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## Spatial network structure and robustness of detritus-based communities in a patchy environment

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**Abstract** The mechanisms that regulate the spatial distribution of species are an essential aid to understanding the effects of the environment on the persistence of populations and communities. The effects of spatial structure on the persistence and robustness of ecological communities can, in turn, prove useful in uncovering their functioning, e.g., in the decomposition of leaf detritus. We applied the framework of complex networks to evaluate the effects of spatial structure on the colonization process of leaf detritus in a patchy aquatic environment, with a spatial network of six pools at different salinity. We found three well-defined modules formed by groups of taxa sharing the same pools, observing an association between modularity and spatial proximity of pools. Modules maximize the number of links within modules, and minimize the number of links among modules, showing the presence of a strong site-specific association between taxa and pools. The topological characteristics of the network show robustness against random perturbations and a lower tolerance of targeted perturbations. These findings suggest that random events, such as flooding or heavy rains, slightly affect the robustness of the system, while localized perturbations on the most connected nodes could have a negative effect on the connectivity of the whole network. The consequences could lead to a structural and functional homogenization of the system, with potential effects for the entire trophic chain. Here we discuss the topological properties of the network in relation to the spatial distribution of pools, showing how network analysis can yield valuable insight for conservation and management.

**Keywords** Detritus colonization · Macroinvertebrate · Network · Perturbation · Spatial homogenization

### Introduction

Network analysis represents a useful tool in the analysis and description of many complex systems (Albert et al. 1999; Newman 2001; Guimerà et al. 2005). In recent years it has been used extensively in the study of many natural systems, such as food webs (Dunne et al. 2002; Melián and Bascompte 2002), plant–animal mutualistic networks (Bascompte et al. 2003; Jordano et al. 2003; Lazáro et al. 2005), and spatial ecological networks (Urban and Keitt 2001; Fortuna et al. 2006, 2009). In the network approach, natural systems are depicted as a set of nodes, typically species in food webs or habitat patches in spatial networks, connected by links that represent some kind of association among nodes, such as interspecific interactions (May 1974; Polis 1991) or dispersal movements (Hanski and Gilpin 1991; Minor and Urban 2008).

The structural characteristics of the networks, such as the ability to regulate the spread of information among nodes (e.g., the spread of parasites or diseases; Fortuna et al. 2009), or the ability to counteract and regulate the effects of alien species invasion (Padrón et al. 2009), are related to their robustness against disturbances (Albert et al. 2000). The use of network analysis can also give useful information about the effects of spatial structure on migration, colonization, species distribution, and species persistence (Moilanen and Nieminen 2002). The rationale behind this view is that the mechanisms that generate the spatial distribution of organisms are of great importance for our understanding of the consequences of environmental changes on ecosystems structure and functioning (Crain et al. 2004).

The colonization process of leaf detritus by macroinvertebrates can be described by using a spatial network approach where the links (or potential links) between taxa and sites are constrained by the spatial arrangement

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of sites, which reflects the “costs” associated with the formation of links between nodes (Barthélemy 2003). In aquatic ecosystems, the decomposition of leaf detritus involves three main mechanisms: (1) the rapid weight loss of soluble constituents; (2) the modification of detrital matrix by microorganisms; and (3) the feeding activity of macroinvertebrates, whose activity regulates the rate of detritus processing (Petersen and Cummins 1974). Understanding the decomposition process is critical since detritus is able to sustain higher species diversity, a larger biomass of predators, and longer food chains than would be supported by primary production alone (Hairston and Hairston 1993), stabilizing the dynamics of consumers populations and food webs that would be otherwise unstable (for a complete review, see Moore et al. 2004). Moreover, the spatial characteristics (e.g., the spatial extent) were found to influence the decomposition dynamic (Sangiorgio et al. 2004), showing how control of the decomposition process may vary across spatial scales (Tiegs et al. 2009).

Here we studied six detritus-based communities in six pools subjected to different salinity conditions in the artificial aquatic ecosystem of the Biological Reserve of Tarquinia saltern (Italy), in order to uncover patterns in the colonization process of *Phragmites australis* (Cav.) Trin. ex Steud leaf detritus. We used network analysis to answer some specific questions about: (1) the role of the spatial arrangement of the pools and the environmental constraints on the colonization process of leaf detritus in aquatic environment; and (2) the consequences of the spatial pattern for robustness against perturbations. In order to answer these questions we first analyzed the modular structure of the network, to locate closely connected subgroups of nodes formed by groups of taxa sharing the same pools, identifying the role of each taxon with respect to their position within and among identified modules. Next, we explored the individual use of substrates by macroinvertebrates by applying a nested analysis, which might reveal an asymmetric use of pools by taxa, where macroinvertebrates using a few pools are a subset of the macroinvertebrates that use pools used by a high number of macroinvertebrates.

