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RESEARCH ARTICLE

# Evaluating nestedness in a spatially structured detritus-based systems

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## Abstract

1 - Evaluating patterns and mechanisms behind species aggregation represents a fundamental issue in community and conservation ecology.

2 - The extent to which species colonize or disappear from habitats and resources is mostly related to several different factors, such as random processes of birth, death and migration, or complementarity in species responses to environmental disturbances, habitat heterogeneity or spatial distributions.

3 - Patterns of species aggregation can be evaluated by considering the network structure of such assemblages, where the use of ad-hoc null-models could help our understanding of the mechanisms underlying these structures.

4 - Here we evaluated the possible mechanisms underlying the nested assemblage of macroinvertebrates on leaf detritus in different sites of the transitional ecosystem of Tarquinia saltern, by using quantitative networks based on the abundances and frequencies of sampled taxa.

5 - Our results show that the use of quantitative information is able to closely mimic the pattern of incidence observed in the real network, with important outcomes for ecosystem's functionality and its conservation.

**Keywords:** Detritus; macroinvertebrates; patches; network; nestedness.

## Introduction

In small-fragmented areas, species experience environmental variations at small spatial and temporal scales, influencing the pattern of occurrence within patches (Wiens, 1989). Species may differ in their temporal occurrence, with some species occurring only few times and others more frequently, differing at the same time in terms of abundance, with species more locally abundant than others. However, real communities may represent a *continuum* of such aggregation, and a proper evaluation of different colonization mechanisms in promoting nestedness is crucial, also for ecosystem functioning.

We have developed this theoretical and conceptual framework to evaluate the role of multiple determinants in the nested structure of macroinvertebrates on leaf detritus, under different and variable environmental conditions. To date, only few studies have attempted to study the nested structure in detritus-based systems (Yee and Yee, 2007; Bellisario *et al.*, 2010), revealing the importance of habitat quality/heterogeneity and detritus level for the observed community assemblage, and suggesting the

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role of nestedness for species diversity and ecological functioning (Petrin *et al.*, 2008).

Here we use data on the colonization of *Phragmites australis* (Cav.) Trin ex Steud. leaf detritus in a patchy environment. We first defined different probability matrices to mimic the pattern of incidence of macroinvertebrates on leaf detritus, and then compared the likelihood of different determinants to match the nested structure of real dataset. We finally compared the nested structure with the rate at which the leaf detritus was decomposed by macroinvertebrates in different habitats, to look for a correspondence between nestedness and decomposition.

Here we show the importance of considering the jointly effect of multiple determinants in the network structure of detritus-based systems and discuss the causes and consequences of species aggregation for the functional process, also from a conservation point of view.

## Materials and methods

### *Study area and field experiment*

The study area is the aquatic ecosystem of Tarquinia saltern, a transitional artificial environment (central Italy, 42°12' N, 11°43' E), composed by a series of pools whose connection is ensured by a drainage system surrounding the pools, and where the exchange of waters is provided by a single connection with the sea located north of the area (Fig. 1). Isolation and hydrological connectivity give rise to a wide salinity gradient (Bellisario *et al.*, 2010), spanning from hypo-saline (mean annual salinity 8.5 $gL^{-1}$) to hyper-saline waters (mean annual salinity more than 100 $gL^{-1}$).

We chose six sampling sites in the area, covering the full spectrum of salinity variation, to perform a colonization experiment of *Phragmites australis* (Cav.) Trin. ex Steud. leaf detritus under different environmental conditions. We placed 48 protected (mesh size: 5 x 5 mm) and 48 unprotected (mesh size: 10 x 10 mm) leaf packs in each pool and measured, on a monthly sampling with $r = 4$ replicates: i) the number of colonizing taxa, ii) the number of individuals for each taxon (number of individuals per gram leaf pack dry weight, expressed as means with $r = 4$ replicate), iii) the frequency of colonization and, iv) the dry weight loss of leaf detritus in both protected and unprotected leaf packs, after storing at 60°C for at least 72 h (leaf pack weight: 2.000 ± 0.004 g dry mass).

