

The interplay between network structure and functioning of detritus-based communities in patchy aquatic environment

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Received: 30 March 2012 / Accepted: 31 July 2012 / Published online: 19 August 2012
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Abstract Understanding models of networks formation is fundamental to explore the role of the structure in the functioning of the systems they describe, and their ability to respond to change. In this work, we aimed to understand whether and how the modular (or compartmented) structure of a network composed by macroinvertebrates and leaf detritus in six pools of aquatic system was related with the decomposition process. First, we evaluated the relationship between the temporal patterns of leaf detritus colonization and the modular subdivision of the network. Modularity was then related with the clustering of the pools based on convergent traits of leaf detritus consumption and environmental conditions. A significant relationship between the colonization patterns and the distribution of taxa and pools in well-defined modules was found. The modular and clustering subdivision of the pools showed a significant overlap, which revealed the intimate linkage between the structure and functioning of the system. Modularity shapes the functional architecture of the network, by increasing the spatial differences of leaf litter decomposition over time and the diversity of functional traits among detritus feeder.

As a consequence, modularity influences the variability of communities' responses to disturbance, increasing the diversity and robustness of functional processes. Our results have also implications from a conservation point of view, showing the importance of habitat heterogeneity for the robustness of ecosystem functioning, potentially enhancing biodiversity with positive, long-term effect on the whole food web.

Keywords Network analysis · Modularity · Macroinvertebrates · Decomposition

Introduction

One of the most intriguing and controversial issues in community ecology has always been the identification of the patterns and mechanisms of species occurrence (Weiher and Keddy 1999; Ulrich 2004). Early studies showed the importance of simple deterministic rules based on forbidden species composition and reduced niche overlap in the structure of natural communities (Diamond 1975). However, interspecific competition could not be somehow sufficient to describe the abundance and diversity of species. Other stochastic processes may be involved (Hubbel 2001), suggesting the role of environmental variability in determining patterns of communities' composition (Ellwood et al. 2009).

Patterns and mechanisms of species occurrence and interaction have been largely explored in the last

Handling Editor: Piet Spaak

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years, taking advantage of the network theory, a useful framework to represent the structure of many complex systems (see Proulx et al. 2005, and references therein). Food webs, plants/pollinators and spatial networks are examples of how the species, and/or species and habitats can be represented by a set of nodes linked by some specific associations (e.g., predation, competition, mutualism and colonization). Among many, modularity is considered one of the main topological structures often found in many ecological networks (Krause et al. 2003; Olesen et al. 2007; Fortuna et al. 2009; Guimerà et al. 2010).

Modularity is a peculiar topological organization where the nodes (e.g., species and/or habitats) in a network tend to organize themselves into a set of ‘modules’ (or compartments), where the density of the links is greater within nodes of the same module than among nodes of different modules. Several mechanisms, involving diet’s contiguity (Guimerà et al. 2010), habitat heterogeneity (Pimm and Lawton 1980) or past evolutionary history between interacting species (Lewinsohn et al. 2006), are advocated to explain the modular structure in a variety of ecological networks. However, recent findings (Williams 2011) identified the spatial and temporal heterogeneity of species occurrence as the building block able to explain features of the network structure. Patterns of temporal colonization may shed light on the effect of unobserved links, either missing or forbidden (i.e., unobservable), on network formation (Olesen et al. 2011). Phenological uncoupling (Olesen et al. 2011), asynchronous dynamics between interacting species or differential responses to environmental conditions, might influence the capacity to capture the entire complexity of the system (but see Olesen et al. 2008). This may result in a decreased reliability in network constructing, with important implications for our understanding of the communities’ assembly rules, and their implication on ecosystem functioning and stability.

This uncertainty should be carefully addressed, since the structure of complex networks strongly determines their dynamics and stability. Indeed, recent findings (Bastolla et al. 2009) have shown the importance of specific network patterns for biodiversity, able to reduce interspecific competition and enhancing the number of coexisting species. Non-limiting food and habitat resource coupled with high rates of predation and parasitism (Strong 1982),

habitat heterogeneity (Palmer 2003) and environmental filtering (Weiher and Keddy 1999) may prevent competition in natural communities. The ability of species to use an extended range of resources and their capacity to exploit each one (the ‘jack-of-all-trades is master of none’ hypothesis, MacArthur 1972) can thus be considered a general rule able to explain the assembly of communities (Weiher and Keddy 1999).

