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- XXII CICLO -

Ecofunctionality in artificial aquatic ecosystem: linking abiotic dynamics to community stability

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TALKS

Bruno Bellisario, Fulvio Cerfolli, Giuseppe Nascetti - *Leaf detritus colonization in a patchy environment: the spatial structure of detritus-based communities in Tarquinia saltern* – 3rd Italian Conference on Lagoon research – LAGUNET - Orbetello (GR, Italy) 1-3 Ottobre, 2009

Bruno Bellisario - *Centralization measures of donor – controlled communities on P. australis leaf detritus in Tarquinia Saltern* – Annual Meeting of Italian PhD Student in Ecology, Parma, Italy, 2009

Bruno Bellisario, Fulvio Cerfolli, Claudia Novelli, Giuseppe Nascetti - *Macroinvertebrates colonization process of Phragmites australis leaf detritus in Tarquinia saltern* – 2nd Italian Conference on Lagoon research – LAGUNET - Tarquinia (VT, Italy) 23-25 Ottobre, 2008

Fulvio Cerfolli, Claudia Novelli, **Bruno Bellisario**, Giuseppe Nascetti - *Donor control model in the transition ecosystem of Tarquinia salterns: the functional role of bottom up pressures* – 3rd European Conference on Lagoon Research – LAGUNET – Napoli (NA, Italy), 19 – 23, 2007


NON DIRMI CHE HAI UCCISO L'ULTIMO "GUFO A BECCO CURVO!"
CALMATI, AMICO...
HO SALVATO UN MASCHIO E UNA FEMMINA, VEDI, PER LA PROPAGAZIONE DELLA SPECIE.
...BE', SCUSA SE T'HO AGGREDITO.
NIENTE FIGURA'TI.
ALLORA CIAO GEORGE.
EI VEDIAMO BILLY.

INTRODUCTION

The influence of environmental conditions on the structuring process of detritus-based communities is of great importance in order to understand the consequences of environmental changes on ecosystems structure and functioning [30].

Natural and human induced alterations in space and time have sparked widespread changes in the global distribution of biota, and this results in the expansion of allochtonous, non-native species and contractions of autochthonous, native species, the so-called "biotic homogenization". Homogenization is not a random process, because invasion success and extirpation vulnerability are defined by the interaction between species traits and environmental conditions [107].

Therefore, since species contribute individually and collectively to the stability of communities and ecosystems, the modification of community structure could lead to a structural and functional homogenization, involving the replacement of ecological specialists by the same widespread generalists [134]. Homogenization of communities might also reduce ecosystem functioning, stability and resistance to environmental change by restricting the available range of species-specific responses [164].

The structural composition of communities defines the range of functional traits that influence ecosystem functions (such as the decomposition of organic matter [120]), and the homogenization might limit the pool of species that can compensate for local extinctions (i.e., reduce spatial patterns in functional redundancy). Homogenized communities might therefore have a decreased resistance to environmental perturbations, as the high degree of similarity among communities might dampen or eliminate potential recolonizations by species with locally extirpated traits.

In this work, I wanted to assess the consequences for ecosystem structure and functioning of changing environmental conditions over space and time. Since the effects of biotic homogenization might be particularly high in areas, such as small and fragmented ecosystems that experience more frequent and severe disturbance events, the Biological Reserve of Tarquinia saltern represents a suitable candidate to test hypotheses about functional ecology [26].

The aim of this work is to understand how the steepest gradients of environmental conditions influence the structure and functioning of detritus-based communities. The importance in the study of decomposition processes and dynamics lies in the ability of detritus to sustain higher species diversity, larger predator biomass, and longer food chains than would be supported by primary productivity alone [60], stabilizing the dynamics of consumer populations and food webs that would be otherwise unstable (for a complete review see [120]).

The experimental approach carried out for this work comes from a twelve months field experiment under non-manipulative conditions in six sites in the area of Tarquinia saltern, to cover the full spectrum of environmental gradients, using the allochtonous leaf detritus of *Phragmites australis* (Cav.) Trin. ex Steud. The

choice of use the allochtonous detrital resource of *P. australis* comes from its wide spatial distribution, able to be colonized from a variety of organisms, independently from their life history and phenology (e.g., marine and/or freshwater).

Here I applied the network analysis to understand how the whole community assembly and the spatial distribution of macroinvertebrates on leaf detritus are influenced by the environmental conditions under which they are structured, and the consequence for ecosystem functionality and stability.

In this work I also evaluated the role of the spatial assembly of the pools in Tarquinia saltern on the colonization process of leaf detritus. Spatial patterns could affect any of the many processes in communities, such as decomposition [185], spatial subsidies and food-web dynamics, and thereby have cascading effects elsewhere on the landscape. Moreover, an increased spatial similarity in the species identity could have direct and indirect effects on species at lower and higher trophic levels by increasing extirpation rates via intensified species-specific interactions (e.g., functionally similar species might utilize the same resources increasing competition and decreasing functionality), giving useful insights for conservation and management.

This work is divided in two main sections. The first section gives the background in the ecology of detritus-based systems (Chapter 1) and in the framework of complex networks (Chapter 2). The second section represents the core of my work, describing the raw results about the field experiment (Chapter 3), the more fine analyses about the role of salinity on driving the structuring process of communities and the consequences for decomposition (Chapter 4), and the influence of spatial structure on the robustness of ecological communities (Chapters 5 and 6). After the references, the reader can find a series of appendices describing the most used concept in functional and network ecology (Appendix 1), the derivation of the equations used to measure the potential interferences among taxa in the detritus-based communities (Appendix 2), the interaction matrices derived for each community (Appendix 3), and the codes written in R [154] to measure the network parameters and statistics (Appendix 4).

PART I

The ecology of detritus-based systems

1. THE ECOLOGY OF DETRITUS-BASED SYSTEMS

This chapter gives the background in the ecology of detritus-based systems. Detritus represent a source of energy for many organisms and is able to sustain higher species diversity and longer food chain than would be expected by primary production alone. Environmental conditions influence the decomposition dynamic in aquatic ecosystem *via* direct and indirect effects, influencing the rate at which detritus is leached by water and conditioned by microfungi and bacteria, and influencing the colonization process by macroinvertebrates, in terms of species diversity and abundance, both of detritivores and their predators. This chapter aims to introduce my work following one main question about the role of the structural patterns of detritus-based communities and their influence on the degree of system functionality, under variable environmental conditions in time and space.

1.1 Introduction

Traditional approaches in ecology emphasize the transfer of local primary productivity through trophic levels. However, detritus is a common feature in most of ecosystems and plays an often-overlooked role of a dynamic heterogeneous resource and habitat for many species. The importance of detritus comes from the ability to regulate the regeneration of carbon and nutrients, being an important link between primary and secondary production [42]. Indeed, most primary production is not consumed by herbivores, but is returned to the environment as detritus, to play a critical role in organizing and sustaining ecosystems [200] [60] [151]. Detritus also physically alters habitats [169] [207], facilitating some species and inhibiting others [64].

Therefore, the importance of decomposition (especially in aquatic ecosystems) comes from the ability to sustain higher species diversity, larger predator biomass, and longer food chains than would be supported by primary productivity alone [60]. Decomposition can also stabilize the dynamics of consumers populations, alter habitat complexity, and stabilize food webs that would be otherwise unstable [120].

This chapter aims to introduce a fundamental question in the study of detritus-based systems: what are the structural patterns that influence the degree of ecosystem functionality under variable environmental conditions in time and space? To answer this question it is necessary to introduce some fundamental concepts in the study of these systems, in order to better understand the role of detritus within ecosystems.

1.2 Definition of detritus

Detritus can be defined as any form of non-living organic matter, including different types of plant tissue (e.g., leaf litter, dead wood, aquatic macrophytes), animal tissue, dead microbes, faeces, as well as products secreted, excreted or exuded from organisms (e.g., extra-cellular polymers).

In the studies of decomposition dynamic in aquatic ecosystems, detritus can be subdivided on the basis of its dimensional classification [32]:

1. **DOM**: Dissolved organic matter, with a diameter less than 0.5 μm, deriving from soluble organic matter
2. **FPOM**: Fine particulate organic matter, with a diameter ranging between 0.5 μm and 1 mm, deriving from leaf fragment
3. **CPOM**: Coarse particulate organic matter, with a diameter up to 1 mm, deriving from leaf, flower and wood

This classification follows a particular dynamic, in which the fractions are in dynamic equilibrium following the order $\mathrm{CPOM} \rightarrow \mathrm{FPOM} \rightarrow \mathrm{DOM}$.

However, this nomenclature derived from the size classification of detritus is far from be standardized. For example, aquatic ecologists usually subdivide particulate detritus into large particles (coarse POM) and small particles (fine POM). In terrestrial ecosystems, where it is difficult to separate aged detritus from the soil matrix, the density distinguishes more labile (the so-called “light fraction” or LF) from the less degradable POM fraction that is incorporated into aggregates, association with clay and silt, and chemical/biological transformation into recalcitrant molecules [176]. The chemical quality of detritus and its decomposition products, combined with physical mixing by organisms, influence nutrient availability, soil chemistry, and soil architecture that, in turn, influence species diversity [22]. Indeed, detritus, other than a source of energy, serves as a habitat and habitat modifier for a variety of organisms.

As highlighted by several authors, both in terrestrial [179] [77] [16] and in aquatic ecosystems [168] [206], detritus modifies the physical structure and conditions of habitats, such as soil moisture, light, temperature, and flow velocity

of wind and water. The turbidity of many estuaries, reservoirs, large rivers, and lakes comes from the high concentrations of detritus, where the attenuation of the light by particulate detritus suspended in water column may reduce the photosynthetic rates and the feeding efficiencies of visually oriented predators [160].

The origin of dead organic matter is often particular, observing how in some ecosystems (e.g., floodplain), a great amounts of detritus, nutrients, and sediments rich in organics are exchanged reciprocally between the river channel and the riparian land via flooding. Allochtonous detritus among habitats is ubiquitous in diverse biomes and is often a central feature of population, consumer-resource, food web and community dynamics, representing a substantial source of energy for many ecosystems.

Indeed, one of the most biomass-rich community on earth is supported entirely by allochtonous detritus, where 15–300 m mats of detrital surfgrass and kelp are converted into 1 kg/m^3 of benthic crustaceans (up to 36 individuals/m^3), and a large numbers of trophically distinct fish feed in these hotspots [195] (but see [113] for many other examples).

This supports the need to understand the mechanisms that regulate the spatial dynamics of detritus, nutrients, consumers and prey, because ecosystems dynamics are rarely confined within a focal area and that factors outside a system may substantially affect (and even dominate) local patterns, dynamics and stability.

1.3 The decomposition of detritus

Decomposition dynamic in aquatic ecosystems involves three main mechanisms: i) the rapid weight loss of leaf soluble constituents, ii) the modification of leaf matrix by microorganisms and iii) the feeding activity of macroinvertebrates.

Detritus begins to lose soluble organic and inorganic materials shortly after immersion in water. The general pattern of leaching from immersed whole leaves is a rapid loss over the first 24 hours, followed by a gradual decline [119]. It has been found [143] [142] that some variables such as water temperature, turbulence,

salinity and leaf species/quality, influence the decomposition dynamic of leaf detritus.

After leaching, leaves are colonized by a variety of aquatic microbes within a few days of deposition. In general, fungi, principally hypmomycetes, dominate early colonization, gradually giving way to bacteria as decay advances [182]. Aquatic hypmomycetes produce polysaccharide-hydrolyzing exoenzymes including pectinases [181], hemicellulases and cellulases [175], all of which are potentially important in the decomposition of plant material.

However, the structural polysaccharides, cellulose and hemicellulose of plant cell walls are physically and chemically bound to lignin, forming lignocellulose, a resistant complex that renders cellulose and hemicellulose less accessible to enzymes [84], producing a refractory fraction of detritus persisting in the system.

A second mechanism of fragmentation is that promoted by invertebrates. Leaf-shredding invertebrates, or shredders [31], preferentially colonize and feed on microbially conditioned leaves [32] and may contribute significantly to leaf breakdown, especially in aquatic systems.