Modularity measures the degree to which the nodes of a system can be decoupled into relatively discrete components (or compartments), enhancing the robustness of the networks since are more easily countered in compartmentalized systems disturbances (May 2008). On the other hand, nestedness measures the order in which species are related to area (Atmar and Patterson 1993), or the extent to which specialized species interact with increasingly large subsets of generalists (Bascompte et al. 2003; Olesen et al. 2007; Graham et al. 2009). Nestedness has been shown to increase network robustness, since nested networks appear less prone to the detrimental effects of habitat loss (Fortuna and Bascompte 2006). Therefore, modularity and nestedness can be viewed as two complementary measures of network complexity (Olesen et al. 2007), playing a critical role in both the functioning and stability of networks (May 1974).

Here we focus on the spatial characteristic of the network, suggesting the importance of habitat heterogeneity in community structure and dynamics, and show how network analysis can yield valuable insights for conservation and management.

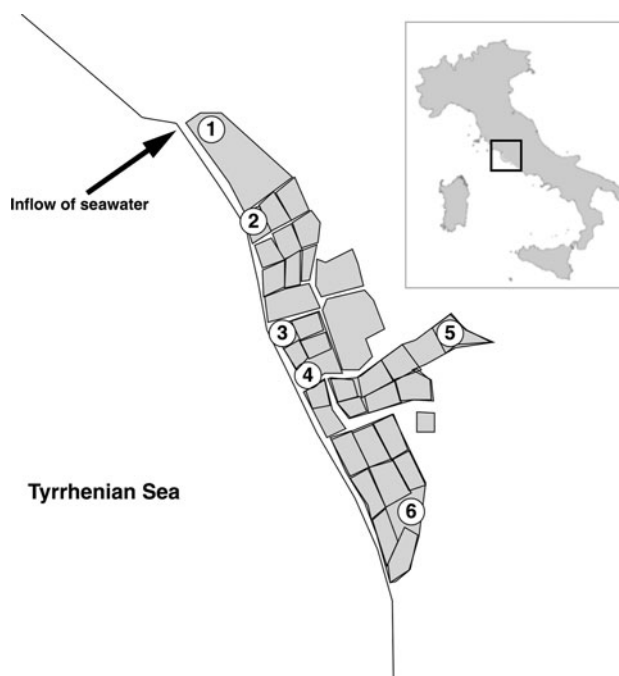
## Materials and methods

### Study area and field experiment

We studied six different detritus-based communities, whose structuring process being made according to different salinity conditions and where a strong component of temporal dynamic was expected, i.e., with a marked turnover of taxa that colonize the detrital substrates, which is determined by the seasonal variations of salinity conditions.

The study area was the artificial aquatic ecosystem of the Biological Reserve of Tarquinia saltern (Italy) (42°12'N, 11°43'E), whose spatial network comprises 36 pools characterized by a wide salinity gradient (Fig. 1), from hyposaline (mean annual salinity 8.5 g L<sup>-1</sup>) to hyperaline (mean annual salinity up to 100 g L<sup>-1</sup>) waters. 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, which is located north of the area.

To measure the decomposition and colonization process of leaf detritus, we placed 48 mesh bags in six



**Fig. 1** Schematic representation of the Biological Reserve of Tarquinia saltern and spatial location of the sampled pools (circles). The inflow of seawater is the point of water refill located north of the area; mean annual salinity values are given in Table 2

sampling sites, covering the full spectrum of salinity variation (Fig. 1). Mesh bags were filled with *P. australis* leaf fragments weighed to the nearest milligram after drying at 60°C for at least 72 h (leaf pack:  $2.000 \pm 0.004$  g dry mass). The mesh bags had dimensions of  $10 \times 10$  cm with a coarse mesh of  $5 \times 5$  mm, to allow colonization of substrates by macroinvertebrates. We also used 48 bags with a fine mesh ( $0.5 \times 0.5$  mm) to avoid animal colonization and to measure only the leaching and conditioning rate of leaf detritus.

Mesh bags were recovered, with a total number of  $r = 4$  replicates for each type (coarse and fine) for each site, and with a time step  $t$  of 1 month for a total of 12 months. The following parameters were measured: (1) the loss of leaf detritus weight in both fine and coarse mesh bags; (2) the number of taxa colonizing the detrital substrates; and (3) the number of individuals for each sampled taxon, averaged over the  $r$  replicates.