Within the communities, species are often ordered along a generalist/specialist gradient, separating species with large ecological niches from those with smaller ones. This differentiation is often associated with several life-history traits, with more generalist species supposing to maintain higher dispersal abilities and to cope more easily with environmental stochasticity than specialist species (Sol et al. 2002; Brouat et al. 2004). Recent findings (Clavel et al. 2011) have also shown the relationship between the degree of specialization/generalism and the functional homogenization of biodiversity in natural communities. This effect refers to the consequence of biological homogenization, observing how the replacement of specialists by more generalist species could lead to a decreased capacity to perform specific functions (Clavel et al. 2011), given by similarities in niche partitioning. Therefore, more specialized species within the communities can stabilize ecosystem processes (Hooper et al. 2005), on account of greater niche complementarity.

With up to 90 % of global terrestrial plant production entering the dead organic matter pool (Cebrian 1999), decomposition and the sequestration of organic carbon in soils and sediments stand out as central components of ecosystem functioning (Gessner et al. 2010). The decomposition of dead organic matter is often related to the chemical quality of leaf litter (e.g., C:N, lignin:N), able to influence the degree of microbial colonization and the diversity of detritivores decomposer (for a complete review, see Moore et al. 2004). One of the earliest models explaining the complexity of detritus-based systems was the ‘top-down bottom-up’ approach, which considers the effect of consumers and litter diversity on the decomposition dynamics (McQueen et al. 1986).

To date, many empirical evidences suggest the role of competition and predation in regulating the decomposition of dead organic matter (Wardle and Yeates 1993). Therefore, the diversity and abundance of the organisms involved in the decomposition process are

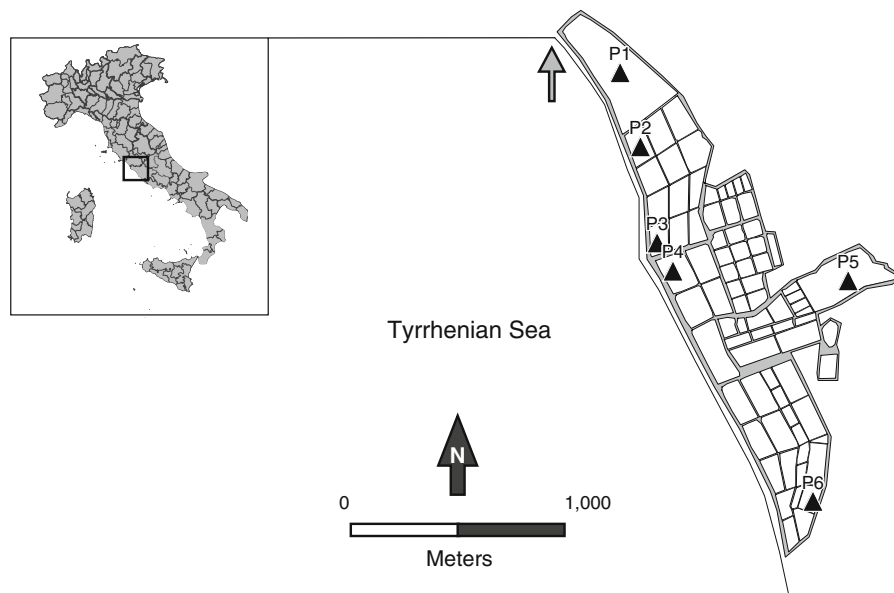


Fig. 1 Spatial location of the six sampling sites (black triangles) in the Natural Reserve of Tarquinia Saltern. The dark gray arrow indicates the main point of water refill between

the sea and the study area, while the surface highlighted in gray shows the drainage system surrounding the pools

by no mean sufficient to describe the richness–functioning relationship (Mouillot et al. 2011). Predation, facilitation and competition have the potential to influence the population dynamics of the organisms that feed on detritus and, generally, biodiversity, which is controlled by within- and between-trophic-level interactions (Yee et al. 2007). Further, differences in habitat conditions may create contrasting selection pressures that shape the evolutionary trajectories of the organisms involved in the colonization of the detrital resources in different ways, altering the type and strength of interactions that can translate into diversity effects on litter decomposition (Gessner et al. 2010).