In ecology, one of the most used models to describe the decomposition dynamic is the negative exponential model, originally developed by Jenny et al. [75] and Olson [136]:

$$W_t = W_0 e^{-kt} \tag{1}$$

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 time.

From Eq.1 it is easy to derive the decomposition coefficient, k, expressing the rate at which detritus is decomposed in time t:

$$k = \frac{\ln W_t - \ln W_0}{t} \tag{2}$$

This model has been criticized for two major reasons: first, other mathematical equations often describe the data more precisely, second, variables

known to affect rates of organic matter breakdown, such as temperature, pH and salinity, are not present in the negative exponential model.

The useful of the negative exponential model can be developed from the assumption that the rate of weight loss (or absolute decomposition rate) from organic material is a constant fraction of the amount of remaining material. The major problem encountered in using this model is that breakdown rates are seldom constant.

As noted by Levins [93], there is no single all-purpose model, because models might be built for generality, realism, or precision, but it is not possible to maximize all of these qualities simultaneously. The aim of any model is to maximize realism, such as some of the various modifications of the negative exponential model (see for references [116] [165] [172]), useful for the insight they provide to the mechanisms of breakdown under natural conditions.

Despite these criticisms, the advantage of the exponential model is its generality, because it provides a single number that describes the progress of breakdown in a particular situation, posing the basis for comparing breakdown rates in different situations.

1.4 The detritus-based food webs

Detritus in food webs is a source of energy and nutrients to living organisms. As noticed by Moore and Hunt [123], most of the known food webs available in literature contain both detritus and primary producers. In their work, the authors deconstructed the 40 food webs compiled by Briand [18] into 138 pathways (or energy channels) that originated with a basal resource (i.e., detritus) and ended with a top predator, revealing as many of which could be traced back to detritus.

Food webs normally exhibit a high degree of inter- and intraguild predation and omnivory across the pathways, to the point that a significant amounts of biomass can be traced back to detritus [120]. Some food webs are based almost entirely on detritus [71], as the food webs structured in caves and small stream in forested watersheds, while for others the detritus can have strong influence on the structure and dynamics of grazer pathways [121]. One example is provided by the

reservoirs in the Midwestern USA, where detritivorous fish attain high biomass *via* detritus consumption, excreting nutrients that stimulate phytoplankton biomass [190].

A detritus-based trophic chain in aquatic environment is mainly composed by four elements (also called trophic levels, see Appendix A1). These are the basal level, or the source of dead organic matter, the 1st order consumers (fungi and bacteria), the 2nd order consumers (micro and macrodetritivores, mainly macroinvertebrates) and 3rd order consumers, predators. A constant interlink between the grazer and detritus food chain can be observed by the fact that the 3rd order predators in detritus food web can be a source of food for vertebrates predators of the grazer food web. The complexity of the whole community assemblage may end with the presence of top-predators, those species able to feed at the same time between the grazer and detritus chain.

Detritus has often-important implications for the interpretation of many classic ecological theories, such as the stability of food webs, trophic height or food chain length, the distribution of biomass among trophic levels, trophic cascade and biodiversity (see Appendix A1). The stabilizing effect of detritus is achieved not through self-limitation of the resource (as in classic primary-producer models) but, rather, as a result of the constant inputs of detritus. Indeed, several authors [122] [127] have shown how detritus represents a more stable and persistent reservoir of energy than primary producers alone, over a wide gradient of productivity.

As noticed by many [123] [60] [83] detritus was found to support long food chains. The number of trophic levels is a central issue in the study of food chain dynamics [133] and the structuring of ecosystems *via* trophic cascades [25], as well as mediating the relationship between species diversity and ecosystem function [209] [37].

One of the earliest explanations for what constrains the number of trophic levels was forwarded by Elton [39]. His productivity hypothesis posited that, due to the inherent inefficiency of trophic transfers, available energy becomes insufficient to support more than a small number of trophic levels. A testable prediction of this hypothesis is that more productive ecosystems should have

longer food chains. Because of the resident time of energy within detrital systems is longer owing to the absence of death, and the internal cycling in detritus-based systems enhances the efficiency of detrital *vs*. grazer-dominated food webs, this source of energy can support species at higher trophic levels, longer food chains and greater food web complexity [120].

This latter represents one of the fundamental and controversy issue in the study of ecological communities. Early theoretical consideration suggested that the presence of more feeding link (complexity) among more species (diversity) generally reduces the risk of species dependence on a few resources [98].

Starting from the late 1950's, the notion that *complexity begets stability* was considered by many ecologists one of the basic ecological theorem [73]. However, the apparent inevitability of this relationship was challenged by mathematical models of food webs dynamic, which showed how diversity and complexity might destabilize ecosystems through increasing the chance of positive feedback [101]. In particular, Pimm and Lawton [149] concluded that long food chains tend to be dynamically fragile, and less able to recover from environmental perturbation. A resulting prediction was that food chains should be shorter in ecosystems subject to environmental fluctuations and disturbances [147]

Thus, understanding the role of complexity (e.g., the number of interactions among species in a community) and diversity (e.g., the number of species in a community) represents a fundamental issue in the face of our understanding of ecosystem function. Which species are important and how they interact to create and maintain species diversity patterns represents a key issue to understand the mechanisms of decomposition processes.

Several authors have shown a significant decrease in the rate of leaf litter decomposition with declining species richness, both in terrestrial [125] and in aquatic ecosystems [200]. However, decomposition may be only weakly correlated with species richness and the total abundance of detritivores organisms, because some species are far more important than others.

This view supports the idea that the presence of keystone taxa (i.e., topological keystone species [80]) may be more important for decomposition

[196] than species diversity *per se*. Many laboratory and field studies suggest that species richness can be related to the rate at which leaf detritus is broken in stream ecosystems [78], showing a little redundancy among species in their effect on ecosystem process, on the contrary of what observed in marine environment [0], where the functional diversity among species seems to be more correlated whit the decomposition rate. Thus, understanding how the environment constraints the structural pattern of ecological communities will provide a more understanding of our knowledge about functionality, also in the face of environmental change.

Related to the above discussion is the fundamental question of what determines how many species are to be found in a given place and how they interact to maintain ecosystems functioning. One can ask why there are a well-defined number of species co-occurring in a given place and why not more or fewer similar species.

In the late 1961's, Hutchinson [72] posed the paradox of plankton, noticing how phytoplankton communities generally exhibit high species number despite apparent limited opportunities for niche partitioning of their resource. Niche differentiation is obviously an important aspect, however, it is clear that other mechanisms must be involved, as similarity in coexisting species. High diversity of coexisting species can results from spatial heterogeneity [186], temporal variability [92], spatial structure and interactions between competition and colonization [48], and trophic complexity [139]. In addition, high diversity of competitors could result from the interplay of speciation and extinction process in systems in which all competing species were functionally identical (the so called neutral theory of biodiversity [70]).

The question early posed by Hutchinson and MacArthur reaches answers in the intuition of many naturalists that niches of all of seemingly similar species really differ in aspects that are not easily detected [166]. Another, slightly less intuitive, class of explanations for the coexistence of so many species in nature is that various mechanisms may help to prevent competitive exclusion. As noticed, these mechanisms might be predation [139], chaotic population dynamics [167], environmental variability [177] [27] and incidental disturbances [28]. The

interaction of such mechanisms at multiple scales of space and time may maintain much of the biodiversity observed in nature [91].

Niche differentiation, or facilitative interactions among species within trophic levels, maximizes ecosystem processes such as productivity [70] or decomposition [178] as diversity increases. Ecological niche differentiation may be correlated with phylogenetic divergence among species, and so indicates the potential for complementarity in function [100].

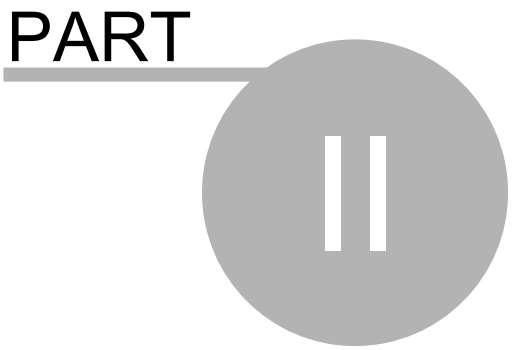
The role of the mixing pattern of interactions in ecological communities is a fundamental issue to understand species coexistence and to make prediction about ecosystems functioning. Indeed, species interactions are found to be of greater influence on decomposition dynamic, suggesting how the richness-functioning relationship may be driven by direct (abundances) and indirect (predation and competition) mechanisms [35]. Factors such as competition between the organisms involved in detritus decomposition have been suggested to regulate the dynamics between trophic levels [197], and the increased trophic complexity (i.e., the presence of predators) will potentially enhance the consumption rate by detritivores [120].

It has been found how the interlink among uncertainty in environmental conditions, predation and competition in ecological communities may determine relative abundances of species [202]. This regulation in populations and the determination of relative abundances are determined by complex interactions among the life histories of the species, their defenses against predators, and their competitive abilities.

The size-structured interactions among species in community may change connections through seasonal shifts in trophic links. This allow a different way of thinking about food webs, moving away from the static concept of stable linkages among taxa to include some of the spatial and temporal mechanisms that make actual food webs constantly changing tangles of trophic relationships [201]. Thus, the impact of detritus into food webs analyses must be focused not only on the characterization, classification and transformation of detritus, but often on the role that the detritus has for community organization. This is because detritus goes

through a series of changes through time, and these changes are both mediated by and have large effects upon the organisms that process the detritus.

These transformations represent multiple entry points into the system and the infusion of this energy into the community and its passage to top predators affects the diversity, structure and dynamic properties of the community.



Network theory

2 NETWORK THEORY

In the past few years, the framework of complex networks has provided new insight into the organization and function of many biological systems, representing a useful tool to describe many physical, biological and social systems. Network theory is now a truly interdisciplinary topic, and ecology has drawn heavily upon algorithms developed in other areas, such as social science and information theory. In this chapter I want to introduce the basic concept in network analysis, and highlight the most used network properties in the study of ecological and spatial networks. After the necessary introduction to the common statistical measures I briefly look inside the network measures I used to analyze data in this work.

2.1 Introduction

A network can be defined as a set of items called vertices or nodes, with connections (called edges) between them (Fig. 2.1).

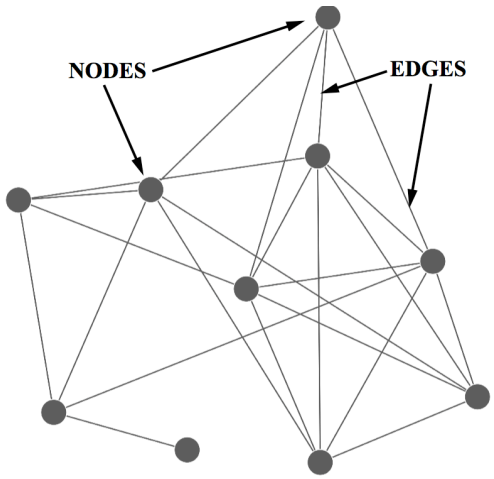


Figure 2.1 – Example of network with 10 nodes and 26 edges.

In real life, there are many examples of systems taking the form of networks, also called graphs in mathematical literature. Some examples include the Internet, the World Wide Web, social networks of acquaintance or other connections between individuals, organizational networks and networks of business relations between companies, neural networks, metabolic networks, food webs, distribution networks such as blood vessels or postal delivery routes,

networks of citations between papers, and many others.

The study of networks, in the form of mathematical graph theory, is one of the fundamental pillars of discrete mathematics. Recent years, have witnessed a substantial new movement in network research, with the focus shifting away from the analysis of single small graphs and the properties of individual vertices or edges within such graphs to consideration of large-scale statistical properties of graphs. The body of theory in network analysis focuses mainly on three fundamental aspects: i) the statistical properties able to characterize the structure and behavior of networked systems, and to suggest appropriate ways to measure these properties, ii) the models of networks that can help us to understand the meaning of these properties - how they came to be as they are, and how they interact with one another, and iii) what the behavior of networked systems will be on the basis of measured structural properties and the local rules governing individual vertices.