The decomposition rate was measured according to Olson (1963),  $k = (\ln W_t - \ln W_0)/t$ , where  $W_t$  is the dry weight of leaf detritus at time  $t$ ,  $W_0$  the initial dry weight of leaf detritus and  $t$  the total time of immersion, expressed in days. The total decomposition rate ( $k_t$ ) was measured by the loss of detritus weight in the coarse mesh bags, while the leaching and conditioning process ( $k_l$ ) was measured by the loss of detritus weight in the fine mesh bags. Thus, as a first approximation, we measured the macrodetritivores activity as  $k_d = k_t - k_l$ . We also measured the frequency of colonization ( $f_i$ ), defined as the sum of the number of times a taxon has colonized the detrital substrates in each pool, averaged by the total time of the experiment.

## Network analysis

We studied the network of Tarquinia saltern as a bipartite network, establishing links between two sets of nodes, taxa ( $S$ ) and pools ( $P$ ), but not between nodes of the same set, looking at two main properties of network structure: modularity and nestedness. We first compiled the incidence matrix (Table 1), whose values express the presence of a particular taxon  $S$  (row) in a given pool  $P$  (column). The incidence matrix was then converted into a bipartite graph, in which a single edge was created for every non-zero element. We used only presence/absence data to standardize the dataset for modularity and nestedness. Since the chosen algorithm for nestedness works only with binary data, we chose to use the same unweighted dataset for the network analyses.

## Modularity

An interesting measure of network structure is its modularity—defined as non-overlapping groups of nodes in the network, where the links are not homogeneously distributed, and the density of links inside modules is higher than among modules (Newman 2006).

There are several algorithms used to detect community structure in networks (Newman and Girvan 2004; Guimerà and Amaral 2005). In this work we used an algorithm implemented in R (R Development Core Team 2009) to find communities in a graph via a spin-glass model based on simulated annealing (SA; Kirkpatrick et al. 1983). This approach explicitly admits the possibility that no good division for a network can exist a priori, using a heuristic procedure to find the optimal solution for modularity, based on a slightly modified version of the function given by Newman and Girvan (2004; for more details see Reichardt and Bornholdt 2006).

The algorithm requires some specific parameters, such as the number of spin states that can be populated, and the starting temperature for SA. The number of spin states represents the upper limit for the number of communities, and during the SA algorithm some spin states will be unpopulated, according to the optimization of the modularity function. The community structure of the network is interpreted as the spin configuration that minimizes the energy of the spin-glass, with the spin states being the community indices (Reichardt and Bornholdt 2006). We chose six spin states because, in our spatial network, the maximum number of modules that we expected to observe was equal to the six sampled pools.

Each step of the SA algorithm replaces the current solution by a random approximated one, with a probability that depends on the difference between the corresponding function values and on a global parameter  $T$  (defined temperature), decreasing gradually during the process towards deep minima (i.e., low-cost configuration) of the network partition (Guimerà and Amaral 2005). To test the significance of the modular structure, we compared the measured modularity with those of 100 random networks with the same degree distribution as our empirical one, and examined whether the empirical network was significantly more modular than the random ones.

The spin-glass with SA algorithm returns the modularity score of the whole network, assigning to each graph vertex a specific module. Modularity ranges between 0 and 1 and tends towards a maximum when the bulk of links occur within the same module, and the probability of a random association among different sets of nodes is small. Therefore, in our analysis, a high modularity corresponds to a configuration in which taxa and pools are separated into distinct modules, indicating a non-random pattern of colonization.

We then identified the role of a taxon within the network by its within-module degree ( $z$ ) and its among-module connectivity ( $c$ ), which define how the node is positioned in its own module and with respect to other modules (Guimerà and Amaral 2005). This approach is based on the idea that nodes with the same role should have similar topological properties. If we define  $l_{im}$  as the number of links  $l$  of node  $i$  to other nodes in its own module  $m$  and  $\bar{l}_m$  and  $\sigma_{lm}$  as the average and standard

**Table 1** Incidence matrix. Each entry represents the association between the *S* taxon (row) and the *P* pool (column)

	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	$\sum_{i=1}^P x_i^a$
Detritivores							
<i>Chironomus</i> spp.	1	1	1	1	1	1	6
<i>Gammarus aequicauda</i>	1	1					2
<i>Perinereis cultrifera</i>	1	1					2
Gordiidae	1						1
<i>Hydrobia acuta</i>	1	1	1	1			4
<i>Cerastoderma glaucum</i>	1	1	1	1			4
<i>Cerithium rupestre</i>	1						1
(other) Diptera (larvae)		1			1		2
<i>Corophium insidiosum</i>		1					1
<i>Idotea baltica</i>		1					1
Predators							
Dytiscidae					1		1
Hydrophillidae					1	1	2
(other) Coleoptera (larvae)	1				1		2
Nereidae	1	1					2
Polichetae		1					1
<i>Haliplus</i> sp.			1	1	1	1	4
<i>Micronecta</i> sp. (larvae)					1		1
Anisoptera (nymphae)					1		1
$\sum_{j=1}^S x_j$	9	10	4	4	8	3	