In this work, we evaluated the interplay between the structure and functioning of a network composed by macroinvertebrates and the leaf detritus of *Phragmites australis* (Cav.) Trin. ex Steud in six different pools of a patchy-connected system. The temporal variation in the number of individuals per taxon in each sampled pool was used to explore whether the degree of specialization in the use of habitat could be related to the modular structure of the network. Afterward, we checked whether modularity did affect the functioning of the system, defined as the rate at which the dead organic matter was decomposed by macroinvertebrates. Habitat heterogeneity is expected to influence the pattern of leaf detritus colonization, determining

the structural and functional architecture of the network. Our findings showed the intimate linkage between network structure and functioning, with modularity decreasing the spatial similarity of leaf litter decomposition over time, increasing the diversity of functional traits among detritus feeder. This may have important outcomes for conservation, showing the importance of habitat heterogeneity for the robustness of ecosystem functioning, with positive, long-term effects on biodiversity.

Materials and methods

Study area and field experiment

The study area is the transitional aquatic ecosystem of Tarquinia saltern (central Italy, 42°12'N, 11°43'E), a patchy ecosystem composed by a series of pools connected by a drainage system where the exchange of waters is provided by a single connection with the sea located north of the area (Fig. 1). The spatial characteristics of the pools within the study area (e.g., isolation and connectivity, Bellisario et al. 2011) give rise to a wide environmental gradient, showing the existence of a geographic pattern in the variability of the salinity levels, pH and dissolved oxygen concentration.

Table 1 Main chemical–physical parameters measured in the six sampling pools

Pool	Salinity (mg L ⁻¹)	[O ₂] (mg L ⁻¹)	pH
P1	44.769 (±4.746)	5.765 (±2.543)	8.112 (±0.243)
P2	50.531 (±5.126)	6.068 (±2.703)	8.104 (±0.252)
P3	87 (±10.083)	5.505 (±1.568)	8.067 (±0.296)
P4	100.154 (±12.548)	5.865 (±1.216)	8.134 (±0.236)
P5	8.515 (±4.292)	10.03 (±1.644)	8.953 (±0.566)
P6	115 (±29.958)	5.536 (±1.779)	8.034 (±0.187)

Values are expressed as the mean ± SD

To measure the colonization process, 48 litterbags have been placed in six sampling pools, chosen to cover the full spectrum of environmental variability (Table 1). Litterbags had dimension of 10 × 10 cm with a mesh size of 5 × 5 mm, filled with a known weight (2 ± 0.004 g of dry mass, after drying at 60 °C for 72 h) of *Phragmites australis* (Cav.) Trin ex Steud. leaf detritus. To quantify the colonization of leaf detritus, litterbags in each pool were sampled on a monthly basis with 4 replicates for 12 months and measured the number of individuals for each taxon. The abundances were calculated as the mean number of individuals per taxon, averaged over the 4 replicates. To reduce as much as possible the sampling biases, samples were recovered directly into the pools and stored in separate containers filled with water taken in situ. To avoid the presence of singletons (i.e., taxa represented by single individuals), only those taxa whose average number of individuals was at least equal to one were recorded. Thus, taxa must have colonized all replicates with at least one individual, or with greater abundances in at least a half of the replicates.

Data source

To investigate the degree of specialization during the colonization process of leaf detritus, data were first organized as taxa × time matrices for each sampled pool, which entries represent the mean number of sampled individuals. The degree of specialization of a species may be described as the variance in species' performance across a range of environmental conditions. We therefore measured specialization as the response in species' abundance to a given resource gradient (Devictor et al. 2010), here considered as the

set of all environmental conditions under which the communities are structured in different pools (Grinnell 1917). In this work, taxa whose abundances vary little across time have been considered as more generalists than those with more variable abundances through out the sampling periods. This degree of temporal specialization (TS) was measured, in first instance, as the coefficient of variation (SD/mean) of taxa abundance across the sampling periods. Therefore, for each pool, one can obtain the degree of specialization for each taxon, where low values of TS (i.e., a more even distribution of abundances through time) indicate a high degree of generalism than higher values.

Network structure and modularity

Data were rearranged as a bipartite network, a kind of network assemblage where the links are established between two different sets of nodes but not within nodes of the same set. In our bipartite network, links are established between macroinvertebrates and the leaf litter in different pools. We also measured the weights of the links, by reversing the TS values through their ranking across sites (TS*), so that high values indicate high degree of generalism. The rationale behind this operation was to make the degree of specialization comparable across taxa and, more important, allow the more generalist taxa to have higher probability of incidence in modularity analysis (see after in Null models).