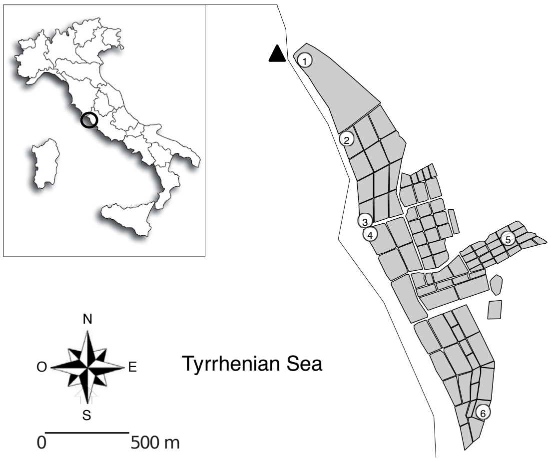

Figure 1. Tarquinia saltern (central Italy, 42°12' N, 11°43' E). Sketch of the study area with sampling sites (white circles) and black triangle representing the point of water refill. Mean (± SD) annual salinity values: 1 = 44.8 ± 2.63 $gL^{-1}$; 2 = 50 ± 2.84 $gL^{-1}$; 3 = 88 ± 5.60 $gL^{-1}$; 4 = 100 ± 7.09 $gL^{-1}$; 5 = 8.5 ± 2.45 $gL^{-1}$; 6 = 115 ± 16.62 $gL^{-1}$.

Starting from the dry weight loss of leaf detritus we also measured the decomposition rate following the negative exponential model of Olson (1963), $k = (\ln W_t - \ln W_0)/t$, where $W_t$ is the dry weight of remaining leaf detritus at time $t$ (expressed in days, $d^{-1}$) and $W_0$ the initial dry weight. The total decomposition rate ($k_t$), given by the jointly effect of leaching, microbial and fungal conditioning and macrodetritivores activity, was measured by the weight loss of leaf detritus in unprotected leaf packs. Moreover, we measured the effect of leaching and microbial and fungal conditioning by the loss of leaf dry mass in protected leaf packs. As a consequence, the macrodetritivores activity ($k_d$) was assumed to be $k_d = k_t - k_l$.

### *Determinants of macroinvertebrates assemblage on leaf detritus*

The starting hypothesis was that species with greater niche breadths are both more locally abundant and more widely distributed than species with narrower environmental niche breadths (Brown, 1984), assuming that variability in colonization ability among species is not an impediment to dispersing to and establishing in areas with appropriate environmental niches.

The pattern of association between macroinvertebrates and leaf detritus in different pools was drawn as a bipartite network, where links have been established between two distinct set of nodes, taxa and substrates in different pools, but not between nodes of the same set. Hereafter, we use the word 'pools' as reference term to indicate the unprotected leaf packs in different sites. The pattern of incidence of macroinvertebrates on leaf detritus can be described by a probability matrix **M**, whose incidences could be determined by different explanatory variables, such as the relative species abundance (**N**) and the frequency of colonization (**F**).

The frequency of colonization has been defined as the frequency with which a generic taxon colonized each pool during the field experiment

$$f = \sum_{i=1}^{T} i_i^P / T \qquad (1)$$

with $i_i^P$ the number of observed colonization of taxon $i$ on pool $P$, and $T$ the total time of experiment. Given this formulation, a value of $f = 1$ was assigned if a given taxon was found in a pool every sampling.

We also defined the colonization ability (hereafter $c_A$) as a measure dependent on both species abundance and their frequencies of colonization, $c_A = f(n_{ij}, f_{ij})$, with $n_{ij}$ and $f_{ij}$ the abundance and the frequency of colonization of taxon $i$ in pool $j$, respectively. Thus, $c_A$ measures to what extent the abundances (log-transformed to account for a skewed distribution in the number of individuals *per* taxa) and the proportional use of the spatial resource influence the distribution of taxa on a patchy environment.

### *Calculation of the incidence probability matrices*

Abundances, frequencies of colonization and colonization ability were used to derive three different incidence probability matrices, $\mathbf{N} = [n_{ij}]$, $\mathbf{F} = [f_{ij}]$ and $\mathbf{CA} = [n_{ij}f_{ij}]$. The probability of incidence was drawing as the evenness of quantitative information within the matrix (Albrecht *et al.*, 2007; Bluetghen *et al.*, 2008), which quantifies the dominance structure of incidences between macroinvertebrates and pools.