<sup>a</sup> $x_i$  and  $x_j$  are the total number of pools colonized by each taxon and the total number of sampled taxa in each pool, respectively

deviation of within-module  $l$  of all nodes in  $m$ , the within-module degree is defined simply as:

$$z = \frac{l_{im} - \bar{l}_m}{\sigma_{l_m}}$$

High values of  $z$  indicate a high within-module degree, which measures how well node  $i$  is connected to other nodes in the module, and vice versa. The among-module connectivity (sensu Olesen et al. 2007, identical to the participation coefficient of Guimerà and Amaral 2005) expresses the position of node  $i$  with respect to other modules, and is defined as:

$$c = 1 - \sum_{k=1}^M \left( \frac{l_{ik}}{l_i} \right)$$

where  $l_i$  is the degree of node  $i$  and  $l_{ik}$  the number of links from node  $i$  to other nodes in module  $k$  (including  $i$ 's own module). If  $i$  has all its links  $l$  within its own module, then  $c \rightarrow 0$  and, if these are distributed evenly among modules,  $c \rightarrow 1$ . Once the modules are identified, the role of a taxon can be identified in the  $zc$ -parameter space (see Guimerà and Amaral 2005; Olesen et al. 2007).

### Nestedness

We quantified nestedness  $N$ , a complementary measure of modularity (Olesen et al. 2007), by using the matrix temperature  $T^*$ . Generally, matrix temperature is measured as the ratio of sum of squared deviations from the isocline of a maximally packed matrix of unexpected

presences and absences, and the maximum possible value in a given matrix (Atmar and Patterson 1993). Nestedness temperature ( $T^*$ ) was estimated from the BINMATNEST algorithm (Rodríguez-Gironés and Santamaría 2006) implemented in the “bipartite” package of R (R Development Core Team 2009, library bipartite). We followed Bascompte et al. (2003) and expressed the degree of nestedness as  $N = (100 - T^*)/100$ , ranging between 0 and 1 and expressing the distribution order of taxa among pools.

The significance of nestedness was tested by comparing the observed value with the distribution from the 100 resulting randomized matrices for the whole network, using null model 3 implemented in BINMATNEST. This null model assigns a value of 1 to each matrix element with probability equal to the arithmetic mean,  $(p_r + p_c)/2$ , of the presence probability of pools (i.e., the fraction of ones in column  $c$ ) and macroinvertebrates (i.e., the fraction of ones in row  $r$ ; for more details about this null model see Bascompte et al. 2003) and, since this is a conservative model, it is less prone to type I and II error (Ulrich et al. 2009).

## Results

### Decomposition of leaf detritus

We found differences in the remaining dry weight of *P. australis* leaf detritus among the six sampling sites, observing a high proportion of final dry weight in hyperaline waters. In hypoaline waters (mean annual salinity  $8.5 \pm 2.45 \text{ g L}^{-1}$ ), the percentage of final



dry weight in the coarse mesh bags was about 25%, while in hyperaline waters (mean annual salinity  $115 \pm 16.62 \text{ g L}^{-1}$ ) this value was about 80% of the initial dry weight. The same trend can be observed for the final dry weight of leaf detritus measured in fine mesh bags (Table 2). The loss of leaf dry mass followed a negative exponential model in each sampled pools, according to Olson (1963), with  $P < 0.001$ . Decomposition rates followed the salinity gradients, decreasing with increasing salinity (one-way ANOVA,  $F_{3,23} = 17.12$ ,  $P < 0.001$ ).

### Structure of detritus-based communities

During the field experiment we sampled a total of 2,406 individuals belonging to  $S = 18$  taxa of macroinvertebrates on  $P = 6$  pools, resulting in a total of  $L = 38$  links between taxa and pools; among sampled taxa, ten were classified as detritivores and eight as predators, according to the available literature (McCafferty 1983 and literature cited; Bramucci 2009; see Table 1 in Materials and methods). The mean number of individuals per taxa was highly skewed, where a few taxa were most abundant and a bulk of taxa were much lesser abundant (Fig. 2a).