Modularity represents a peculiar topological organization where nodes in a network can be grouped by their membership to well-defined 'communities' (Newman and Girvan 2004). Communities (also modules or compartment, Guimerà et al. 2010) identify non-random structures within a network, where the bulk of links occur within nodes belonging to the same module rather than between nodes of different modules. To date, several algorithms to find communities have been developed (Newman and Girvan 2004; Guimerà and Amaral 2005; Barber 2007), most of which converge on the problem of finding, if any, the best partition of the network (Q , see Newman and Girvan 2004 for more details), by comparing the distribution of the links in original network to those of an appropriate randomization model. However, a common problem in community finding algorithms relies in their application to

bipartite networks, where the randomization of the links should be avoided within nodes of the same set (Barber 2007).

In this work, we used a recently developed algorithm (BRIM, bipartite and recursively induced modules, Barber 2007), which is based on a greedy search algorithm, where vertices are moved among existing communities to ensure the resulting partition is at a local optimum of modularity. As many other developed algorithms, this technique identifies modules maximizing the measure of modularity, Q , by splitting large modules in smaller modules, until the optimal solution for Q is reached. The procedure starts by assigning all vertices to the same module, so that $Q = 0$. The number of modules, c , is then iteratively increased up to an imposed limited value, here set as the maximum number of modules that could be observed (i.e., the six pools). For each increasing, half of the vertices are randomly reassigned to the newly defined modules, and a new, locally optimal solution is found. This process continues, with c being repeatedly increased so long as Q continues to increase, and the maximization of modularity is then reached once Q drops for increasing number of c .

Null models

To search for the maximum modularity, the randomization in BRIM algorithm keeps the degree of real network (i.e., the number of links per node), along with the additional constraint that links must be established between nodes of different sets. However, since one of the aims of our analyses was to search for a significant modular structure, and the contribution of TS^* on modularity, we compared the results obtained for the real network with benchmark null models.

The first null model is the one derived from Vázquez et al. (2007) and implemented in the ‘bipartite’ package of R (R Development Core Team 2011) as ‘vaznull.’ This null model first assigns links according to link-specific probabilities, requiring that each row had at least one entry. Then, once the number of filled cells in the original matrix was reached, the remaining links are distributed among the filled cells, so that connectance in the original and randomized matrices is the same (Vázquez et al. 2007). Although similar, this null model has lower systematic bias than the swap algorithm, which yields, for instance, more high values than necessary (Artzy-Randrup and Stone

2005). Therefore, this null model maintains the total number of taxa and pools and randomizes the links proportional to the TS^* values. The higher the TS^* , the higher will be the probability of occurrence of a given taxon within the pools.

A second null model was chosen to test the contribution of TS^* to modularity. This null model maintains the same degree of connectance (the proportion of all possible links observed in a network), keeping the number of rows and columns of the original matrix and randomly reshuffling the distribution of the links, so that the probability to obtain a link between the nodes is independent from the TS^* values.

To test for a significant modular structure, 1,000 replicates of the original matrix under each null model were performed. We used the software Netzscope (Barber et al. 2011) to find the maximum modularity for each ensemble of simulated networks and reported the value as the mean \pm SD. Since the ‘vaznull’ model aims to replicate accurately the original network structure, we expected that the mean modularity of random networks should not deviate significantly from empirical data, since the distribution of the links follows specific constraints based on link-specific probability (i.e., the TS^* values). Conversely, a completely random reshuffling should return values significantly different from the modularity measured in real network, on account of the independence between the occurrence of macroinvertebrates and TS^* .

Finding ‘functional modules’

The degree of functional activity in different pools was measured as the rate at which the detrital resource was consumed by macroinvertebrates, by measuring the coefficient of decomposition following the negative exponential model of Olson (1963), $k = (\ln W_t - \ln W_0)/t$, with W_t the dry weight of leaf detritus at time t and W_0 the initial dry weight. To disentangle the effect of macroinvertebrates activity, k_d , from other decay processes (e.g., leaching and microbial–fungal activity), in each of the six pools have been placed 48 litterbags with a fine mesh, to avoid animal colonization. Therefore, the macroinvertebrates activity has been measured (as a first approximation) as the difference between the global decomposition rate measured in coarse litterbags, k_r , and the decomposition rate measured in fine litterbags, k_f .