This is because structure affects the functioning of systems and, therefore, a proper understanding of the structural characteristics of the network involves a greater understanding on their functioning.

2.2 Types of networks

In real world, there may be more than one different type of vertex in a network, or more than one different type of edge, and vertices or edges may have a variety of properties, numerical or otherwise, associated with them. The edges of graphs may also be imbued with directedness so, a normal graph in which edges are undirected is said to be undirected.

In the most common sense, a network (or graph) is an ordered pair $G := (V, E)$, comprising a set V of vertices or nodes together with a set E of edges or lines, which are 2-element subsets of V. Otherwise, if arrows may be placed on one or both endpoints of the edges of a graph to indicate directedness, the graph is said to be directed.

A directed graph in which each edge is given a unique direction (i.e., edges may not be bidirected and point on both directions as once) is called an oriented graph. An undirected graph, is a graph in which edges have no orientation, i.e.,

they are not ordered pairs, but sets $\{u, v\}$ (or 2-multisets) of vertices. A directed graph (or digraph), is an ordered pair of $D := (V, A)$, with V as a set whose elements are called vertices or nodes and A, a set of ordered pairs of vertices called arcs, directed edges or arrows. A directed graph D is called symmetric if, for every arc in D, the corresponding inverted arc also belongs to D. A symmetric loopless directed graph $D := (V, A)$ is equivalent to a simple undirected graph $G := (V, E)$, where the pairs of inverse arcs in A correspond one-to-one with the edges in E; thus the edges in G are $|E| = |A|/2$, or half the number of arcs in D.

A further essential aspect in network theory is to consider not only the number of connections (edges) among nodes, but also the weight that each connection has. This is the case of a weighted graph, having a numerical label $w(E)$ associated with each edge E, called the weight of edge. Edge weights can be integers, rationale numbers, or real numbers, which represent a concept such as distance, connection costs, or affinity.

Mathematically, a network or graph can be expressed in two different ways, a one-mode data matrix and a two-mode data matrix. A one-mode data matrix is the classical representation in which the elements in rows are the same in columns, and each matrix element x_{ij} represents the presence/absence (in a binary 0-1 representation) of a relationship among them. Clearly, matrix element can be weighted, expressing a quantitative relationship between i and j.

In ecology, a one-mode matrix depicts a kind of direct relationship among nodes that can be represented as a set of species in a community, typically a food web expressing who eat whom in a community. A two-mode data consist of a data matrix **A** over two sets U (rows) and V (columns). Such data can be viewed also as a bipartite network, in which links are established between two sets of nodes (U and V) but not within the same set (Fig. 2.2). A 2-mode network is a structure (U, V, R, w), where U and V are disjoint sets of vertices (nodes or units), where $R \subseteq U$ x V is a relation, and $w : R \rightarrow \Re$ is a weight. If no weight is defined we can assume a constant weight $w(U, V) = 1$ for all $(U, V) \in$ R. A 2-mode network can be viewed also as an ordinary one-mode network on the vertex set $U + V$, divided into two sets U and V, where the arcs can only go from U to V (a bipartite directed graph).

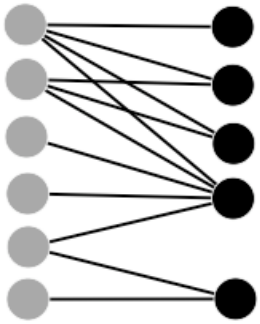


Figure 2.2 – A bipartite graph in which links are established between two sets of nodes but not within nodes of the same set.

2.3 Properties of networks

The simplest, useful model of a network is the first studied by Rapoport [155] and Erdós and Rényi [40]. In this model, undirected edges are placed at random between a fixed number n of vertices to create a network in which each of the $1/2(n - 1)$ possible edges is independently present with some probability p, and the number of edges connected to each vertex - the degree of the vertex - is distributed according to a binomial distribution, or a Poisson distribution in the limit of large n. Real networks are non-random in some revealing ways that suggest both possible mechanisms that could be guiding network formation, and possible ways in which we could exploit network structure to achieve certain aims.

Here I briefly explore some of the basic features in network analysis, referring to Newman [129] for a complete review in network theory.

2.3.1 The small world of real networks

The significance of small world lies in the fact that most pairs of vertices in most networks seem to be connected by a short path through the network, the so-called six-degree of separation, following Milgram's experiment [114], set in a more mathematically rigorous way by Pool and Kochen [152].

Consider an undirected network with l as the mean geodesic (i.e., shortest) distance between vertex pairs in a network with n nodes:

$$l = \frac{1}{0.5n(n+1)} \sum_{i \geq j} d_{ij} \tag{3}$$

where d_{ij} is the (geodesic) distance from vertex i to vertex j.

The quantity l can be measured for a network of n vertices and m edges in time $O(mn)$ using simple breadth-first search, also called a *burning algorithm* in the physics literature [1]. In Table 1, are shown the values of l takes from the literature for a variety of different networks, in which the values are in all cases much smaller than the number n of vertices, for instance.

Table 2.1 – Shortest paths among different types of networks.

	Network	Type	n	l
Social network	Film actors	Undirected	449913	3.48
	Physics coautorship	Undirected	52909	6.19
	Citation network	Directed	783339	5.22
	Email messages	Directed	59912	4.95
Biological network	Metabolic network	Undirected	715	2.56
	Protein interactions	Undirected	2115	6.8
	Marine food web	Directed	135	2.05
	Freshwater food web	Directed	92	1.9
	Neural network	Directed	307	3.97

The small-world effect has obvious implications for the dynamics of processes taking place on networks. For example, if one considers the spread of information across a network, the small-world effect implies that spread will be fast on most real-world networks. Networks are said to show the small world effect if the value of l scales logarithmically or slower with network size for fixed mean degree.

2.3.2 Clustering

A fundamental measure that has long received attention in both theoretical and empirical network research is the clustering coefficient, measuring the degree to which nodes tend to cluster together. Evidence suggests that in most real-world networks, nodes tend to create tightly knit groups characterized by a relatively high density of ties [199].

As I previously shown, a graph $G = (V, E)$ consist of a set of vertices V and a set of edges E between them, and an edge e_{ij} connecting vertex i with vertex j. The neighborhood N for a vertex v_i is defined as its immediately connected neighbors as follows:

$$N_i = \left\{ v_j : e_{ij} \in E \wedge e_{ij} \in E \right\} \tag{4}$$

In this context, I introduce the next statistical properties of the networks, the degree k_i of a vertex, defined as the number of vertices, $\left|N_i\right|$, in its neighborhood N_i. The local clustering coefficient C_i for a vertex v_i is then given by the proportion of links among the vertices within its neighborhood, divided by the number of links that could possibly exist among them. In a directed graph it is possible to observe two distinct edges, $e_{ij} \neq e_{ji}$, and therefore for each neighborhood N_i there exist $k_i (k_i - 1)$ links among vertices.

This means that a generic node i could have an ingoing and an outgoing link (the in- and out-degree). The clustering coefficient for the whole system [199] is defined as:

$$\overline{C} = \frac{1}{n} \sum_{i=1}^{n} C_i \tag{5}$$

where

$$C_i = \frac{\left|\left\{ e_{jk} \right\}\right|}{k_i (k_i - 1)} : v_j, v_k \in N_i, e_{jk} \in E \,^{1} \tag{6}$$

[1] For directed graphs

and

$$C_i = \frac{2\left|\{e_{jk}\}\right|}{k_i(k_i-1)} : v_j, v_k \in N_i, e_{jk} \in E^2 \quad (7)$$

2.3.3 Degree distribution

The degree of a vertex is the number of edges incident on (or connected to) that vertex, and it is defined as the fraction p_k of vertices in the network that have degree k. In network theory, the degree distribution of a vertex could be represented by a filled histogram showing the distribution of the number of links each node has. Clearly, the distribution can be highly skewed, meaning that the distribution has a long tail of values that are far above the mean.

An alternative (and more useful) way of presenting degree data is to make a plot of the cumulative distribution function, expressing the probability that the degree is greater than or equal to k:

$$P_k = \sum_{k'=k}^{\infty} p_{k'} \quad (8)$$

Several studies [199] have shown how real life network may follow an exponential degree distribution, $P(\geq L_i) \propto \exp(-\gamma L)$, which indicates that nodes inside the network have a well-defined average number of links. Some others follow a power-law distribution [3], $P(\geq L_i) \propto L^{-\gamma}$, characterized by the asymmetry in the frequency distribution of link per node, where the bulk of nodes have a few links and a few nodes are much more connected than expected by chance. Some networks have found to follow a truncated power-law, $P(\geq L_i) \propto L^{-\gamma} \exp(-L/L_x)$ where, at some critical level of connections (L_x), it can be observed a change in network topology, from a typical scale-free distribution to a single-scale distribution with a faster exponentially decay.

[2] For undirected graphs

The rationale for the importance in degree distribution lies behind the fact that it affects the robustness to node deletion [3] and, thus, the stability of the network.

2.3.4 Centrality

Centrality is one of the most studied concepts in social network analysis.

Numerous measures have been developed, including degree centrality, closeness, betweenness, eigenvector centrality, information centrality, flow betweenness, the rush index, the influence measures. What is not often recognized is that the formulas for these different measures make implicit assumptions about the manner in which things flow in a network.

For example, some measures, such as Freeman's closeness and betweenness [47], count only geodesic paths, apparently assuming that whatever flows through the network moves only along the shortest possible paths. Other measures, such as flow betweenness [46], do not assume shortest paths, but do assume proper paths in which no node is visited more than once. Still other measures, such as Bonacich's eigenvector centrality [15] and Katz's influence [82], count walks, which assume that trajectories can not only be circuitous, but also revisit nodes and lines multiple times along the way.

Regardless of trajectory, some measures (e.g., betweenness) assume that what flows from node to node are indivisible (like a package) and must take one path or another, whereas other measures (e.g., eigenvector) assume multiple paths simultaneously (like information or infections).

Here I discuss the eigenvector centrality because this measure is defined in a way that a node centrality depends not only on the topological characteristic of nodes (e.g., the number of connections), but also on their weight (e.g., some properties of interaction strength) (but see Chapter 5 for discussion about other measures of centrality). Eigenvector centrality is defined as the principal eigenvector of the adjacency matrix defining the network.

The defining equation of an eigenvector is:

$$\mathbf{A}\vec{x} = \lambda\vec{x} \tag{9}$$

where **A** is the adjacency matrix of the graph, λ is a constant (the eigenvalue), and $\vec{x}$ is the eigenvector.

The equation lends itself to the interpretation that a node that has a high eigenvector score is one that is adjacent to nodes that have themselves high scorers. The idea is that even if a node influences just one other node, which subsequently influences many other nodes (who themselves influence still more others), then the first node in that chain is highly influential.

It can be shown [15] that an eigenvector is proportional to the row sums of a matrix **S** formed by summing all powers of the adjacency matrix, weighted by corresponding powers of the reciprocal of the eigenvalue:

$$\mathbf{S} = \mathbf{A} + \lambda^{-1}\mathbf{A}^2 + \lambda^{-2}\mathbf{A}^3 + ..\lambda^{-n}\mathbf{A}^{n+1} \qquad (10)$$

It is also well known that the cells of the matrix powers give the number of walks of length *k* from node *i* to node *j*. Thus, the measure counts the number of walks of all lengths, weighted inversely by length, which emanate from a node. Eigenvector centrality is consistent with a mechanism in which each node affects all of its neighbors simultaneously, as in a parallel duplication process hence, is ideally suited for influence type processes.

2.3.5 The resilience of networks

Related to degree distributions is the property of resilience of networks to the removal of their vertices.

If vertices are removed from a network, pairs will become disconnected and any kind of communication between them through the network will become impossible. There are also varieties of different ways in which vertices can be removed, and different networks show varying degrees of resilience to these. One could remove vertices at random from a network, or one could target some specific vertex, such as those with the highest degree.

The consequence of node removal on network resilience is related to the *shape* of the links distribution in the network (Fig. 2.3).