The mean abundances ( $n_i$ ) and mean frequencies of colonization ( $f_i$ ) of macroinvertebrates have been normalized to the maximum measured value ( $n_i \text{ max}$  and  $f_i \text{ max}$ ), to standardize these measures on a dimensionless interval between 0 and 1. The parameters  $n_i$  and  $f_i$  were positively correlated (Spearman's  $\rho$  correlation;  $\rho = 0.92$ ,  $P < 0.01$ ), revealing how the most abundant taxa were also those with a higher frequency of colonization, with a best fit given by a power-law (Fig. 2b). The most abundant and widespread taxa were larvae of *Chironomus* spp., *Gammarus aequicauda*, *Hydrobia acuta* and *Haliphus* sp.

### Network analysis

Results on modularity showed how the network structure was significantly more modular ( $M = 0.360$ ) than expected by a random colonization of leaf detritus by macroinvertebrates ( $M_{\text{null}} = 0.220 \pm 0.0009$ ,

$P < 0.001$ ), revealing three well-defined groups of pools ( $P_1 = 2$ ,  $P_2 = 3$  and  $P_3 = 1$ ) and taxa ( $S_1 = 10$ ,  $S_2 = 2$  and  $S_3 = 6$ ). Among taxa, we found a different, yet specular, modular distribution of predators and detritivores, where the bulk of predators (75%) and detritivores (80%) were assigned to only one module (Module 3 and Module 1 in Fig. 3, respectively). The modular structure of the network maximized the number of links within modules ( $L_1 = 15$ ,  $L_2 = 6$  and  $L_3 = 6$ ) and minimized the number of links among modules ( $L_{12} = 6$ ,  $L_{13} = 2$  and  $L_{23} = 3$ ). Many links in the network were between taxa and pools belonging to the same module (on average 40% of all links in the network, Module 1 in Fig. 3), which revealed the degree of ecological specialization of macroinvertebrates (i.e., the lower tolerance to different environmental conditions). On the other hand, the most widespread taxa were assigned to one module (Module 2 in Fig. 3).

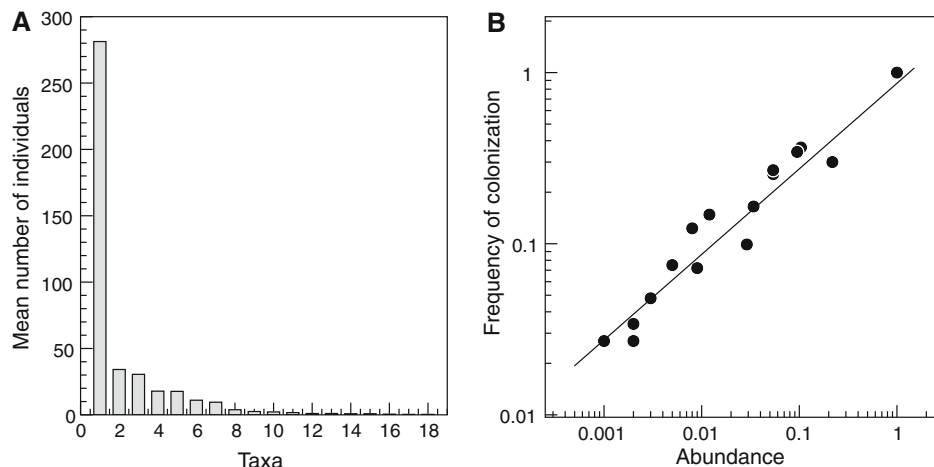
The modular structure of the network appeared to be built on modules connected by those links between taxa and pools connecting the modules (Fig. 4a). This may be indicative of an asymmetric use of pools by macroinvertebrates, which is representative of a nested pattern. The nested structure of the network was significantly higher ( $N = 0.799$ ) than expected by a random use of pools by macroinvertebrates ( $N_{\text{null}} = 0.674 \pm 0.0023$ ,  $P < 0.001$ ). This finding revealed a heterogeneous pattern in the use of pools by macroinvertebrates, since the bulk of pools were colonized by few taxa and a few pools were used much more than expected by chance (Fig. 4a). This non-random pattern in the use of detrital substrates in the different pools might be a consequence of habitat heterogeneity, which favoured an asymmetric hierarchical pattern through the network.

Almost all sampled taxa (89%) were peripheral nodes (i.e., environmental specialists), with most of their links inside their module (i.e., both low  $c$  and  $z$ ); 61% of these had connections only with pools in their own module ( $c = 0$ , ultraperipheral sensu Guimerà and Amaral 2005; Fig. 4b). The remaining 11% (2 taxa) were generalists, distributed equally between module (the predator *Haliphus* sp.) and network (the larvae of detritivore *Chironomus* spp.) hubs, which is important for the coherence and cohesion of the module and the whole network, respectively.