Let $x_{ij}$ be the quantitative information describing the incidence of the $i^{\text{th}}$ taxon on the $j^{\text{th}}$ pool, then the heterogeneity of quantitative information on rows ($p_r$) and columns ($p_c$) can be described, respectively, by:

$$\begin{aligned} p_r &= -\sum_{j=1}^{P}[(x_{ij}/X_{ij})\ln(x_{ij}/X_{ij})] \Big/ \ln\sum_{j=1}^{P} x_{ij} \\ p_c &= -\sum_{i=1}^{S}[(x_{ij}/X_{ij})\ln(x_{ij}/X_{ij})] \Big/ \ln\sum_{i=1}^{S} x_{ij} \end{aligned} \qquad (2)$$

with $X_{ij} = \sum_{i=1}^{S}\sum_{j=1}^{P} x_{ij}$ .

Recently, a great contribute in studying the complexity of species composition within habitats was given by considering the network structure and properties of such aggregations (Fortuna *et al.*, 2006, 2009). Differences in dispersal ability, tolerance to stress, niche width and competitive ability, among many, are thought to influence the dynamics of colonization/extinction processes and, ultimately, the distribution of species across space (Vázquez and Simberloff, 2002; Azeria *et al.*, 2006). Nested analysis can potentially indicate the mechanisms underlying the structuring of ecological communities, and whether certain species in a fragmented system are likely to colonize new areas or face extinction. A nested pattern emerges when species found in progressively richer assemblages form a series of subsets (Atmar and Patterson, 1993), indicating the tendency of specialized species to colonize a subset of sites with more generalized species. Several mechanisms can cause nestedness, such as passive sampling (Higgins *et al.*, 2006), selective extinction and colonization (Simberloff and Levin, 1985) or habitat nestedness (Honnay *et al.*, 1999). All of these can be defined as probabilistic filters (Mc Abendroth *et al.*, 2005), and different circumstances might determine whether or not one or more filters will produce a consistent ordering of species across sites (Stiles and Scheiner, 2008). Although a common tendency in nested analysis is to disentangle and prioritize the effects of all involved mechanisms, most of them show the tendency of an intimate linkage (Ulrich *et al.*, 2009), and only few studies have combined them simultaneously to examine their roles in generating nestedness (Schouten *et al.*, 2007).

This formulation then considers the probability of drawn a connection (i.e. the incidence) as a measure depending on the amount of homogeneity/heterogeneity in the distribution of quantitative information among rows and columns. Evenness approaches 0 for the most heterogeneous distribution and 1 for a perfectly homogenous distribution. A value of $p_r \rightarrow 1$ implies a homogenous distribution of taxa within all the pools, indicating a greater probability of incidence. The same occurs for $p_c \rightarrow 1$, where a greater probability of incidence is given for an even distribution of taxa within a given pool.

We also defined a further probability matrix, named **Null**, as a benchmark null model for comparison with other probability matrices. In **Null** matrix all pairwise incidences had the same probability, $1/SP$, of occurrence, where $S$ and $P$ are the number of taxa and pools in the network. For all matrices (**N**, **F**, **CA** and **Null**) we imposed only one constraint based on matrix dimension, that is, the size of the original matrix ($S$ x $P$) must be the same of the original one.

### *Evaluating nestedness and likelihood of incidences*

Nestedness is commonly defined in terms of matrix temperature $T$, giving a measure of disorder in the observed matrix, where low temperatures indicate nestedness (Atmar and Patterson, 1993). The common procedure to find $T$ starts with the reordering of rows and columns leading for the minimum matrix temperature of given size and fills. $T$ is hence derived as the ratio of sum of squared deviations from the isocline of a maximally packed matrix of unexpected presences/absences and the maximum possible value for an interaction matrix (Atmar and Patterson, 1993).

However, the observed inconsistencies found in matrix temperature are associated with two basic properties derived from the concept of nestedness: decreasing marginal totals, and paired overlaps (Almeida-Neto *et al.*, 2008). To overcome these flaws in the estimation of nestedness, we chose to use a metric based on overlap and decreasing fill, NODF (Almeida-Neto *et al.*, 2008). This metric calculates nestedness independently among rows and among columns, which allows evaluating nestedness only among sites (i.e. species composition) or only among species (i.e., species occupancy), varying from 0 (random assemblage) to 100 (perfectly nested assemblage). Therefore, NODF considers matrix row and column fill differences, as well as the overlap of row and column presences. Nestedness was measured on 1,000 replicates of each probability matrix and compared with those of the original incidence matrix.