By definition, a power-law distribution shows a much more robustness against random removal of nodes, but high sensitivity to the removal of most

connected nodes, as showed in [4]. This is because bulks of nodes have a few links, and a few nodes are much more connected than expected by chance so, the probability to disconnect the system with a random *attack* is very small. On the contrary, a less skewed distribution reveals a much more sensitivity to random removal of nodes and, thus, on network resilience. Following these studies, many authors have looked into the question of resilience for other networks, observing how most networks are robust against random vertex removal but considerably less robust to targeted removal of the highest-degree vertices (as in metabolic networks [76], or food webs [38]).

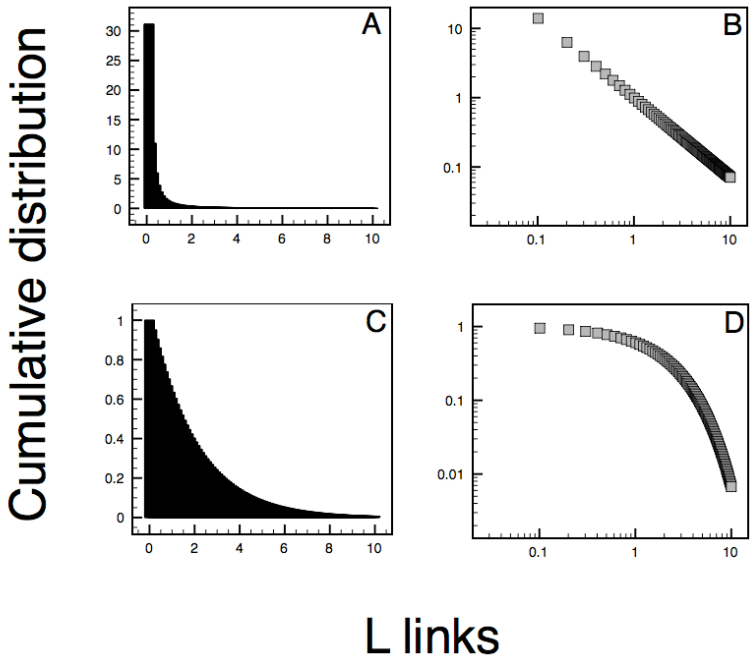


Figure 2.3 – Histogram of degree distribution**.** On the left, the histogram for a power (A) and exponential distribution (C). On the right, the same distribution expressed as the cumulative degree distribution in a log-log graph of *P* (*y*-axis) and the number of links *L* (*x*-axis) for a power (B), and exponential distribution (D). The power-law has a much more skewed distribution than an exponential. In a log-log graph, a straight line expresses a power-law.

2.4 Networks in ecology

The origins of networks in ecology date back to the early years of graph theory [65], developed by receiving input from economical network analysis [62] and sociometry [66].

An ecological network is the representation of the biotic interactions in a given ecosystem, in which species (nodes) are connected by pairwise interactions (links). These interactions can be trophic (predator/prey), non trophic (competition, apparent competition) or mutualistic (as in plant-pollinator network). Historically, research into ecological networks developed from descriptions of trophic relationships in aquatic food webs. However, recent works have expanded to look at other food webs as well as webs of mutualists, identifying several important properties of ecological networks.

In this section I show some of the fundamental structural measures in ecological network analysis, shown in more detail in the next section:

1. **Connectance**: the proportion of possible links among species that are realized. In food webs, the level of connectance is related to the statistical distribution of links *per* species.

2. **Clustering**: the proportion of species that are directly linked to a focal species. A focal species in the middle of a cluster may be a keystone species, and its loss could have large effects on the network.

3. **Compartmentalization**: the division of the network into relatively independent sub-networks. Compartmentalization can be related to body size [170] [158], spatial location [86] or temporal niche availability [96].

4. **Nestedness**: the degree to which species with few links have a sub-set of the links of other species, rather than a different set of links. In highly nested networks, guilds of species that share an ecological niche contain both generalists (species with many links) and specialists (species with few links, all shared with the generalists).

Given the network-like quality of many ecological phenomena, network analysis may be ideally suited for understanding ecological systems. For example, it may help to identify the processes by which species are able to coexist in communities [33].

However, the use of graph-theoretic approaches by ecologists is limited to a few specific contexts, and most ecological studies involving graph-theoretic approaches focus on the structure of food webs [19] [145] [203], with occasional forays into landscape ecology [189] and nearest-neighbor analysis in plant ecology [34].

The relationship between ecosystem complexity and stability is one of the major topics of interest in ecology, and the use of ecological networks makes it possible to analyze the effects of network properties on the stability of ecosystems (see Appendix A1). Ecosystems complexity was once thought to reduce stability by enabling the effects of disturbances, such as species loss or species invasion, to spread and amplify through the network.

However, other characteristics of networks structure have been identified to reduce the spread of indirect effects and, thus, enhance ecosystem stability. Interaction strength may decrease with the number of links among species, damping the effects of any disturbance [192], and cascading extinctions are less likely in compartmentalized networks as effects of species losses are limited to the original compartment [86].

The community of species in ecosystem is expected to affect both the ecological interactions and coevolution of pairs of species. Related, spatial applications are being developed for studying metapopulations, epidemiology, and the evolution of cooperation. In these cases, networks of habitat patches (metapopulations) or individuals (epidemiology, social behavior) make it possible to explore the effects of spatial heterogeneity. Furthermore, as long as the most connected species are unlikely to go extinct, several studies have shown as stability increases with complexity (e.g., connectance in [38], and nestedness in [23]).

2.4.1 Connectance

Connectedness is a general term describing the degree to which components of a system are connected to each other [5]. Its application in ecology focuses on interactions resulting in energy transfers and food webs. Martinez [103] assessed different aspects of connectedness from the ecological literature, and showed that connectance, and particularly directed connectance, was the most robust measure under different resolutions of food web data.

Mathematically, connectance refers to the ratio of the observed links (L) on the maximum possible number of feasible links in the system (S^2) [49]:

$$C = \frac{L}{S^2} \tag{11}$$

Eq.11 measures the direct connectance, where the denominator expresses all the possible links in an S x S matrix, including self-connectance or cannibalism. Connectance can be also expressed as the interactive connectance, where the denominator is given by $S(S - 1)$, ignoring or disallowing self-connectance or cannibalism.

As any structural properties in network analysis, also the connectance implies a minimum value for any web of S species that can be estimated from the minimum number of links, $L_{\min}$, required to interlink species into a single web [50]. This is because a connectance of zero is a contradiction in terms, because network with a connectedness of zero (e.g., a food web) is not a web.

In a network, or food web of S species, the minimum number of possible links is clearly $S - 1$ so, it is possible to rewrite the Eq.11 as:

$$C_{\mathrm{MIN}} = \frac{(S-1)}{S^2} \tag{12}$$

The denominator can take any value from the type of connectance you want to measure. Normalizing Eq.12 it is possible to derive a measure of connectance with no bias for network size:

$$C_N = \frac{C - C_{MIN}}{1 - C_{MIN}} \quad (13)$$

The set of equations 11, 12 and 13 expresses the way in which connectance can be measured in a one-mode matrix, or S x S matrix.

For a two-mode matrix, and thus for a bipartite web in which links are established between two different set of nodes (a and b), but not among nodes of the same set, connectance (C_b) must be expressed as the number of observed links (L) divided by all the possible links: $C_b = L / ab$.

2.4.2 Clustering

Aggregations of biological species on the basis of trophic similarity (namely trophospecies, see Appendix A1) are the basic units of study ecological networks as food webs, but little attention has been devoted to articulating objective protocols for defining such aggregations [211]. Quantitative patterns in food webs have been the subject of the controversy for several years [103]. The clustering of species on the basis of their trophic similarity helps ecologists to investigate resolution-related issues with statistics commonly used to describe the patterns. To cluster species in the raw food web, the nodes are hierarchically clustered based on the amount of trophic overlap among taxa [103].

In deciding whether two trophospecies should be assigned a trophic link, the maximum linkage convention (in which a link is included if any pair of original trophic entities are linked) produced more aggregation than the minimum linkage convention (in which a link is included only if every pair of original trophic entities is linked).

A one usually way to measure clustering among species is the trophic overlap given by the similarity index (I), calculated using the algorithm defined by Jaccard [74]:

$$I = c/(a + b + c) \quad (14)$$

where c = number of predators and prey common to the two nodes, a = number of predators and prey unique to one node, and b = number of

predators and prey unique to the other node. When two nodes have the same set of predators and prey, $I = 1$, and when two nodes have no common predators or common prey, $I = 0$.

However, as highlighted in the work of Yodzis and Winemiller [211]: '[*The*] *choice of similarity level for defining trophospecies remained an unresolved issue based on our analysis of our dataset. Perhaps, the greatest challenge is posed by sampling bias within empirical datasets, and we ultimately conclude that it is difficult to identify trophospecies [..] by strictly objective criteria*'.

A fundamental contribution may result from the use of modern isotopic techniques [153], used to trace the migration of organisms and the flow of water and nutrients through organisms and ecosystems. They can be used to reconstruct the diet and trophic position of animals, evaluate trophic structure of entire ecosystems and explore niche differentiation among individuals, populations, and communities.

2.4.3 Compartmentalization

Compartments are subgroups of nodes in which many strong interactions occur within the subgroups and few weak interactions occur between the subgroups, increasing the stability of networks. In social sciences, cohesive subgroups in human communities have been an important concept since the 1950's, when it was proposed that social systems were more efficient and durable when composed of subgroups in which interactions were concentrated [174].

As showed by several authors [101] [147], the structure of food webs is an important property for understanding their dynamic and topological stability. Food web structure was represented in many studies composed by guilds [162], blocks and modules [101], cliques and dominant cliques [212], compartments [147] and sub-webs [138]. Current studies show that groups of species are more connected internally than they are with other groups of species [118], showing how the weak links connecting these subgroups of nodes are the *glue* that maintains systems stability [105].

An interesting measure in network compartmentalization is given by its modularity. The importance of modularity has been discussed for a long time, but no consensus on its prevalence in ecological networks has yet been reached, because progress in modularity analysis has been hampered by inadequate methods and a lack of large ecological datasets [135]. One main critique in finding compartments (also defined "communities" or modules in the physical literature) in networks is given by the assumption that with hierarchical clustering methods (e.g., Eq.14) one needs to decide where to cut in order to obtain the relevant modules.

Recent development in statistical mechanics showed how it is possible to find modules (also called communities) in a variety of ecological (e.g., food webs, plant-animal mutualistic webs) and non-ecological (e.g., spatial webs) networks, assuming that the network of interest divides naturally into subgroups, whose number and size are determined by the network itself. One of the central algorithm used to find modules in networks, explicitly admits the possibility that no good division of network can exists *a priori*.

This algorithm is based on a process derived from the physical process of simulated annealing (SA), using a heuristic procedure to find an optimal solution [85]. The name and inspiration come from annealing in metallurgy, a technique involving heating and controlled cooling of a material to increase the size of its crystals and reduce their defects. The heat causes the atoms to become unstuck from their initial positions (a local minimum of the internal energy) and wander randomly through states of higher energy; the slow cooling gives them more chances of finding configurations with lower internal energy than the initial one.

In analogy, each step of the SA algorithm replaces the current solution by a random approximated solution, with a probability that depends on the difference between the corresponding function values and on a global parameter T (defined “temperature”), gradually decreased during the process.

Among the many algorithms implemented to detect community structure in networks during the last few years [131] [58] [57], is of great interest the one developed by [157], implemented in the *igraph* package of R [154]. 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. In physics, a spin-glass is a magnet with frustrated interactions augmented by stochastic disorder, where usually ferromagnetic and ant ferromagnetic bonds are randomly distributed. Its magnetic ordering resembles the positional ordering of a conventional, chemical glass.

Through this analogy, the spin states of a network are viewed as the number of communities that can be populated during the SA algorithm and the properties of the ground state spin configuration lead to a direct interpretation of the result in terms of graph theoretical measures, which give an exact definition of what a "community" is, corresponding to the local minima of the spin states energy.