**Table 2** Percentage of final dry weight (values in parentheses are the % measured in the fine mesh bags) and decay rates of *Phragmites australis* leaf detritus

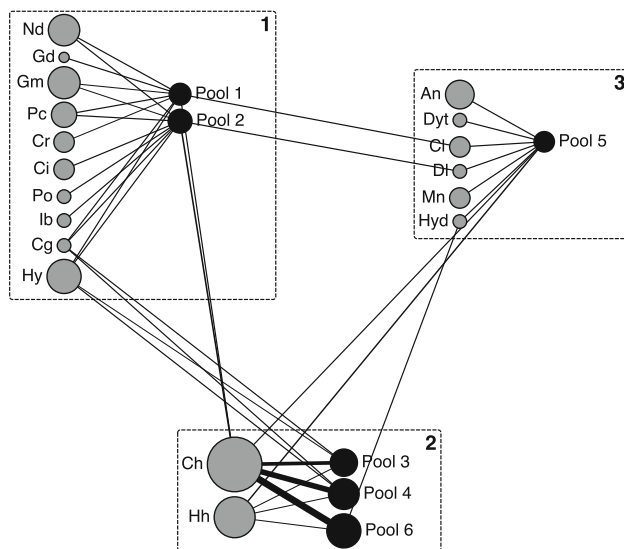
	Salinity ( $\text{g L}^{-1}$ )	% Final dry weight	$k_t$ ( $\text{day}^{-1}$ )	$k_l$ ( $\text{day}^{-1}$ )	$k_d$ ( $\text{day}^{-1}$ )
Pool5	$8.5 \pm 2.45$	25.43 (47.89)	$0.0058 \pm 0.00060$	$0.0027 \pm 0.00050$	$0.0031 \pm 0.00030$
Pool1	$44.8 \pm 2.63$	31.88 (60.12)	$0.0038 \pm 0.00080$	$0.0016 \pm 0.00040$	$0.0022 \pm 0.00030$
Pool2	$50.0 \pm 2.84$	34.38 (62.14)	$0.0035 \pm 0.00060$	$0.0016 \pm 0.00050$	$0.0019 \pm 0.00030$
Pool3	$88.0 \pm 5.60$	56.53 (71.57)	$0.0022 \pm 0.00040$	$0.0014 \pm 0.00040$	$0.0008 \pm 0.00040$
Pool4	$100.0 \pm 7.09$	49.60 (79.77)	$0.0016 \pm 0.00050$	$0.0009 \pm 0.00008$	$0.0007 \pm 0.00030$
Pool6	$115.0 \pm 16.62$	78.70 (78.20)	$0.0007 \pm 0.00002$	$0.0004 \pm 0.00005$	$0.0003 \pm 0.00001$

$k_t$  Total decomposition rate,  $k_l$  leaching + conditioning,  $k_d$  consumption rate by macrodetritivores. Decomposition rates are measured following Olson (1963). Values are expressed as the mean ( $\pm 2$  SE) and ordered following the salinity gradient, from hyposaline to hyperaline waters



**Fig. 2** **a** Frequency distribution showing the asymmetry in the mean number of individuals per taxa in the detritus-based communities of Tarquinia saltern. **b** The abundances ( $n_i$ ) and frequencies of colonization ( $f_i$ , a proportion of how many times a taxon colonized the detrital substrates in the pool during the field experiment) show a

positive correlation. The log-log graph shows the best fit given by a power law ( $y = 0.866 x^{0.5}$ ,  $R^2 = 0.867$ ).  $n_i$  and  $f_i$  are expressed by their means normalized over their maximum. Note how the measured values of abundance and frequency of some points in (**b**) are similar and therefore superimposed in the figure



**Fig. 3** Modular structure of the spatial network. *Light gray nodes* Taxa, *black nodes* pools; *dashed numbered boxes* identified modules. The size of nodes is proportional to the mean log-transformed abundances of taxa and the mean annual salinity value of the pools. The thickness of a link represents the mean normalized frequency of colonization ( $f_i$ ) and indicates the proportion of how many times a taxon colonized the detrital substrates in the pool during the field experiment. Taxa: Ch, *Chironomus* spp. (larvae); Gm, *Gammarus aequicauda*; Pc, *Perinereis cultrifera*; Gd, *Gordiidae*; Hy, *Hydrobia acuta*; Cg, *Cerastoderma glaucum*; Cr, *Cerithium rupestre*; Dt (other), *Diptera* (larvae); Ci, *Corophium insidiosum*; Ib, *Idotea baltica*; Dyt, *Dytiscidae* (larvae); Hyd, *Hydrophilidae*; Ct (other), *Coleoptera* (larvae); Nd, *Nereidae*; Po, *Polychaeta*; Hh, *Haliphus* sp.; Mn, *Micronecta* sp. (larvae); An, *Anisoptera* (nymphae)