To evaluate the ability of each probability function to replicate the incidences of the original matrix, we used the methodology introduced by Vazquez *et al*. (2009) based on the likelihood analysis $\mathbf{L}_l$ of pairwise interaction probabilities (in our case the incidence) based on multinomial distribution. As in the work of Vazquez *et al*. (2009), we used the Akaike's Information Criterion, $AIC = \mathbf{L}_l - 2\varphi$, to measure the contribute of each involved parameter $\varphi$ to generate a particular probability matrix; thus, probability matrices **N** and **F** has one parameter and **CA** two parameters. The evidence for each alternative model m can be determined by evaluating the difference between model AIC and the minimum AIC, $\Delta_m = AIC_m - \min(AIC)$, with min(AIC) as the best model given by fitting the incidence matrix by itself (Vazquez *et al*., 2009). The larger the $\Delta_m$, the smaller the likelihood of that model being the best model in the set of candidate models considered. Models having $\Delta_m \leq 2$ can be considered as having substantial support as candidate models (Burnham and Anderson, 2002). We finally compared the ranking of sites derived from NODF measured for each probability matrix and real dataset with the ranking yielded by the macrodetritivores activity, to look for a correspondence between nestedness and decomposition.

## Results

During the field experiment, we sampled a total of 2,406 individuals distributed on 18 taxa of macroinvertebrates that have colonized the leaf packs in the six pools (Table 1). Abundances and frequencies of colonization showed a skewed distribution, with few taxa occurring up to 50% of times with high abundances and the bulk of taxa occurring less than 20% of times with low abundances (Fig. 2). We found a significant correlation between these two variables (Spearman's $\rho$ correlation: $\rho = 0.92$, $P < 0.01$), showing that the most frequent colonizers were also those with highest abundances (Fig. 2).

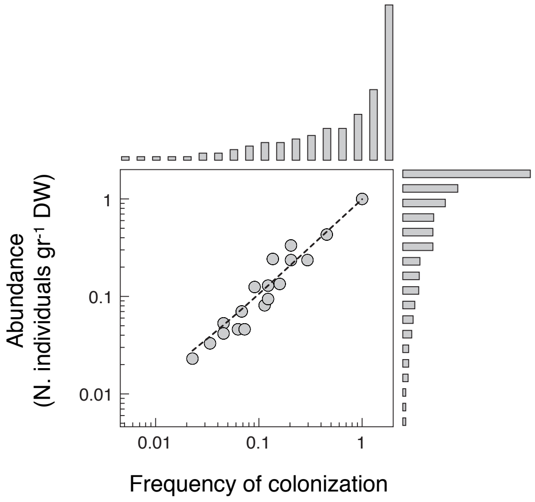

Figure 2. The abundances (histograms on the right panel) and frequencies of colonization (histograms on the upper panel) show a skewed distribution, with the bulk of taxa occurring few times with low abundances. The best-fit model is given by a power-law relationship (dashed line in the central log-log panel), which shows the tendency of the most common taxa to occur with high abundances.

Abundances (**N**) and frequencies of colonization (**F**), alone, did not predict the nested pattern of observed network, overestimating and underestimating, respectively, the pattern of incidence of macroinvertebrates on leaf detritus (Fig. 3). Conversely, we found how the mixed-probability function given by the colonization ability (**CA**) showed a very similar value as the original one, whose confidence intervals included observed values of nestedness (Fig. 3). Here we would expected that if a model was

Table 1 - Incidence matrix. Entries represent the association between taxa (on rows) and sampling sites (on columns).

| | | Pool1 | Pool2 | Pool3 | Pool4 | Pool5 | Pool6 |
|---|---|---|---|---|---|---|---|
| Detritivores | *Chironomus* spp. (larvae) | 1 | 1 | 1 | 1 | 1 | 1 |
| | *Gammarus aequicauda* | 1 | 1 | | | | |
| | *Perinereis cultrifera* | 1 | 1 | | | | |
| | Gordiidae | 1 | | | | | |
| | *Hydrobia acuta* | 1 | 1 | 1 | 1 | | |
| | *Cerastoderma glaucum* | 1 | 1 | 1 | 1 | | |
| | *Cerithium rupestre* | 1 | | | | | |
| | (other) Diptera (larvae) | | 1 | | | 1 | |
| | *Corophium insidiosum* | | 1 | | | | |
| | *Idotea baltica* | | 1 | | | | |
| Predators | Dytiscidae | | | | | 1 | |
| | *Hydrophilus* sp | | | | | 1 | 1 |
| | (other) Coleoptera (larvae) | 1 | | | | 1 | |
| | *Nereis diversicolor* | 1 | 1 | | | | |
| | *Spio decoratus* | | 1 | | | | |
| | *Haliplus* sp. | | | 1 | 1 | 1 | 1 |
| | *Micronecta* sp. (larvae) | | | | | 1 | |
| | Anisoptera (nymphae) | | | | | 1 | |

