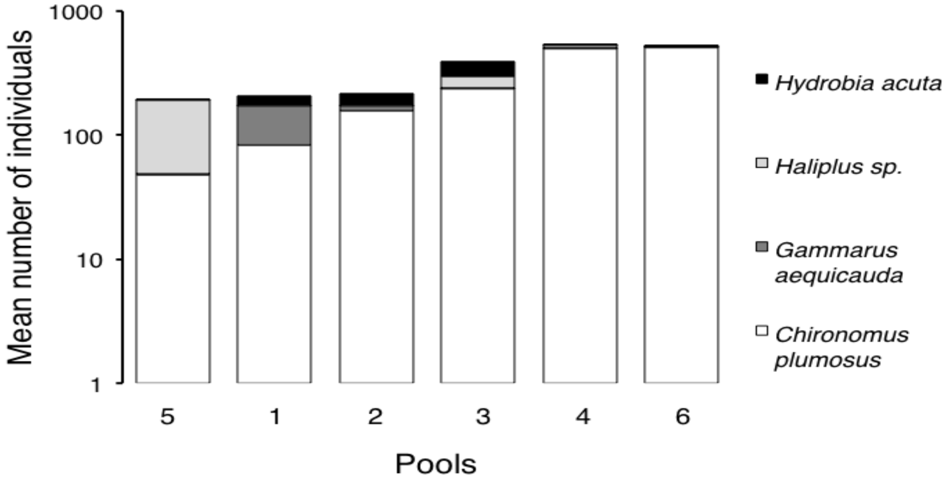

Figure 3. Frequency distribution of the mean number of individuals of the most abundant and widespread taxa, showing the distribution under different conditions of salinity. The *x*-axis is expressed in increasing order of salinity (mean annual salinity is given in Figure 1) and the *y*-axis is given in logarithmic scale.

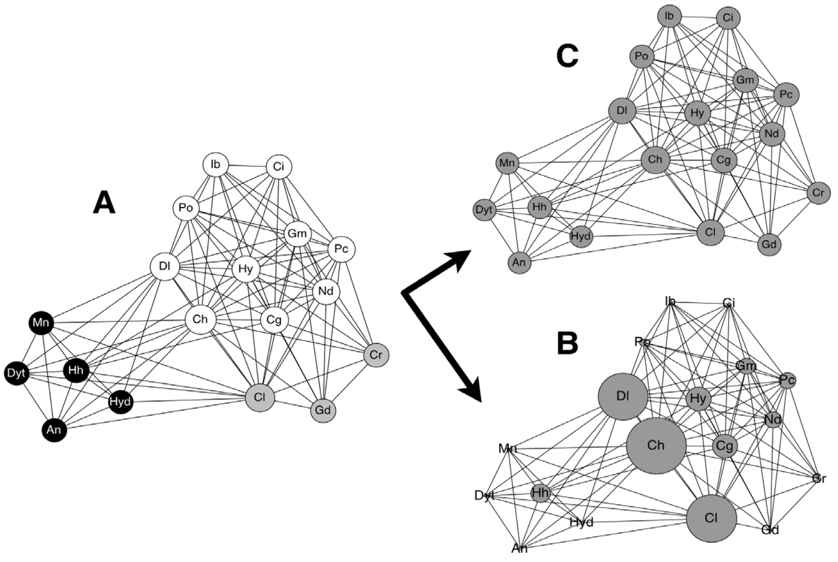

Figure 4. The *k*-core partition (A) of the unipartite projection of macroinvertebrates on leaf detritus shows three well-defined subnetworks (black nodes = peripheral taxa, white nodes = central taxa, grey nodes = low-peripheral to central taxa). Closeness centrality (B) is almost equal for all sampled taxa while betweenness centrality (C) shows the role of environmental generalists for the cohesion of network.