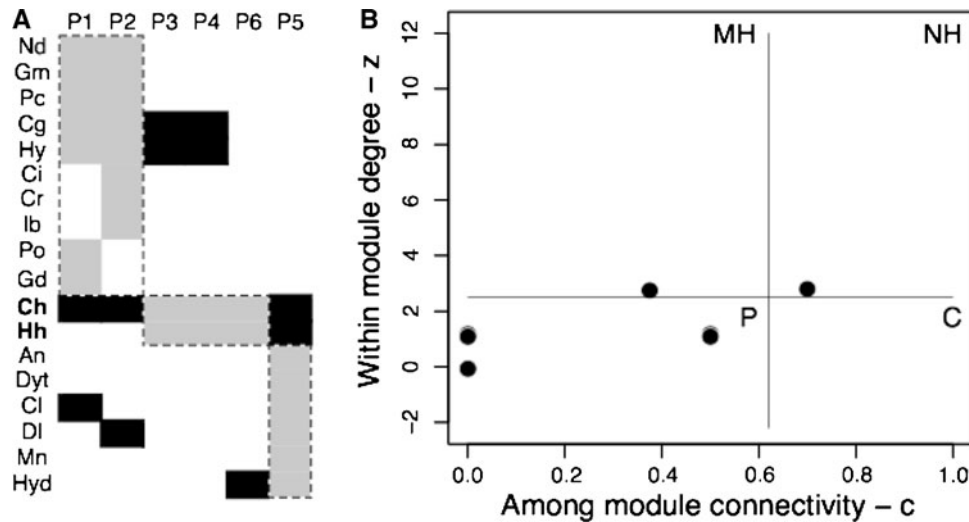
Thus, the network of Tarquinia saltern was characterized by a clear subdivision between high within-connected modules, revealing an association between the spatial proximity of the pools (e.g., the distance from the

point of water refill), and modularity. Therefore, network analysis has proved a useful tool for characterizing the spatial pattern of species distribution, allowing predictions about robustness against perturbations and their consequences.

## Discussion

The present distribution of macroinvertebrates on leaf detritus revealed that colonization pattern is a process driven mainly by the environmental conditions under which the communities are structured, which influences the abundance, richness and frequency of colonization, where a few taxa are more abundant and widespread than others. The scarce water refill among the pools favors a greater variation in salinity conditions throughout the seasons due to high evapotranspiration, and the colonization process seems to favor the occurrence of predators when a marked change in salinity conditions occurs with the changing seasons. On the other hand, minor variations (i.e., more stable salinity conditions during the seasons) lead to an ecological adaptation to salinity of a narrow pool of taxa. This may place some physiological limitations on the abundance and diversity of predators (Herbst 2006), which may imply a reduction in predation activity (Connel 1975), with possible consequences on the feeding activity of macrodetritivores. Indeed, interference between taxa, such as competition among organisms involved in detritus decomposition, have been suggested to regulate the dynamics between trophic levels, and the increased trophic complexity (i.e., the presence of predators) will potentially enhance the consumption rate by detritivores (Wardle and Yeates 1993).

Modularity analysis shows a dense core of within-module connections and sparse connections between



**Fig. 4 a** Modular matrix of the network (with nodes sorted according to their modular affinity as in Fig. 3) showing differences in the colonization of detrital substrates in the different pools. *Dashed boxes* Identified modules, *black cells* links between taxa and pools connecting the modules. **b** Plot showing that almost all

sampled macroinvertebrates are peripheral nodes with one module hub and one network hub (*bold in a*). Taxa abbreviations as in Fig. 3. *MH* Module hubs ( $z > 2.5$ ,  $c \leq 0.62$ ), *NH* network hubs ( $z > 2.5$ ,  $c > 0.62$ ), *P* peripheral nodes ( $z \leq 2.5$ ,  $c \leq 0.62$ ), *C* connectors ( $z \leq 2.5$ ,  $c > 0.62$ )

different modules, revealing the partition of the network into three well-defined subgroups of nodes. This result highlights the strong association between taxa and pools under different conditions of salinity, and the role of the most widespread taxa in linking the modules. The taxon acting as a connector among modules in the network (i.e., network hub) is the most abundant and widespread, i.e., the larvae of *Chironomus* spp. a group of species well adapted to changing and extreme salinity conditions (Velasco et al. 2006). At whole network level, taxa that associate with only a few pools are not a subset of those taxa that associate with pools colonized by different taxa. This reflects in a “coherent noise” (Patterson and Atmar 2000), given by the presence of ecologically distinctive taxa, which create idiosyncratic peaks corresponding to pools that contribute much more to network “noise” (e.g., pool 5, hyposaline waters).