able to closely match the nested structure of observed network, this would have to replicate more accurately the incidence of macroinvertebrates on leaf detritus. Taking both the abundances and the frequencies of colonization as reference model, the combined probability matrix **CA** had the lowest $\Delta$AIC, with a difference with the next best fitting probability matrix **N** of 6.802, and of 108.081 with **Null** (Fig. 4). Although significant, the small differences between models, and the high differences between models and the perfect fit given by a $\Delta$AIC value of 0, suggest that abundances and frequencies of colonization, alone, was by no mean sufficient to predict the nested structure of macroinvertebrates on leaf detritus. The ranking of pools yielded by NODF in real dataset match significantly the ranking given by $k_d$ (Spearman's $\rho$ correlation: $\rho = 0.83$, P = 0.041), which showed the relationship of a nested structure with the rate at which the leaf detritus was decomposed by macrodetritivores in different pools (Fig. 5). However, the non-significant association between the rankings of nestedness yielded

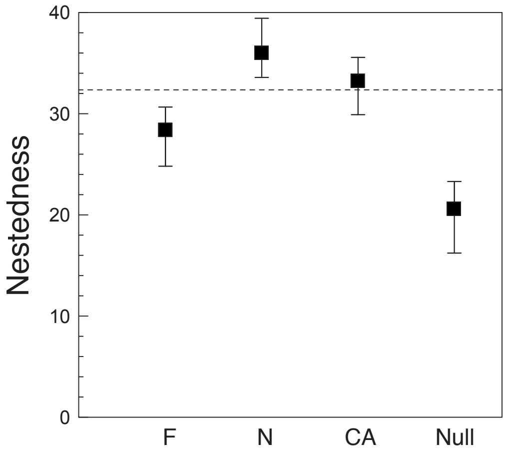

Figure 3 - Comparison between observed nestedness (horizontal dashed line) and that predicted by different probability matrices, with error bars indicating 95% confidence intervals. Results are shown for 1,000 replicates of each probability matrix based on frequencies of colonization (**F**), abundances (**N**), colonization ability (**CA**), and null probability matrix (**Null**) with homogeneous incidence probability.

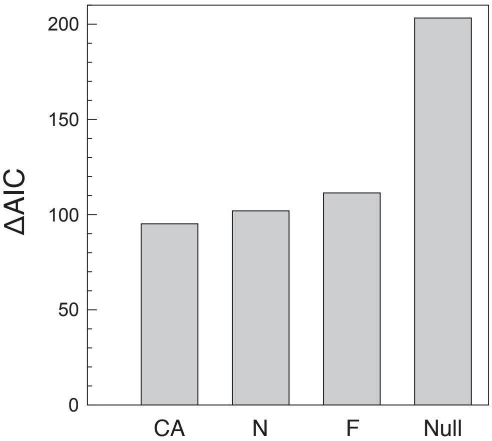

Figure 4 - Likelihood analysis of incidence probabilities showing the ΔAIC for each model. The probability of incidence was designed as a function of the colonization ability given by: i) the aggregate effect of abundances and frequencies of colonization (**CA**), ii) abundances (**N**) and, iii) frequencies of colonization, (**F**). **Null** represents the reference null-model with homogenous incidence probability.

by the probability matrices with $k_d$ (Fig. 5), again suggested how, although **CA** was found to be the best model able to describe the pattern of incidence of macroinvertebrates on leaf detritus, some others determinants should be incorporated for an accurate prediction of the amount of unexplained variation.