The modularity (Q) is defined as [131]:

$$Q = \sum_{s} e_{ss} - a_s^2 \tag{15}$$

with $a_s = \sum_{r} e_{rs}$

where e_{ss} is the fraction of links that fall within the s set, and e_{rs} is the fraction of links that fall between nodes in group r and s, i.e., the probability that a randomly drawn link connects a node in group r to one in group s. The probability that a link has one end in the group s is expressed by a_s. From this, a fraction of a_s^2 links is expected to connect nodes in the group s among themselves.

Eq.15 can be rewritten as:

$$Q = \frac{1}{2M} \sum_{i \neq j} \left(A_{ij} - \frac{k_i k_j}{2M} \right) \delta(\sigma_i \sigma_j) \tag{16}$$

Any quality function for an assignment of nodes into communities should therefore follow the simple principle: group together what is linked, keep apart what is not.

Therefore, Eq.16 is rewritten as:

$$Q = -\frac{1}{M} H(\{\sigma\}) \tag{17}$$

where M are the number of links and H is the Hamiltonian[3] given by:

$$H(\{\sigma\}) = -\sum_{i \neq j} (A_{ij} - \gamma p_{ij}) \delta(\sigma_i \sigma_j) \quad (18)$$

where A_{ij} denotes the adjacency matrix of the graph with $A_{ij} = 1$ if an edge is present, 0 otherwise, σ_i is the spin state (or group index) of node i in the graph, p_{ij} the probability that a link exists between i and j (normalized such as $\sum_{i \neq j} p_{ij} = 2M$) and γ the parameter that relates the weight given to missing and existing links and allows for an assessment of overlapping and hierarchical community structures. Therefore, maximum modularity is reached when the Hamiltonian in Eq.18 (with $p_{ij} = k_i k_j / 2M$ and $\gamma = 1$) is minimal. To maximize the modularity of a community structure is equivalent to finding the spin configuration that minimizes this Hamiltonian.

A possible explanation to the modular structure of some observed ecological and non-ecological networks is that modularity may reflect habitat heterogeneity, divergent selection regimes, and phylogenetic clustering of closely related species [148] [94], leading to non-random patterns of interactions and contributing to the complexity of ecological networks.

2.4.4 Centrality and network centralization

Since species are involved in complex interaction networks in natural communities, one major aspect of importance is how the effects starting from a focal species reach the others, both directly and indirectly [113]. Functionally important species could be the ones being in key positions of the topological space of interactions [80], playing relatively more important roles in the community either through many direct links or indirectly-mediated by only a few neighbors [7].

The importance of species in a community is not easy to define and is even more complicated to quantify, and the choice of using a particular index is a direct

[3] See Appendix A3

consequence of whether our community data are directed, signed and/or weighted [191].

2.4.5 Nestedness

Nestedness is a common measure of order (or disorder) in ecological systems, referring to the order in which the number of species is related to area or other factors. The more a system is "nested", the more it is organized. Nestedness is a common response to faunal relaxation, as dramatically shown by frogs on Amazonian forest fragments [210]. Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships, and passive sampling may all shape local assemblages into a nested pattern [173].

The most common measurement unit for nestedness is the system “temperature”, introduced by Atmar and Patterson [8], in analogy with physical disorder. This measures the order in which species extinctions would occur in the system (or from the other side - the order of colonizing a system). The “colder” the system is, the more fixed the order of extinction would be. In a warmer system, extinctions will take a more random order so, temperatures go from 0, coldest and absolutely fixed, to 100 absolutely random.

The algorithm first reorganizes the matrix by arranging rows (e.g., species) and columns (e.g., sites) from the most generalist to the most specialists in the way that maximizes nestedness. Given a particular number of S species, distributed in A sites, an isocline of perfect nestedness can be calculated for each matrix (Fig. 2.4).

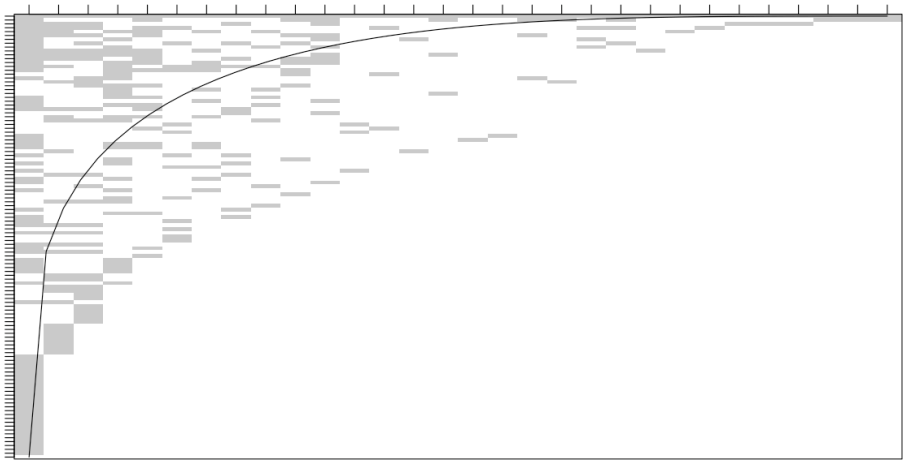


Figure 2.4– Nestedness matrix with species on rows and sites on columns. The line represents the isocline of perfect nestedness. Isolate cells under the line of perfect nestedness show idiosyncratic species, identified by an idiosyncratic temperature higher than the whole system temperature, revealing that species is in some manner disconnected form the system.

For each site (column), all of the absences before the isocline and all of the observed presences beyond the isocline are recorded as unexpected. Recently, Bascompte et al. [11] have derived a measure of nestedness order instead of disorder, called the maximum nestedness order, given by:

$$N = \frac{(100 - T)}{100} \tag{19}$$

with values ranging from 0 and 1.

To assess the significance of nestedness, one must compare the measured nestedness value with a benchmark provided by a null model. The goal is to test whether the observed level of structure can be explained by simple rules (e.g., a derived probability of cell occupancy) or by randomness. In the last few years, an intensive discussion has revolved around null models, and how the conclusions on community structure may depend on our choice of a null model. For a zero-depth on null models in ecology, I would refer to the review of Ulrich et al. [188] and cited literature, giving a useful insight into null models in ecology.

Some potential implications of nestedness for community persistence concern cohesiveness (strictly related to clustering and compartmentalization). In

a common sense, cohesiveness is referred to the way in which nodes (e.g., species) are linked among them generating a dense core of interactions to which the rest of the community is attached. The nested pattern also occurs in spatial network, creating a core in which a set of species using a high number of sites uses a small set of highly used sites.

This cohesive pattern can provide alternative routes for system responses to perturbations. For example, a species is more unlikely to become isolated from the network after the elimination of other species when embedded on a highly cohesive network, and a nested and modular structure can provide useful insight about the spread of information inside the network (e.g., parasite or pathogens as showed by [43]).

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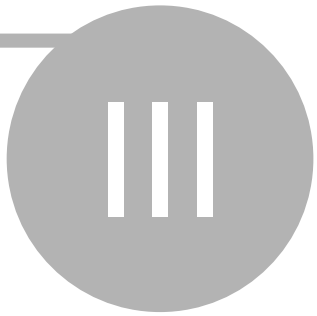

An overview of the study area

3 AN OVERVIEW OF THE STUDY AREA

This chapter shows the main ecological characteristics of saline environments and, in particular, the ecology of Tarquinia saltern. The aim is to introduce the field experiments carried out between the 1st March 2007 and the 1st April 2008 on the colonization and decomposition process of *Phragmites australis* leaf detritus. The saltern shows a strong environmental gradient, following the spatial distribution of the pools and the distance from the inflow of seawater. Among all, salinity was found to be the main structuring parameter of ecological communities, and its influence on the decomposition dynamic revealed its inhibitory effect allowing the persistence of high percentage of leaf detritus that accumulates in sediments. The non-significant association between the number and the abundance of consumers taxa and the decomposition rate by macrodetritivores, and the significant correlation between this latter and the whole community assembly revealed a greater complexity than previously expected. I discuss these preliminary results introducing the next chapters, where more fine analyses were applied to identify the role of temporal and spatial assembly of detritus-based communities on system functionality.

3.1 Introduction

Salt environments, such as coastal lagoon, reservoirs, estuaries and salterns are transitional zones between marine and freshwater environment, characterized by a high instability of environmental parameters. Among the chemical-physical parameters, salinity represents the fundamental variable able to influence the ecology of the entire system.

Because of the limited hydrodynamic, it can be observed the accumulation of organic material, such as limo and detritus where, under high temperatures, the evapotranspiration lead to a drastically decrease of dissolved oxygen in the water column. Because of these characteristics, these environments can be considered as "harsh" environments [68].

As water evaporates, gypsum and other minerals precipitate (e.g., the sodium chloride, NaCl) and salinity increase above 300 gL^{-1} [137]. An example of extreme hyperaline environment is the crystallization ponds or solar salterns, providing a diversity of environments where different conditions of salinity, pH, temperature, light intensity, oxygen and nutrient concentrations are found. Harsh environments are found to exert a controlling influence on the composition and interactions in biological communities, often evident in the simple and productive ecosystems of saline lakes [61]. Low species richness may be due both to severe chemical stress and to high population growth rates of generalist species, as the *Chironomus* spp., a species well-suited to extreme salinity conditions and

variations [194].

In saline systems, two main aspects about species composition are found to be more important: the poor number of species and the high abundances of these latter. Saline systems are extremely selective environments, due to the steepest and variable environmental gradients, such as the salinity variability or their ephemeral characteristics, which allow the adaptation of only a narrow pool of marine and freshwater taxa due to their osmoregulative mechanisms. The selective conditions under which communities are structured allow species to maximize the resources given by the habitat, showing opportunistic reproduction strategies (*r -selected*). The species colonizing these habitats can be subdivided in those that use the habitat only as a source of food and those that develop their life cycle entirely in the salt waters. Saline managed wetlands (e.g., the common salterns) and evaporation ponds are biologically productive aquatic habitats, attracting large numbers of migrating and breeding waterfowl and shorebird populations, representing a fundamental issue for the conservation and management of these ecosystems.

3.2 The Tarquinia saltern

The Tarquinia saltern is an artificial aquatic ecosystem, separated from the sea by a sandy cordon of modest size, that grows at sea level (between 2 and 4 m), in which the salinity and the isolation of the pools represent the main limiting factors for macroinvertebrates communities [20]. This is a Natural Reserve covering an area of about 193 ha, of which about 70% are occupied by the pools used for salt production, and is therefore classified as a hyperaline area. Like all sites for salt extraction in the Mediterranean area, the water passes among various basins to facilitate the separation of solutes and compounds suspended in seawater, the precipitation of dissolved salts and the crystallization of sodium chloride. This led a change in the concentration of salinity, from 35 gL^{-1}, to the point of salt precipitation, 250 gL^{-1}.

The pools are around 100 rectangular basins delimited banks in local limestone or wood of fir, and the water flow between them is ensured through of closed timber and a canal system that surround the pools, needed to transfer water.

All pools are shallow basins (from 0.3 to 0.8 m) and progressively reduced in both area and depth. Water salinity has given rise to an ecosystem characterized by aquatic and terrestrial habitats, rich in animal and plant species adapted to these hyperaline conditions. For instance, it is possible to observe rare plant species, as *Sarcocornia fruticosa* and *Arthrocnemum glaucum*, especially halophytes that form the belt of vegetation in direct contact with the water, tolerating salinity higher than seawater. It is also worth noting the presence of *Phragmites australis*, which grows along the edges of the pools, that constitutes a substantial input of allochtonous vegetable detritus.

From an ornithological point of view, the area of Tarquinia saltern is extremely significant, both as a wintering place and stop-over area during the spring and autumn migration for many species of birds. At least 56 species of birds have been reported during the migration periods, these include *Himantopus himantopus* (Linnaeus 1758), *Egretta garzetta* (Linnaeus 1766), *Recurvirostra avosetta* (Linnaeus 1758), *Sterna sandvincensis* (Latham 1878), *Sterna albifrons* (Pallas 1764), *Sterna caspia* (Pallas 1770), *Chlidonias niger* (Linnaeus 1758), and *Phoenicopterus ruber* (Linnaeus 1758). Macrozoobenthos community is composed of typically opportunistic species [126], among these, the most representative are the gastropods *Hydrobia acuta*, the larvae of chironomids and the amphipods *Corophium insidiosum*.