Modules are linked by the most widespread (generalist) taxa, and this creates an asymmetric association between taxa and pools that is representative of a nested pattern. The taxa colonizing more than one pool (e.g., *Chironomus* spp. and *Haliphys* sp.) are also those that colonize the most shared pools, and this might create a core in which a small set of macroinvertebrates using a high number of pools uses a small set of the highly used pools. We also observed an association between modularity and the spatial proximity of the pools; pools located near the point of water refill (Pool 1 and 2 in Fig. 1), and pools far away from this point (Pool 5, and Pools 3, 4 and 6 in Fig. 1) belong to different modules. The modularity of the network may thus reflect habitat heterogeneity (Pimm and Lawton 1980; Brown 2007) driven by the different environmental conditions of the

pools, and the clustering of closely ecologically related species (as observed in plant-pollinator networks by Lewinsohn et al. 2006).

Therefore, habitat heterogeneity and the ecological adaptation of taxa to the salinity conditions involve a non-random pattern of colonization that contributes to network complexity. The spatial structure of the network can also favor the formation of clusters among spatially close nodes (as in communication and transportation networks, Guimerà et al. 2005), and we observe the same trend in the spatial network of the Tarquinia saltern (Fig. 3). These results may have far-reaching conservation implications because, in modular networks, disturbances are expected to spread more slowly than in a non-modular structure due to the strong within-module connections and the few links between modules.

As well reported in the ecological literature, decomposition is a key process in regulating the regeneration of carbon and nutrients, and is an important link between primary and secondary production (Fenchel and Jørgensen 1977). The importance of decomposition in aquatic ecosystems comes from the ability to sustain higher diversity, larger predator biomass, and longer food chains than would be supported by primary productivity alone (Hairston and Hairston 1993). Decomposition can also stabilize the dynamics of consumers populations, alter habitat complexity, and stabilize food webs that would be otherwise unstable (for a complete review, see Moore et al. 2004). Thus, any kind of alteration to the network structure of detritus-based communities could have implications for the highest levels of trophic chain (e.g., migratory birds).

We note that the network seems to be less sensitive to random removal of nodes but highly sensitive to the removal of the most connected ones, and we suggest that the gradual loss of the latter could signal growing system fragmentation. The distance between pools in the area reflects the differences in their ecological characteristics (e.g., differences in chemical–physical parameters), reducing the probability of connections between taxa and pools. The distance among nodes in a network may be expressed by any quantity that measures the “costs” associated with the formation of links (such as social distance measured by salary or socio-professional category differences, see Barthélémy 2003). This can produce the clustering of spatially closed pools, characterized by the occurrence of ecologically related species. Network topology reveals that random events, such as floods or heavy rains, affect network connectivity slightly. However, the effect of non-random events (e.g., localized flooding on the most connected pools) could seriously affect system connectivity. The consequences of localized perturbations may depend strongly on the role played by a node in the network, since the selective removal of nodes may cause fragmentation of modules or the whole network (Olesen et al. 2007).

The spatial structure of the detritus-based communities in Tarquinia saltern shows a greater structural and functional heterogeneity than expected by chance. Our results reveal how increased functionality (i.e., the higher consumption of leaf detritus) is observed in the presence of a higher site-specific association (Pool 5, Table 2, Fig. 3). Therefore, the effect of non-random perturbations could result in the homogenization of both the structure and function of the system, involving the replacement of ecological specialists by the same widespread generalists (Olden et al. 2004), and this may cause fusion of modules with long-term effects on network functioning.

The effects of alterations in system connectivity at higher trophic levels deserve further investigation. It can be assumed that increased spatial similarity could have effects on species at higher trophic levels by increasing extirpation rates via intensified species-specific interactions (e.g., functionally similar species might utilize the same spatial resources, thus enhancing competition). Since saline ecosystems are artificial aquatic environments, the need for constant maintenance, which involves water management inside the pools, should take into account these findings for conservation practices.

The case study discussed here so far demonstrates how the application of network theory can yield valuable insights for conservation and management practice. Future studies linking topological structure and attachment dynamics of macroinvertebrates on leaf detritus (also on multiple resources) will provide insight into spatio-temporal variations in network structure, increasing our knowledge of the ecological processes behind the dynamic processes of networks and their consequences for functional processes.

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