## Discussion

Evaluating determinants in the assemblage of ecological communities represents a key issue for understanding the ecological, functional and evolutive implications of such structures (Strauss and Irwin, 2004). Differences in the traits of taxa, such as dispersal ability, niche width and competitive ability among others are likely to translate into differences in their distribution across space (Vázquez and Simberloff, 2002; Azeria *et al.*, 2006). These may arise from the dispersal of populations among patches or from the dependence of all population dynamics on some common environmental 'noise'. In real ecosystems, all communities are subjected to fluctuations in their environment, observing a general synchronization of the species in their responses. This is often related to a correlation between changes in the abundances of different populations in different patches (Leibold *et al.*, 2004), able to influence the pattern of colonization/extinction and, ultimately, nestedness.

Nestedness reflects a consistent hierarchy in species likelihood of occurrence across sites (Wright *et al.*, 1998), resulting from predictability in extinction/colonization order among species; i.e., certain species could be more extinction-prone and others more extinction resistant (Patterson and Atmar, 1986). Several hypotheses on what determines a nested structure in ecological communities have been formulated, including habitat nestedness (Honnay *et al.*, 1999), selective extinction (Lomolino, 1996), or

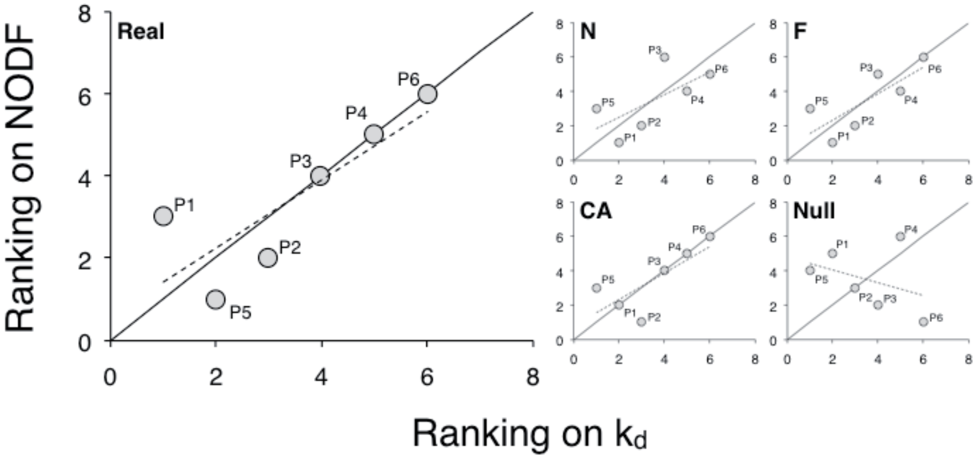

Figure 5 - Comparison between the ranking yielded by NODF and the decomposition rates given by the macroinvertebrates activity ($k_d$), where sites are ranked following a decreasing order of nestedness and $k_d$. Solid line represents the line of a perfect correlation and dashed line the linear correlation for real dataset and for different probability matrices, with the probability matrix based on colonization ability (**CA**) showing quite similar values of ranking with Real dataset.

abundance bias, a natural tendency of the unequal species abundance in the ecosystems (Vázquez and Aizen, 2004). More recently, the co-evolutionary history and phylogenetic signals between species have been found to explain the nested pattern in networks of interacting species (Rezende *et al.*, 2007). Network analysis represents a fascinating way of describing the structure of ecological systems, in which species and habitats may be depicted as nodes, and a particular kind of association between nodes as links that describe the pattern of species incidence within habitats (Bunn *et al.*, 2000; Urban and Keitt, 2001; Fagan, 2002). Some specific mechanisms in species-specific responses posit that patterns of assemblage could result from additional constraints imposed by specific processes (e.g. neutrality), and this might be given by the complementarity in species responses to environmental disturbances (Fleishman *et al.*, 2006), habitat heterogeneity or spatial distributions (Fisher and Lindenmayer, 2005). Moreover, the observed patterns may change through time because of local extinction and colonization of species, often related to changes in abiotic factors such as climatic fluctuations (Alarcón *et al.*, 2008), suggesting how a nested ordering of species and sites should condense long-term dynamics of metacommunities (Azeria and Kolasa, 2008).Our results have shown how, nor the abundances neither the frequencies of colonization, alone, are able to describe the observed pattern of incidence, suggesting the role of habitat heterogeneity in mediating some species-specific traits (i.e. colonization ability and other unknown determinants) on neutral processes of network assembly (abundance-based probability of incidence). Here we posit the importance of spatial-temporal processes in combination with the ability of species to distribute among habitat patches (Schouten *et al.*, 2007). In fragmented areas, the probability of colonization decreases with increasing isolation and limited dispersal of species (Cook and Quinn, 1995), reducing the exchange capacity between patches. Furthermore, the increasing