Spatial heterogeneity of small scale has been observed across the salinity gradient, from North to South, related to the particular conditions of some pools where it can be observed an enrichment of organic sediments. Under these conditions it is possible to highlight the presence of polychaetes species*, Spio decoratus* (Bobretzky 1871) and *Capitella capitata* (Fabricius 1780). The pools are also populated by *Mugil cephalus* (Linnaeus 1758), *Anguilla anguilla* (Linnaeus 1758) and *Aphanius fasciatus*. Therefore, despite the ecological limited conditions, this area is capable of supporting complex communities of fauna and flora.

In this section I introduce the methodological approach followed to measure the colonization and decomposition process of *Phragmites australis* leaf detritus, reporting only the raw results. Most of the elaborations will be presented in the

next chapters, where I tried to answer in more depth about the role of communities structure in maintaining ecosystem function under variable environmental conditions in time and space.

3.3 Materials and methods

Field experiment was carried out between 1st March 2007 and the 1st April 2008 in six sampling pools of the Biological Reserve of Tarquinia saltern, covering the full spectrum of salinity variations (Fig. 3.1).

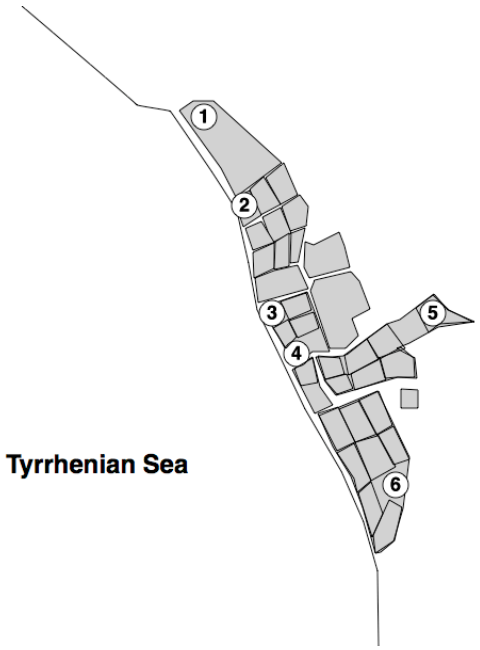

Figure 3.1 – Location of sampling sites in the Biological Reserve of Tarquinia saltern. Mean annual salinity values: **1** = 44.8 ± 2.63 gL^{-1}; **2** = 50 ± 2.84 gL^{-1}; **3** = 88 ± 5.60 gL^{-1}; **4** = 100 ± 7.09 gL^{-1}; **5** = 8.5 ± 2.45 gL^{-1}; **6** = 115 ± 16.62 gL^{-1}.

Two different types of artificial food traps were made up of 2.000 ± 0.004 g dry mass of *Phragmites australis* leaves (leaf-pack technique [143]), weighed to the nearest mg after drying at 60 °C for at least 72 h, and measuring of 10 x 10 cm. The first type had a coarse mesh of 5 x 5 mm, in order to allow substrates colonization by macroinvertebrates. This made it possible to measure the whole decomposition process, taking in account the leaching, conditioning and the consumption rate by detritivores. The other type had a fine mesh of 0.5 x 0.5 mm,

to avoid animal colonization and to measure only the contribution of leaching and conditioning. In each of six sampling stations were immersed 48 coarse and 48 fine mesh bags.

The recovery of mesh bags was done directly into the pools, to avoid the loss of sampled individuals, with a number of $r = 4$ replicates (four fine + four coarse) for each pool with a time step t of one month, for a total of twelve months. For each sampling it was measured the pH, salinity (expressed as gL^{-1}), dissolved oxygen concentration and temperature, using a multi-probe. After the recovery, leaf fragments were weighed to the nearest mg after drying at 60 °C for at least 72 h, and the loss of leaf detritus was derived by the difference with the original weight. For each sampling and for each pool were measured: i) the loss of leaf detritus weight in fine and coarse mesh bags, ii) the taxonomical and functional classification of sampled macroinvertebrates and iii) the number of individuals for each sampled taxon.

Decomposition rates of *P. australis* leaf detritus were estimated starting from Eq.1 and Eq.2 (Chapter 1.3). The global decomposition rate (k_t) was measured from the loss of detritus weight in the coarse mesh bags, while the leaching and conditioning process (k_l) by the loss of detritus weight in fine mesh bags. Thus, the rate of macrodetritivores activity (k_d) was measured as $k_t - k_l$. Sampled taxa were subdivided on the basis of their feeding habits, identifying those with a strictly detritivores diet and those characterized by predatory feeding relationships, according to the available literature [106] [17].

The number of individuals N per taxon i at each time step t, was averaged over the r replicates:

$$\overline{N}_{it} = N_{it} / r \tag{20}$$

with $i = (1, 2,.., S)$ the number of sampled taxa and $t = (1, 2,.., T)$ the number of samplings.

Starting from the above equation it is possible to derive an a-dimensional estimate of the abundance of the i^{th} taxon at time t (n_{it}) by the normalization with the total value, $N_{\mathrm{TOT}} = \sum_{t=1}^{T} \overline{N}_{it}$:

$$n_{it} = \overline{N}_{it} / N_{\mathrm{TOT}} \tag{21}$$

For the quantitative analysis of colonization pattern I considered a proportion of how many times a taxon colonized the detrital substrates in the pools during the field experiment. I defined this proportion, f_i, as the summed number of times a taxon colonized the detrital substrates (i.e., c_i, the number of observed colonization), averaged over the total time T of experiment:

$$f_i = \frac{\sum_{i=1}^{T} c_i}{T} \tag{22}$$

To compare the frequency of colonization (f_i) with the measured dimensionless abundances, both these measures were normalized above the maximum measured value (f_i max and n_i max).

3.4 Results

Results showed how the measured temperatures did not differ significantly among pools (one-way ANOVA $F_{5,65} = 1.757$, $P = 0.996$), and the same trend can be observed for the dissolved oxygen concentration (one-way ANOVA $F_{5,65} = 0.334$, $P = 0.888$). The ANOVA indicated a significant difference among pools as regards the pH (one-way ANOVA $F_{5,65} = 5.655$, $P < 0.001$) and salinity (one-way ANOVA $F_{5,65} = 89.06$, $P < 0.001$) (Table 3.1 and Table 3.2).

Table 3.1 – ANOVA with Bonferroni post-hoc test for pH. Bold font is for significant values. pH1 and pH2 are for the comparison between the pH measured in pool 1 and pool 2, and so on.

Comparison	Mean Difference	*t*-Value	*P* - Unadjusted	*P* - Bonferroni	η^4
pH1 and pH2	0.165	2.447	0.034	0.516	0.353
pH1 and pH3	0.192	4.364	0.001	**0.021**	0.634
pH1 and pH4	0.185	3.135	0.011	0.159	0.472
pH1 and pH5	0.270	2.316	0.043	0.645	0.328
pH1 and pH6	0.277	3.025	0.013	0.192	0.454
pH2 and pH3	0.356	4.074	0.002	**0.034**	0.601
pH2 and pH4	0.349	5.777	0.000	**0.003**	0.752
pH2 and pH5	0.435	3.861	0.003	**0.047**	0.575
pH2 and pH6	0.442	4.772	0.001	**0.011**	0.674
pH3 and pH4	0.007	0.092	0.928	1.000	0.001
pH3 and pH5	0.078	0.571	0.581	1.000	0.029
pH3 and pH6	0.085	0.826	0.428	1.000	0.058
pH4 and pH5	0.085	1.137	0.282	1.000	0.105
pH4 and pH6	0.093	1.554	0.151	1.000	0.180
pH5 and pH6	0.007	0.078	0.939	1.000	0.001

Table 3.2 - ANOVA with Bonferroni post-hoc test for salinity. Significant values are bolded. Sal1 and Sal2 are for the comparison between the salinity measured in pool 1 and pool 2 and so on.

Comparison	Mean Difference	*t*-Value	*P* - Unadjusted	*P* - Bonferroni	η^4
Sal1 and Sal2	5.727	3.654	0.004	0.066	0.548
Sal1 and Sal3	40.818	14.845	0.000	**0.000**	0.952
Sal1 and Sal4	55.545	14.681	0.000	**0.000**	0.951
Sal1 and Sal5	36.000	21.584	0.000	**0.000**	0.977
Sal1 and Sal6	70.727	8.624	0.000	**0.000**	0.871
Sal2 and Sal3	35.091	14.425	0.000	**0.000**	0.950
Sal2 and Sal4	49.818	15.685	0.000	**0.000**	0.957
Sal2 and Sal5	41.727	16.108	0.000	**0.000**	0.959
Sal2 and Sal6	65.000	8.347	0.000	**0.000**	0.864
Sal3 and Sal4	14.727	7.264	0.000	**0.000**	0.827
Sal3 and Sal5	76.818	21.117	0.000	**0.000**	0.976
Sal3 and Sal6	29.909	3.816	0.003	**0.050**	0.570
Sal4 and Sal5	91.545	18.072	0.000	**0.000**	0.967
Sal4 and Sal6	15.182	2.409	0.037	0.551	0.345
Sal5 and Sal6	106.727	11.244	0.000	**0.000**	0.920

[4] η is the proportion of the total variance that is attributed to an effect. It is calculated as the ratio of the effect variance (SS_{effect}) to the total variance (SS_{total}): $H_2 = SS_{effect} / SS_{total.}$

As observed in Tables 3.1 and 3.2, the parameters that showed significant differences were the pH and salinity. An interesting question in studying salt environments is whether species diversity of entire macroinvertebrates guild is affected by the salinity conditions. Salinity, to some degree at least, and either directly or indirectly, is a determinant of community structure in inland bodies of saline water, where species diversity gradually decreases with increasing salinity [61].

As pointed out by several authors [55] [187], the attempt to quantify a multidimensional concept such as biodiversity with a single number is an endeavor that is doomed to failure. It is inevitable that certain situations where the arbitrary choice of diversity index will make a difference in which of two samples are found to have higher diversity. Thus, diversity profiles, such as the Rényi entropy, are often used to alleviate this concern, able to compare the diversity indices collected from different locations or from the same location over time. This is because two of the common measures of diversity often used in ecology (Shannon's and Simpson's measures) are special cases of Rényi entropy.

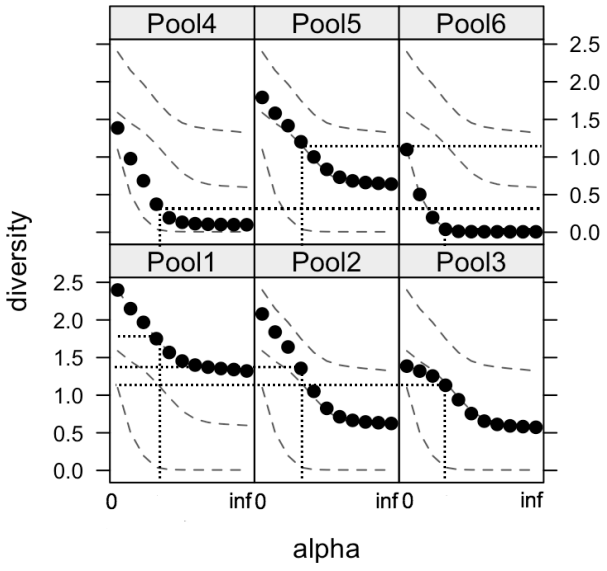

Figure 3.2 – Diversity profiles for sampled pools. Rényi entropy profile is defined as $H_\alpha = \log \sum p_i^\alpha \Big/ (1-\alpha)$, $\alpha \geq 0$, $\alpha \neq 1$. The Shannon index is a limiting function of H_α as $\alpha \to 1$. Ticked lines are, from top to the bottom, the maximum, median and minimum diversity profile found for the six detritus-based communities, and the black circles are the measured diversity profile. Vertical dot lines correspond to $\alpha = 1$, and the crossing with the measured diversity profile gives the Shannon diversity on the *y*-axes.