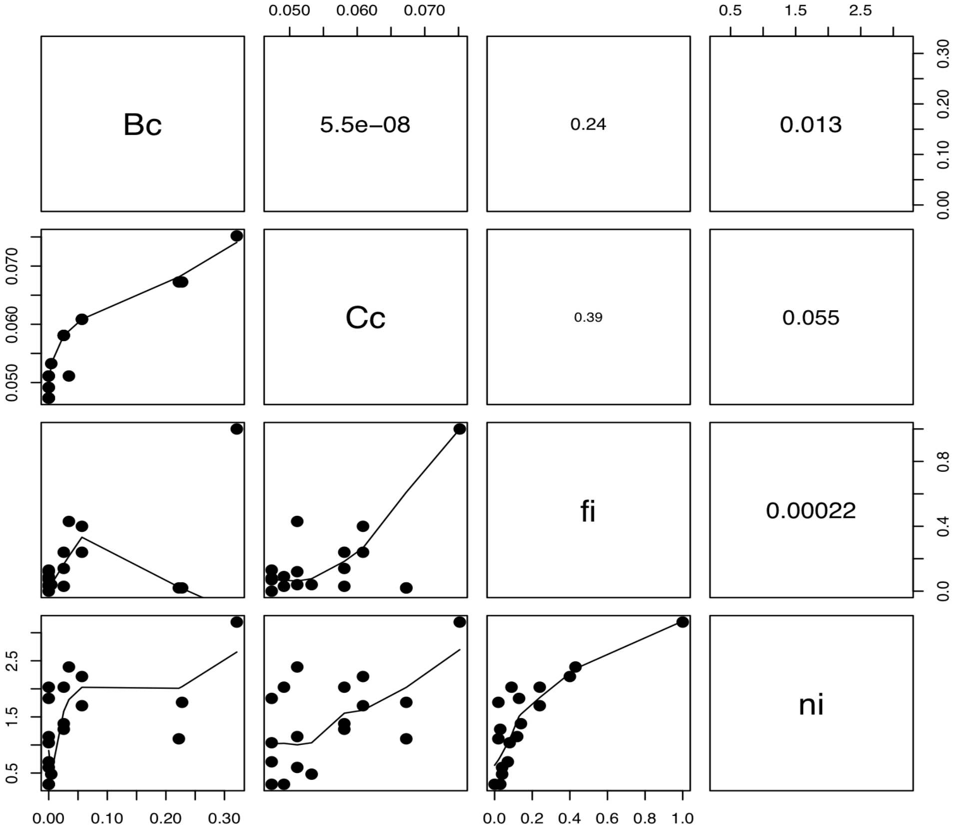

Figure 5. Relationship between the topological parameters and the normalized abundances and frequencies of colonization of macroinvertebrates on leaf detritus. *Bc* = betweenness centrality, *Cc* = closeness centrality, f_i = frequencies of colonization, n_i = abundances. Upper panels show the significance of a correlation (Spearman's ρ correlation) and width of a correlation is proportional to the level of significance. Smooth lines in lower panels show the best curve describing the correlation.

macroinvertebrates on leaf detritus), with possible implications for the robustness and functioning of the whole network.

Discussion

The one-mode network of macroinvertebrates on leaf detritus reveals high clustering and small path-lengths values, that is, a small-world pattern where all taxa are closely linked together (Watts and Strogatz, 1998). The small-world topology reveals strong robustness and fast responses to perturbations (Albert *et al.*, 2000), and its prevalence in many biological systems may reflect an evolutionary advantage of such an architecture (Barabasi *et al.*, 1999). In most ecological systems, a disturbance can be an external signal like invasion by alien species, extinction or change in the behavioural or ecology of species already present in the network. For instance, changes in local ecological conditions might affect the colonization ability of macroinvertebrates, and this may result in increasing opportunities for invaders, if they have an advantage over residents in some places or times via different environmental responses, or *via* differences in life-history trait. Here, we found how the local ecological conditions of the pools in Tarquinia saltern influence the spatial distribution and colonization ability of macroinvertebrates (i.e., abundances and frequencies of colonization), and this may influence the ability of populations to respond to spatio-temporal variations in stochastic environment, regulating network dynamic. This suggests the influence of different array of ecological processes that may operate at different spatio-temporal scales (Hastings, 2004). It has been noticed (Estrada, 2007) how a general correlation among centrality values in networks may exist, since nodes with large degrees show, in general, short average distance to the other nodes in the network. This produces high correlations between node degrees and various measures of centrality, given by a general coincidence in the rankings produced by the different centralities (Estrada, 2007). This result may be a signal of a behavioural synchronicity of nodes, given by a convergent similarity in the traits of taxa and, thus, by the co-occurrence of macroinvertebrates on leaf detritus. The observed differences in the spatial distribution of macroinvertebrates reveal some important characteristics of species traits, such as dispersal limitation or spatial variation in the strength of interspecific interactions. Centralities provide an evaluation of how rich the interaction pattern of a particular taxon is, and this is particularly important in systems where indirect effects (i.e., competition for resource) dominate (Jordán, 2009). The *k*-core partition shows three well-defined subgraphs of taxa, revealing the peripheral position of predators in network topology. This might reflect an ecological adaptation to local environmental conditions, able to influence their life history and phenologies, placing some physiological limitations on the abundances and frequencies of colonization, which may imply a reduction in predation activity over space and time (Herbst, 2006).