To search, if any, for differences in the functional activity and environmental variability in different pools through time, we performed a cluster analysis among the decomposition rates (k_d) and among the measured chemical–physical parameters (Table 1). We used a hierarchical clustering algorithm, implemented in the ‘pvclust’ package of R (R Development Core Team 2011). Hierarchical clustering tries to find relatively homogeneous clusters of cases based on measured characteristics. Here, we used a ‘top–down’ or divisive clustering approach, where all observations start in one cluster and, then, are recursively split until each one is in its own singleton cluster. Uncertainty was measured via multiscale bootstrap resampling, where bootstrap values ≥ 95 provide a minimum level of significance of 0.05. To evaluate the significance of clustering, we used a divisive method with 1,000 replicates based on the analysis of variance.

Linking structure to function

The significance of the association between the structure and functioning of the system was tested by measuring the extent to which the modular and cluster subdivision of the nodes overlapped during the BRIM and clustering algorithms. Both algorithms are hierarchical, meaning that all nodes start in one subset (i.e., a single module or cluster) and then are recursively split into smallest subsets, until the maximum modularity and a significant cluster subdivision were reached. To measure the strength of association, the Mann–Whitney U -test was used to perform a pairwise comparison between (1) the number of modules and clusters in which the network was subdivided during each step of the simulations and (2) the modular and clustering subdivision of the pools. We expected a convergence in the way with which the nodes were rearranged during the modularity and clustering algorithm, meaning that the number of modules and the modular membership of the pools under a significant null model should not deviate from those of clustering.

Results

A total of 18 taxa were sampled along the six sampling pools during the field experiment. Pools differed in terms of the number of colonizing taxa and total

number of individuals (Mann–Whitney U -test, $n_1 = 6$, $n_2 = 6$, $U = 36$, $P = 0.002$). This relationship showed a significant and negative correlation (Spearman’s ρ correlation, $\rho = -0.917$, $P < 0.01$), which showed the tendency of communities composed by highest number of species to have a smaller number of individuals per taxon.

The temporal contribution of each taxon on community composition (TS^*), for example, the presence of rare (present only occasionally with low abundances) or extremely specialized taxa (present in well-defined temporal snapshots with high abundances), varied among the pools (Kruskal–Wallis one-way ANOVA, $H = 11.203$, $P < 0.05$). Communities composed by a smaller number of taxa (P3, P4 and P6 in Fig. 2) were characterized by higher values and greater variability of TS^* compared to communities with greater number of taxa (P1, P2 and P5 in Fig. 2), which might be explained by differences in the temporal distribution of macroinvertebrates within the communities.

The modular structure of empirical network did not differ from the mean modularity of simulated networks under null model 1 ($Q_{\text{real}} = 0.397$, $Q_{\text{sim1}} = 0.377 \pm 0.108$, $P = 0.255$), while had a modular structure significantly higher than the mean modularity of random networks under null model 2 ($Q_{\text{real}} = 0.397$, $Q_{\text{sim2}} = 0.349 \pm 0.078$, $P < 0.01$). Pools and taxa belonged to three different modules, maximizing the number of internal links and minimizing the number of links among other modules (Table 2). These results are consistent with previous analyses (Bellisario et al. 2010), although differing in the membership of sampled macroinvertebrates to different modules. The dispersion of TS^* values (measured as the variance to ratio of mean, VRM) showed different patterns among modules (Table 2), where modules Q_1 and Q_2 had higher VRM values than module Q_3 and, therefore, higher variance of TS^* .

We found a significant difference between the decomposition rates in different pools (Kruskal–Wallis one-way ANOVA, $H = 24.18$, $P < 0.001$), which also differed in the amount of final dry weight of leaf detritus, FDW (Table 2). Considering the modular structure, this resulted in a different distribution of the average amount of persisting resource in the three identified modules, with about 61 % of unconsumed resource in module Q_1 and only 25 % in module Q_3 . The hierarchical clustering showed the partitioning of