Diversity profiles (Fig. 3.2) showed the differences among communities. The highest diversity was found for pool 1 (H_2 = 1.751, water salinity near seawater), while the lowest degree of diversity for pool 6 (H_2 = 0.039, hyperaline waters). Pool 5 and pool 2 showed quite similar diversity values (respectively 1.202 and 1.356), yet differing for species richness (or multiplicity, the points on the extreme left of the graph in Fig. 3.2). Moreover, pool 2, 3 and 5, although differ in the diversity values, had an identical dominance of species (the extreme right points on the graph in Fig. 3.2).

Results also revealed highest species diversity for intermediate values of salinity, with a best fit given by a quadratic model (Fig. 3.3).

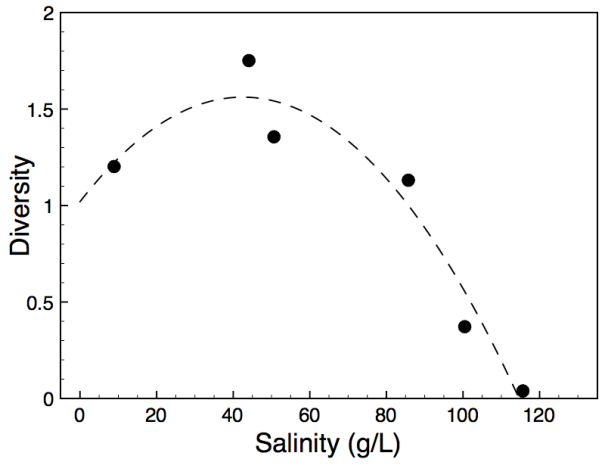

Figure 3.3 – Diversity *vs* salinity relationship. The best fit is given by a non-linear model: $y = -0.0003x^2 + 0.026x + 1.02$, $R^2 = 0.94$.

Salinity influences the diversity and abundance of species, which reveals the asymmetry in the diversity-abundance relationship. The distribution of taxa is highly skewed, observing few taxa with high abundances and a bulk of taxa with a lower number of sampled individuals (Fig. 3.4). However, in comparisons of species richness it is important to account for differences in the number of individuals in the different samples.

Owing to random sampling, a sample of 100 individuals is likely to contain more species than a sample of, for example, 10 individuals. Rarefaction [173] [54] can account for this effect. After rarefaction species richness varies from sites to sites (Fig. 3.5) and, therefore, the environmental characteristics of the pools on the diversity of macroinvertebrates can be detected after adjusting for differences in total abundance of macroinvertebrates.

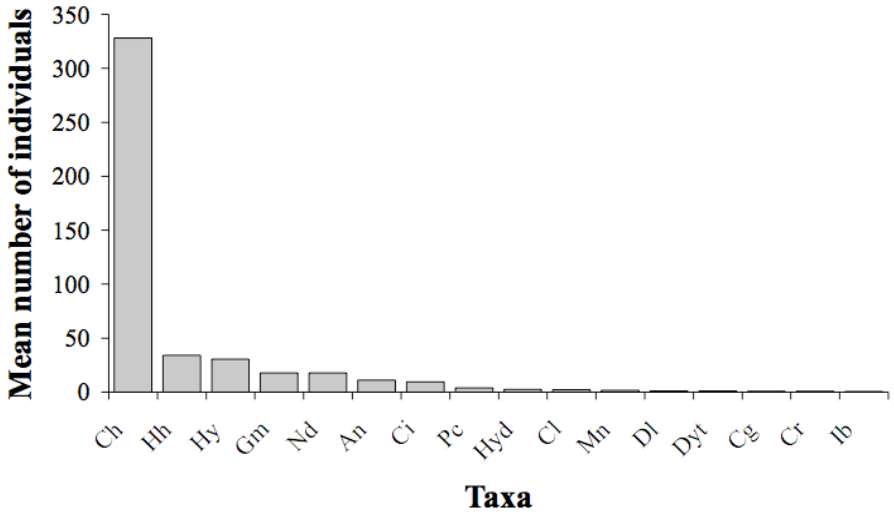

Figure 3.4 – Mean number of individuals *per* taxa. Distribution has a right skewed tail indicating a strong asymmetry in the distribution of sampled individuals *per* taxa. Taxa legend: Ch = *Chironomus* spp. (larvae); Gm = *Gammarus aequicauda*; Pc = *Perinereis cultrifera*; Gd = Gordiidae; Hy = *Hydrobia acuta*; Cg = *Cerastoderma glaucum*; Cr = *Cerithium rupestre*; Dl = (other) Diptera (larvae); Ci = *Corophium insidiosum*; Ib = *Idotea baltica*; Dyt = Dytisicidae (larvae); Hyd = Hydrophilidae; Cl = (other) Coleoptera (larvae); Nd = Nereidae; Po = Polychaeta; Hh = *Haliplus* sp; Mn = *Micronecta* sp. (larvae); An = Anisoptera (nymphae).

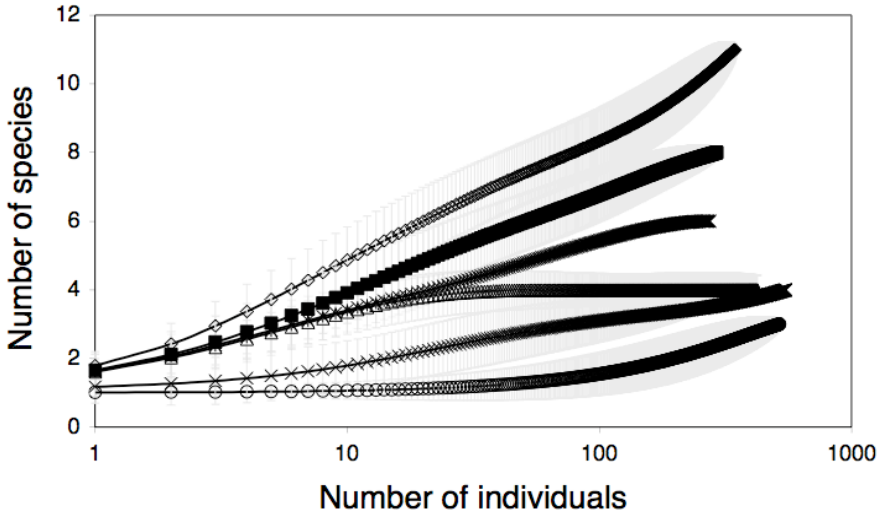

Figure 3.5 – Rarefaction curves for species richness of macroinvertebrates sampled in each pool. Rarefaction calculations were performed using EcoSim software [53]. Continuous lines indicate expected richness; error bars are 95% confidence limits calculated over 1000 iterations of the simulation. ◇: Pool 1; ■: Pool 2; ✱: Pool 5; △: Pool 3; ×: Pool 4; ○: Pool 6. The number (*N*) of individuals is expressed as log(*N*) to reduce the differences of the absolute values of abundance among pools.

Environmental conditions might influence the colonization dynamic of macroinvertebrates because of their seasonal fluctuation and species turnover. The distribution of the frequencies of colonization (Eq.17) and abundances (Eq.18) revealed how the most abundant taxa were also the most widespread (Fig. 3.6). This finding showed how the colonization pattern was a process mainly driven by the salinity conditions under which the communities are structured [156] [68], leading to a nonrandom pattern of colonization.

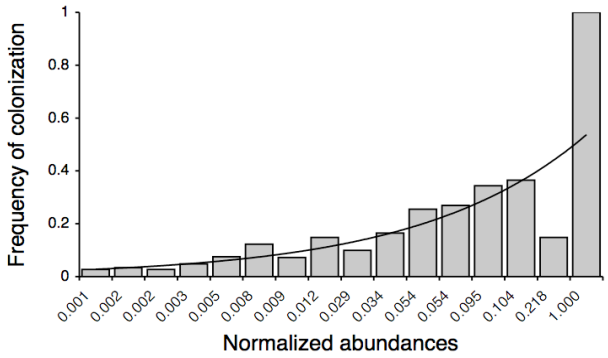

Figure 3-6 – Distribution of the frequencies of colonization and abundances of sampled taxa. The left skew tail of the distribution reveals the asymmetry in frequency of colonization.

The environmental conditions might also influence the decomposition of leaf detritus, enhancing or diminishing the rate at which detritus is consumed by macroinvertebrates. Results showed significant differences in the rates of decomposition of *P. australis* leaf detritus (one way ANOVA, $F_{3,23}$ = 4.54, P = 0.014) (Fig. 3.7).

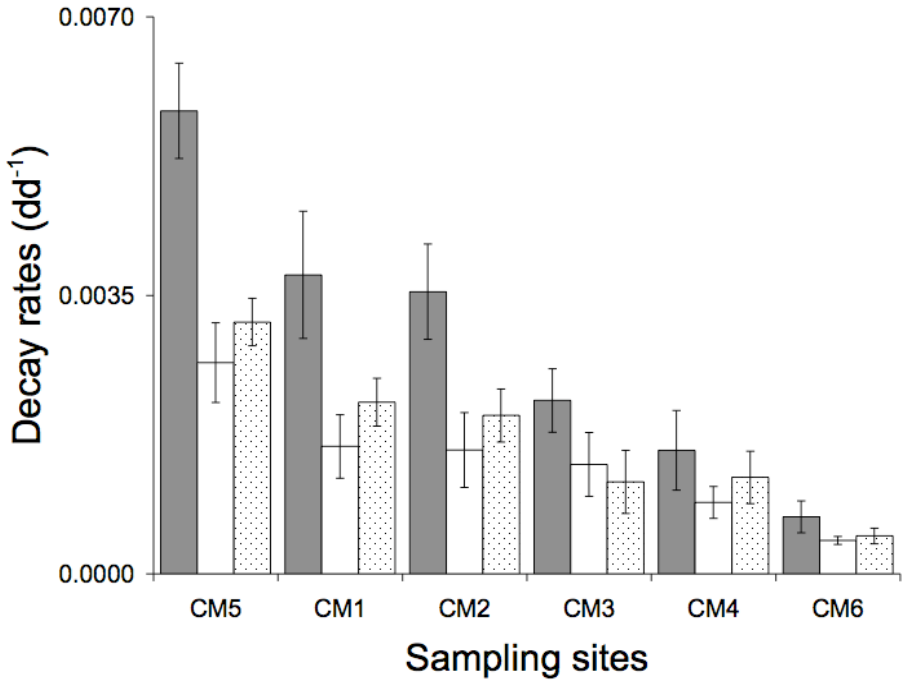

Figure 3.7 – Decomposition rates of *P. australis* leaf detritus. Filled bars: decomposition given by leaching + conditioning + macrodetritivores activity; blank bars: decomposition given by leaching + conditioning; dotted bars: decomposition given by macrodetritivores activity. All values are expressed as dd^{-1} (mean ± 2SE).

Correlation analysis (Spearman's ρ correlation) revealed as none of the decomposition rates was significantly correlated with the temperature, pH and dissolved oxygen concentration. All measured decomposition rates were correlated only with the salinity (Table 3.3), following a negative linear model (Fig. 3.8).

Table 3.3 – Spearman's ρ correlation test between the decomposition rates (columns) and the environmental parameters (rows). Italic font is for the level of significance (*P*), solid for the correlation coefficient (ρ). Significant correlations are bolded.