The most dense subgraph detected by the *k*-core partition is mainly composed by detritivores, indicating the prevalence of nodes characterized by the highest betweenness centrality. This finding indicates how this dense core of environmental generalist may be crucial for the exchange of 'information' within the network (i.e., the spread of potential interactions). Generalism for a species have been defined (McPeek, 1996) in a variety of ways: I) a species that maintain a variety of specialist genotypes that can be expressed depending upon the environmental conditions, II) species in which each genotype has the ability to express various phenotypes depending upon environmental conditions (the so-called phenotypic plasticity), and III) the *jack-of-all-trades*, a species with phenotypes intermediate to the range of environmental conditions experienced. This trade-off can influence the performance of species, predicting that a generalist will outperform a specialist under fluctuating and non-optimal environmental conditions (Richmond *et al.*, 2005) in which the costs of being a generalist are small relative to the benefits of the increased behavioural reduction in performance of the specialist (Gilchrist, 1995). However, comparisons under natural conditions are confounded by the multitude of biotic and abiotic interactions (Lawton, 2000). This suggests how under more permanent habitat conditions (e.g., more stable conditions of salinity through the seasons), the influence of biotic interactions (i.e., competition for resource and predation) will become more important in structuring communities than physico-chemical forces. In this context, the network analysis has shown how it is possible to identify the role of species based on their position within the network, revealing the importance of generalists in maintaining network structure and resilience (Gonzalez *et al.*, 2009).

However, it can be noticed how the effect of the sub-core of extremely peripheral taxa may be important in maintaining network functioning, since an increased trophic complexity (i.e., the presence of predators) will potentially enhance the consumption rate by detritivores (Moore *et al*., 2004), regulating the competition among detritus consumers. The observed characteristics of the spatial network of macroinvertebrates on leaf detritus reveal a well-defined pattern of colonization, which confer to this network robustness against random perturbations. These might be given by occasionally flooding or heavy rains that slightly affect the topological stability of the network.

Since species contribute individually and collectively to the stability of communities and ecosystems, the modification of community structure could lead to a structural and functional homogenization, involving the replacement of ecological specialist by the same widespread generalist (Olden *et al*., 2004). Homogenization might also reduce ecosystem functioning, stability and resistance to environmental change by restricting the available range of species-specific responses (Sankaran and McNaughton, 1999). Network topology reflects the range of functional traits that influence ecosystem functioning (such as the decomposition of organic matter, Moore *et al*., 2004), and the homogenization might limit the pool of species that can compensate for local extinction (i.e., reduce spatial patterns in functional redundancy). An increased spatial similarity could have also effects on species at higher trophic levels, by increasing extirpation rates *via* intensified species-specific interactions, where functionally similar species might utilize the same spatial resources enhancing the effect of competition. Our results indicate how the local ecological conditions may be a key to better understand the whole ecosystem structure and functioning in a patchy environment, giving useful insight for conservation practices. Indeed the different environmental tolerance of a species may play an important role in ecosystem function where human-induced impacts are causing fluctuations to be more severe or more common. Since saline ecosystems are artificial aquatic environments, the need for a constant maintenance, which involves the water management inside the pools, should take into account these findings for the conservation practices of habitat and species.

Conclusions

In this work we show the importance of habitat heterogeneity in community structure and dynamics, revealing how network topology is related to non-random pattern in community structure. Ecological relationships between organisms are rarely, if ever, random because they are constrained by multiple interacting factors, including, in its broadest sense, the coevolutionary history of the (potentially) interacting organisms. This findings allow to make assumptions about the effects of perturbations on network structure and functioning. Our analyses suggest that the environmental tolerances of species can be an important consideration in determining network robustness and function, and should be considered in asking whether human-induced alterations drive the relationship between diversity and ecosystem function. Our analyses also indicate the role of generalists in mantaining ecosystem structure and function, especially when environmental conditions fluctuate with short cycle periods and in presence of low-richness communities. Here we show how the identification of local (individual use of substrates by macroinvertebrates) and global (network properties) patterns in community structure could be of great importance for our understanding on the ecology, evolution and management of complex networks.

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