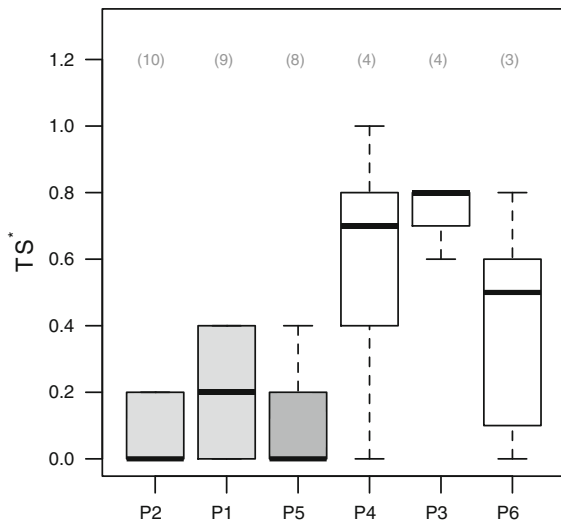


Fig. 2 Boxplots showing the distribution of TS^* values within the pools. The horizontal line dividing boxes in two indicates the median, box limits are the first and third quartiles of the distribution, and whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box. Boxplots are ordered following the decreasing number of sampled taxa (light gray numbers in parentheses). Colors indicate the membership of sampled pools to the identified modules: light gray, Q_2 ; dark gray, Q_3 ; white, Q_1

the pools in three ‘functional’ clusters, given by similarities in the rate of decomposition of *P. australis* leaf detritus. Therefore, sites that had no significant differences in the macrodetritivores activity throughout the sampling period belonged to the same clusters (Fig. 3a), as well as sites that experienced the same environmental conditions during the sampling period (Fig. 3b).

The clustering of the pools, based on convergent traits of decomposition and environmental variability, revealed the correspondence with the modular structure of the network (Fig. 3a, b). Indeed, we did not observe significant differences between the number of modules in which the network was divided under null model 1 and the clusters subdivision based on decomposition rates (Mann–Whitney U -test, $n_1 = 1000$, $n_2 = 1,000$, $U > 5 \cdot 10^5$, $P = 0.709$) and on the variation of environmental parameters (Mann–Whitney U -test, $n_1 = 1,000$, $n_2 = 1,000$, $U > 4 \cdot 10^5$, $P = 0.143$). Furthermore, under null model 1, the modular and cluster subdivision of the pools perfectly overlapped in more than 95 % of cases. Together, these results indicated the relationship between network structure and functioning. Modules composed by more specialized taxa showed highest consumption rates of leaf detritus (Table 2), which did not show a significant correlation neither with the total number of sampled taxa (Spearman’s ρ correlation, $\rho = 0.753$, $P = 0.083$), nor with their abundances (Spearman’s ρ correlation, $\rho = -0.771$, $P = 0.105$).

Discussion

In this work, we showed the intimate linkage between the structure and functioning of complex networks. The modular structure of the network is related to a different use of the detrital resource by macroinvertebrates, on account of the different responses of invertebrate’s populations to different habitat conditions. Therefore, the structure of the network shapes its

Table 2 Structural parameters of observed modules and functional characteristics of the pools

Module	Sampling sites	P	S	L_{in}	L_{out}	k_d (day $^{-1}$)	FDW (%)	VRM
Q_1	P3	3	3	8	6	0.0008 ± 0.0004	56.53	1.600
	P4					0.0007 ± 0.0003	49.60	
	P6					0.0003 ± 0.00001	78.70	
Q_2	P1	2	9	14	2	0.0022 ± 0.0003	31.88	1.142
	P2					0.0019 ± 0.0003	34.38	
Q_3	P5	1	6	6	2	0.0031 ± 0.0003	25.43	0.200

Q identified modules, P number of pools within a module, S number of sampled taxa within a module, L_{in} number of within module links, L_{out} number of outgoing links, k_d estimated coefficient of decomposition given by the consumption of the detrital resource by macroinvertebrates (mean \pm SD), FDW final dry weight of leaf litter detritus, expressed as the percentage of initial dry mass, VRM variance to ratio of mean of temporal specialization, TS^*