isolation of patches within a system could determine local variability in environmental conditions, increasing habitat heterogeneity. Given our results, we suggest the role of isolation in promoting different and variable environmental conditions within the pools (e.g. fluctuations in the level of salinity), which might allows species to selectively colonize different environments (the habitat nestedness hypothesis, Honnay *et al.*, 1999). Thus, the abundances, coupled with synchronous and asynchronous colonization dynamics may result from the local adaptation of species with limited dispersal to changing environmental conditions, particularly when species experience environmental variations at small spatial and temporal scales (a typical situation in transitional aquatic ecosystems).
Although significant, the nested pattern observed in real dataset (and in its probabilistic counterparts) is far from a perfect nested assemblage. A perfect nested structure is often unusual in real ecosystems, with many unexpected presences/absences in species by sites matrices. Several features have been advocated to explain this pattern, such as different responses of species to fragmentation and sampling bias (Fisher and Lindenmayer, 2005). The low nestedness in our study system was most likely a consequence of the number of idiosyncratic species (Atmar and Patterson, 1993), suggesting the pivotal role of disturbance (e.g. fluctuations in the level of salinity within the pools) in influencing the degree of nestedness (Bloch *et al.*, 2007). Indeed, the high level of idiosyncrasy in our system may derive by the presence of well-defined temporal conditions for colonization, given by the environmental fluctuations, which allow the colonization of species otherwise absent.

The order with which species colonize or disappear from a system is also thought to influence the level or rate of key ecosystem properties and functions (Balvanera *et al.*, 2006), suggesting the importance of considering the extinction/colonization order (and therefore nestedness) in explaining the functional consequences of community level processes (Fukami *et al.*, 2010). Correlation between the nested order of sites and decomposition may be due to differences in the colonization and local extinction of macroinvertebrates on leaf detritus. In a perfectly nested matrix, taxa with low **CA** colonize a subset of sites colonized by taxa with high **CA**, and this tendency reflects a more heterogeneous distribution of the abundances and spatial-temporal overlap between species. The significant correlation between the ranking of pools yielded by NODF and $k_d$ illustrates this tendency, where sites with lowest decomposition activities are those colonized by few taxa with similar values of **CA**, which might increase the probability of overlap between species enhancing the effect of interspecific interactions and reducing the efficiency in the use of resource.

Although significant, the colonization ability mediated by habitat heterogeneity cannot be advocated as unique determinant. The amount of unexplained variation could be a consequence of several other factors, such as the degree of microbial and fungal conditioning and the presence of predators, which might influence the complexity of detritus trophic web and its functionality (Gessner *et al.*, 2010). Species interactions are found to be of great influence on decomposition dynamics, suggesting how the richness–functioning relationship may be driven by direct (e.g. abundances) and indirect (e.g. interspecific interactions) mechanisms (Dangles and Malmqvist, 2004). Interferences among taxa have been suggested to regulate the dynamics between trophic levels (Wardle and Yeates, 1993), and the increased trophic complexity will potentially influence the consumption rate by detritivores (Moore *et al.*, 2004).

Regardless of the type of interference among taxa, strong interactions, coupled with variable colonization ability, have the potential to cause multiple trajectories in the structure of detritus-based communities and, consequently, the decomposition of leaf detritus.

Understanding the causes that shape ecological communities may have also important outcomes from a management point of view, especially when deciding the proper management strategies in conservation efforts. Nestedness has been shown to buffer against perturbations, such as habitat loss (Fortuna and Bascompte, 2006), or more generally environmental variability, able to condense the dynamics of metacommunities (Azeria *et al.*, 2006). Here we have shown how a nested structure is likely to condense the dynamic of functional process, and this might give rise important outcomes for the relationship between community's structure and functioning. The maintenance of habitat heterogeneity in small-fragmented areas should be a key conservation strategy, since a decreasing nested structure could be a signal of increasing homogenization of local patches. This could increase the extirpation rates via intensified species-specific interactions, involving the replacement of specialists by the same widespread generalists with long-term effects on the whole system functioning. Thus, to the aim of conservation are of great importance a proper understanding of the causes that shape ecological communities and the functional consequences of such aggregations.

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