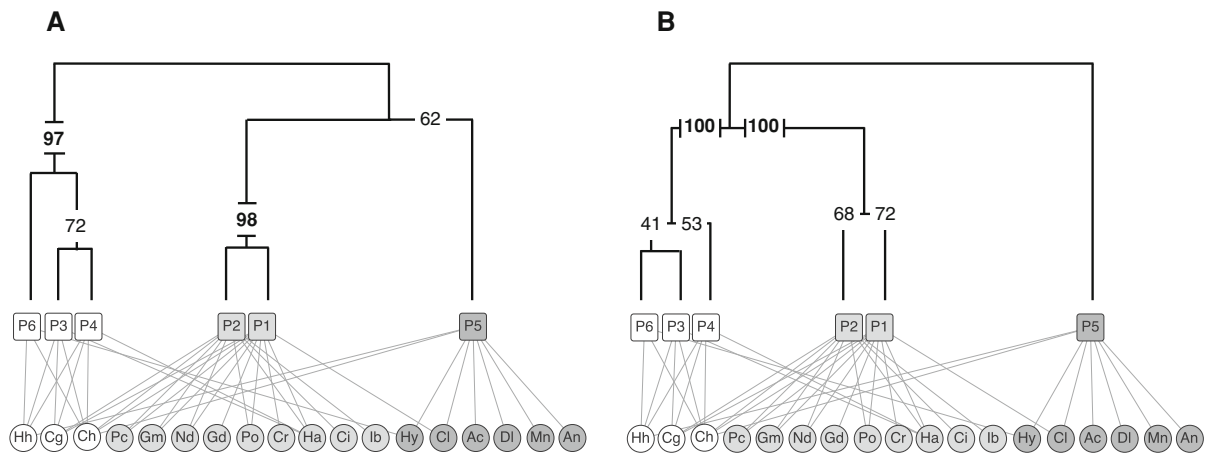


Fig. 3 Relationship between the modular structure of the network and the clustering of the pools based on convergent traits in decomposition rates, **a**, and variations in the main chemical-physical parameters, **b**. Circles are for sampled taxa and round rectangles for pools. Colors indicate the identified modules: white, Q_1 ; light gray, Q_2 ; dark gray, Q_3 . Numbers on the branches are the P -values of cutting, where **bolded values** ≥ 95 indicate an approximately significance of 0.05. *Taxa legend*

Ch, *Chironomus* spp. (larvae); Gm, *Gammarus aequicauda*; Pc, *Perinereis cultrifera*; Gd, *Gordius* sp.; Ha, *Hydrobia acuta*; Cg, *Cerastoderma glaucum*; Cr, *Cerithium rupestre*; Dl (other) Diptera (larvae); Ci, *Corophium insidiosum*; Ib, *Idotea baltica*; Ac, *Acilius* sp. (larvae); Hy, *Hydrophilus* sp.; Cl (other) Coleoptera (larvae); Nd, *Nereis diversicolor*; Sd, *Spio decoratus*; Hh, *Haliplus* sp.; Mn, *Micronecta* sp. (larvae); An, Anisoptera (nymphae)

functional architecture, decreasing the spatial similarity of leaf litter decomposition over time.

Modularity (or compartmentalization) is thought to be a common property in many ecological networks (Olesen et al. 2007) and relies on the concept that modules are structured because of the highest probability of interactions between species (Krause et al. 2003; Olesen et al. 2007) or because of common patterns of co-occurrence within habitats (Fortuna et al. 2009). The mechanisms behind network compartmentalization have been largely explored over a variety of different systems (Olesen et al. 2007; Fortuna et al. 2009; Guimerà et al. 2010; Mello et al. 2011), pinpointing its importance for the robustness against perturbations (Stouffer and Bascompte 2011).

However, the role of topology in explaining some functional aspects of ecological networks is seldom explored (but see Gómez et al. 2011). Regardless the type, nodes within a network always ‘do something,’ and the way with which they are assembled and the mechanisms underlying their topological structures influence the way with which specific functions are discharged. Recently, Gómez et al. (2011) have found how several network properties are associated with variation across populations in the average per-capita production of juvenile plants in network of mutualists, observing how changes in topological attributes

may drive major consequences for plant population performance.

Different mechanisms may be involved in explaining the functional consequences of modularity, including spatial patterns and trophic preferences. The spatial configuration of the sampling sites (e.g., connectivity, Bellisario et al. 2011) may create contrasting environmental conditions, driving the selection of invertebrates able to colonize the detrital resource in different sites. Moreover, in aquatic ecosystems, detritus shows a kind of temporal partition, undergoing a series of transformation following a particular dynamic in which it is subdivided into different fractions based on its dimensional classification in dynamic equilibrium (Cummins and Klug 1979). This transformation is due to the main mechanisms of decomposition dynamic, including the leaching of more soluble constituent and the microbial/fungal colonization, which help the macrodetritivores activity by altering the structural and chemical-physical characteristics of the resource (Lecerf et al. 2005). As a consequence, macrodetritivores in aquatic environments are often classified on the basis of their feeding habits, and then on the use they make of the available detrital fraction (FFG, functional feeding groups, Cummins and Klug 1979). Habitat selection, mostly driven by spatial patterns, can then influence

the topological architecture of the network, suggesting the role of individual response of macroinvertebrates to different and variable environmental conditions.

This reflects the functional partition of the system, with pools experiencing the same variation in macrodetritivores activity belonging to the same modules. The presence of a narrow pool of extremely generalist taxa may then reduce the performance in the use of leaf litter resource (i.e., the rate at which the leaf litter is consumed by macroinvertebrates), reducing the fraction of available detritus used by detritivores and potentially increasing the competition for the use thereof with few, abundant taxa competing for the same resource fraction. This is also suggested by the consistent fraction of leaf detritus accumulated in all sampling sites, whatever the number, abundance and the degree of specialization/generalism.

Modularity is often associated with the ability of a system to resist the spread of disturbances, increasing the robustness against perturbations. The results obtained in this work showed further interesting aspect when considering the modular architecture of a network, that is, the ability to increase the degree of functional diversity within ecosystems. Modularity may enhance the spatial difference of functional activity, as well as the diversity of functional traits among detritus feeder, with positive, long-term effects on the decomposition of leaf litter (Scherer-Lorenzen 2008). Therefore, modularity may have important consequences for the functional stability of the network, decreasing the spatial similarity of leaf litter decomposition over time (i.e., the so-called functional homogenization, Clavel et al. 2011).

This arises from the ability of a modular structure to increase the variability of communities' responses facing disturbances, decreasing the synchronization between connected communities and increasing potential landscape and regional buffering (Olden 2006). The degree of nodes organization into densely connected modules is a direct consequence of a series of different—often concurrent—causes, such as high probability of interaction between species or common patterns of co-occurrence within habitats or resources. Here, we showed how the underlying mechanisms of modules formation could arise from the different responses of macroinvertebrates to different local environmental conditions. Modularity can then influence the functional stability of the system by mediating the complementary in patterns of niche

occupation (sensu Grinnell 1917), increasing the average rates of decomposition.

However, other issues not explicitly investigated in this work, as the temporal diet shift, omnivores, predation and facilitation need to be incorporated for a deeper understanding of the functional consequences of network structure. For instance, Lepoint et al. (2006) found how two dominant detritivores species of *Posidonia oceanica* leaf litter, *Gammarella fucicola* Leach and *Gammarus aequicauda* Martynov, display in reality relatively different diets, showing that a certain degree of trophic diversity may exist among the detritivore community of the seagrass litter. Again, most invertebrates are not restricted to a single feeding mode. Factors including larval size, maturity, food quality, sediment composition and seasonal or environmental change can influence their feeding behavior.

This opens new and intriguing questions about the relationship between network structure and functioning. The use of modern molecular techniques (reviewed in Valentini et al. 2009) proved, for instance, useful information about the feeding ecology of the organisms in a variety of different systems, including freshwater ecosystems (Corse et al. 2010) and insect–host plant associations (Jurado-Rivera et al. 2009), potentially opening new perspective in ecological network analysis.

A clear understanding of the interplay between the functional structure of ecological communities and ecosystem functioning is crucial (Mouillot et al. 2011). The evolutionary trajectories of the organisms involved in the colonization of dead organic matter may alter the type and strength of interactions, which can translate into diversity effects on litter decomposition (Gessner et al. 2010). It follows the importance to disentangle the effect of different types of interactions for the persistence and functioning of ecological communities. Our findings could have also far reaching consequences from a conservation point of view, suggesting the need to maintain a certain degree of spatial heterogeneity through an active water management. Spatial heterogeneity may increase the diversification of the habitats and, therefore, the potential landscape and regional buffering, potentially enhancing biodiversity with positive, long-term effect on the whole food web.

Acknowledgments We wish to thank the State Forestry Department for access to the sampling sites within the Natural

Reserve of Tarquinia Saltern. We are also in debt with the handling editor and two anonymous referees, whose constructive comments and suggestions greatly improved the manuscript.

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