Parameters	k_t	k_l	k_d
T	0.424	0.386	0.371
P-value	*0.40*	*0.45*	*0.47*
pH	0.208	0.105	0.219
P-value	*0.69*	*0.84*	*0.68*
O_2	0.620	0.479	0.576
P-value	*0.19*	*0.34*	*0.23*
p.s.u.	**-0.996**	**-0.961**	**-0.986**
P-value	***0.00***	***0.00***	***0.00***

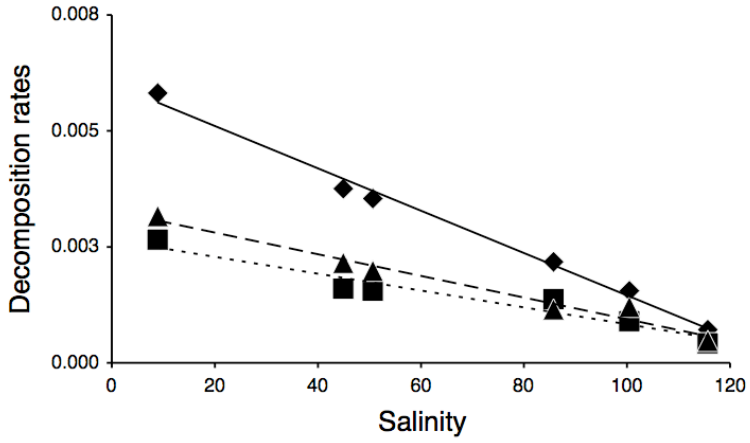

Figure 3.8 – Linear regression between the decomposition rates (mean *k*'s) of *P. australis* leaf detritus and salinity (mean ± 2SE). ◆: k_t; ▲: k_d; ■: k_l. Model fit k_t = -5E-05x + 0.006; k_d = -2E-05x + 0.0033; k_l = -2E-05x + 0.0026.

To account the role of macroinvertebrates on the decomposition of leaf detritus, taxa were identified on the basis of their feeding habits ([106] and literature cited). Correlation test revealed a non-significant association between k_d and the number (ρ = 0.642, P = 0.169) and abundances (ρ = -0.522, P = 0.229) of macrodetritivores. However, results showed a significant correlation between k_d and the total number of sampled taxa (ρ = 0.890, P = 0.018) and the total abundances of macroinvertebrates (ρ = -0.859, P = 0.029).

These findings allow to make hypothesis about how the cumulative effect of the whole community assembly on the decomposition rate of leaf detritus can be much more complex than expected.

3.5 Discussion

Many studies have addressed the effect of salinity on the biota in salt environments [204] [205]. For the most part, these have usually been restricted to determining the salinity tolerance of individual species or species groups and the nature of their physiological adaptations. In broad summary, they show that typical species of moderately saline environments have relatively narrow absolute tolerance ranges, whereas typical species of highly saline environments have very wide absolute tolerances. This account for an important general point: the biota of salt environments can survive over very wide ranges of salinity within the total range of salinity encountered in salt environment. This accords with the results of those studies that have examined the nature of biological communities (as distinct from individual species or species groups) at different salinities.

Relevant studies of this type are basically of two sorts: i) those which have examined differences in community structure, as indicated by changes in species richness and diversity at different salinities in a wide variety of different environments, and ii) those which have described changes in the composition of biota in individual salt environment undergoing increasing in salinity. The present study falls in the middle of above mentioned, since it describes the changes in the composition of biota in individual salt environment, subjected to increasing salinity in a variety of connected patch environments.

As shown by several authors [204] [205], salinity could be considered an indirect determinant of species occurrence, since the major determinants probably included other mechanisms, such as stochasticity in population dynamics, predation, food availability, competition and other forms of biological interaction and mechanisms (e.g. osmoregulatory stress, or the removal of predators).

Results show how salinity influences the number of sampled taxa and their abundances, highlighting how communities undergoing high salinity are composed by generalist (poor) widespread species. I found how, from low to moderate salinity, communities composition differs in terms of richness, diversity and dominance of taxa. On the contrary, for communities undergoing highest salinity, the number of species, the diversity and the dominance have almost the same values (see pool 4 and 6 in Fig. 3.3), and communities are composed by the

same (poor) number of extremely generalist species, such as the larvae of *Chironomus* spp., a species well-suited and adapted to extreme salinity conditions [194].

Generalism for a species have been defined [108] in a variety of ways: i) a species that maintain a variety of specialist genotypes that can be expressed depending upon the environmental conditions, ii) species in which each genotype has the ability to express various phenotypes depending upon environmental conditions (the so-called phenotypic plasticity), and iii) the *jack-of-all-trades* - a species with phenotypes intermediate to the range of environmental conditions experienced. This trade-off can influence the performance of species, predicting that a generalist will outperform a specialist under fluctuating and non-optimal environmental conditions [159], in which the costs of being a generalist are small relative to the benefits of the increased behavioural reduction in performance of the specialist [51].

However, comparisons under natural conditions are confounded by the multitude of biotic and abiotic interactions [87]. In this context, the network analysis will show how it is possible to identify the role of species within a community based on their position within the network, revealing its importance in maintaining network structure, functioning and resilience [52]. Several studies suggest that the cohesive patterns of some ecological networks confer robustness, making them less vulnerable against species deletion and slightly compromising their ability to provide essential ecosystem functions (e.g., nutrient recycling, decomposition) [97].

Salinity was found to be the only environmental parameter significantly correlated with the decomposition rates of *P. australis* leaf detritus [26]. The role of salinity on the leaching and conditioning rates might involve some changes related to decreases in enzymatic activity of microfungi and bacteria on the decaying leaves. As observed by many (see [120] and cited literature), the quality of detritus is tied to the degree of microbial and microfungi colonization, such that it may be more useful in some cases to consider them as grouped entities, as higher consumers in the detrital branch may not distinguish between the consumption of detritus and the microorganisms that feed on it.

This means that the rate of colonization of detrital substrate by macroinvertebrates could be influenced indirectly through changes in salinity to which cascaded to other elements of the biota. This is probably because the indirect effect of salinity on the structuring process of ecological communities involves other mechanisms, such as the effect of competitive and predator/prey type interactions and these mechanisms can be detected only looking at the whole community assembly.

Moreover, as I show in the next chapter, salinity variations affect the number and abundances of predators taxa (this does not happen for consumers), involving a "cascade effect" on the structuring process of detritus-based communities and their ability to process the leaf litter detritus.

Predation in salt environment has been shown to be an effective biological interaction [68] in structuring communities and determining the distribution and abundance of individual species. Herbst [68] studied populations of *Ephydra hians* in two salt lakes in the western USA, founding that species distribution was determined by ecological factors (especially predation) at the lower range of the salinity tolerated by it and by physiological factors at the upper range of salinity. He referred to this idea as the *intermediate salinity hypothesis*, where communities structure and function have been postulated to be optimized between the ecological losses imposed by predation and competition at low to intermediate salinity and the physiological limits of high salinity stress.

Species diversity in the detritus-based communities of Tarquinia saltern seems to follow this trend (Fig. 3.4), revealing the maximum degree of diversity for intermediate levels of salinity. However, decay rates of leaf detritus do not follow this trend, observing a linear negative relationship with increasing salinity (Fig. 3.8).

Therefore, since the process of detritus consumption involves a complex web of interactions, including competition and predation, the cumulative effect of the whole community assembly on the decomposition rate of leaf detritus could be more complex than expected. This is because the stress imposed by the seasonal variations of salinity (e.g., the coefficient of variation, see Chapter 4) probably has a greater influence on the structure and functioning of ecological

communities, altering the effect of ecological adaptation and physiological responses of macroinvertebrates, which in turn may affect the entire system functionality.

PART

Salinity dependent alteration in the network structure of detritus-based communities in a Mediterranean saltern

4 SALINITY DEPENDENT ALTERATIONS IN THE NETWORK STRUCTURE OF DETRITUS-BASED COMMUNITIES IN A MEDITERRANEAN SALTERN

The structural properties of ecological communities are known to influence key ecosystems functions, such as the decomposition of leaf detritus in terrestrial and aquatic environments. However, the identification of a common pattern between communities structure and functioning remains unclear because some species may be far more important than others in maintaining ecosystems functioning. The degree of importance of species may derive from the ecological conditions under which communities are structured, influencing the interactions structure within the network of interspecific interactions. Here I used a methodological approach drawn by network theory to understand the influence of salinity on the structure of detritus-based communities and their ability to process the detrital substrates. My attention has been directed to the degree of network centralization, designed as the effect of each species overall network connectivity and functioning. I studied six different detritus-based communities, which structuring process was made under different condition of salinity in a shallow saline environment, using colonization data on the leaf detritus of *Phragmites australis* during a twelve months field experiment. My results indicate how the different responses of species to changing salinity conditions during the seasons can lead to an increased structural heterogeneity of the networks, which influences the rate at which detritus is consumed by macrodetritivores. This reveals that the presence of structurally important species may have direct and indirect effects on the whole ecosystem integrity and functioning, suggesting a particular attention and management in habitat conservation practice.

4.1 Introduction

Many observations and experiments show how the composition of ecological communities (e.g., species richness and abundances) changes along gradients in environmental factors, observing how those communities sharing similar environmental conditions may converge on similar compositions [186]. Communities composition and species coexistence require some form of temporal niche differentiation by which different species respond differently to variations in their environment [96].

Moreover, the consequences of changes in communities composition may be reflected in a change in their functioning, such as the ability to process the detrital substrates [156] [68], a key process in regulating the regeneration of carbon and nutrients, being an important link between primary and secondary production [42].

In aquatic ecosystems this involves three main mechanisms; i) the rapid weight loss of soluble constituents, ii) the modification of detrital matrix by microorganisms and iii) the feeding activity of macroinvertebrates, where species richness, diversity and abundances influence the consumption rate of detritus.

However, species interactions are found to be of greater influence on decomposition dynamics, suggesting how the richness–functioning relationship may be driven by direct (abundances) and indirect (predation and competition) mechanisms [35]. Which species are important and how they interact to create and maintain species diversity patterns represent a key issues to understand the mechanisms of decomposition processes.

Several studies show a significant decrease in the rate of leaf litter decomposition with declining species richness, both in terrestrial [125] and in aquatic ecosystem [200]. However, decomposition may be only weakly correlated with species richness and the total abundance of detritivores organisms, because some species are far more important than others (for a complete review see [120]). This view supports the idea that the presence of keystone taxa (i.e., topological keystone species *sensu* [80]) may be more important for decomposition [196] than species diversity *per se*.

In network analysis, the role a species plays in a community can be measured by the centrality indices [38] [7], which indicate the relative importance of each node inside the network, and the choice of using a particular index is a direct consequence of whether our community data are directed, signed and/or weighted [191]. Network position considers the neighborhood of each species and provides an evaluation of how rich the interaction pattern of a particular species is, and this is particularly important in systems where indirect effects (i.e., competition for resource) dominate [79]. Beyond the importance to quantify the positional index of species, it is also of interest understand to what extent each species centrality influences the whole network structure, by evaluating the degree of network centralization, a measure able to quantify topological redundancy and the degree of structural heterogeneity in interaction networks.

In this work, I studied the colonization process of leaf detritus by using the network analysis, to understand how the gradients of environmental conditions in artificial aquatic ecosystem may influence the network structure of detritus-based communities and their ability to process the detrital substrates. My attention has been directed to the degree of network centralization, designed as the effect of each node centrality overall network connectivity and functioning. Here I show

how including the colonization ability of species in network analysis may allow a more robust assessment of each species impact on its community and a greater understanding of the relationship between community structure and functioning, giving useful insights for conservation and management.

4.2 Materials and methods

4.2.1 Study area

The study area is the Biological Reserve of Tarquinia Saltern (42°12 N, 11°43' E), a heterotrophic ecosystem where the mean annual respiration exceeds primary and secondary production [126]. The area is divided into 36 pools at different salinity, in a range between hyposaline (8.5 gL^{-1}) to hyperaline waters (up to 100 gL^{-1}), with an input of allochtonous vegetable detritus, especially of *Phragmites australis* (Cav.) Trin. ex Steud (Fig. 4.1).

Pools are shallow (depth range 0.30 - 0.80 m) and closed basins with low surface (ranging from a minimum of 11 to a maximum of 60 ha), making the Tarquinia Saltern a confined environment characterized by a low hydrodynamics increased by a scarce water refill between the pools.

During the field experiment water temperature did not differ among sampled pools and ranged between a maximum of 29 ± 1.7 °C and a minimum of 8 ± 2.3 °C, pH ranged between 8 – 8.32, while dissolved oxygen concentration varied from 5.39 ± 0.900 to 7.38 ± 0.772 mgL^{-1}.

4.2.2 Community approach

I assumed that the availability of detrital resource during the field experiment was equal for all the taxa that have colonized the leaf packs. The proportional use of the resource during each time step t was defined as p_{it}, assuming $\sum_{i=1}^{T} p_{it}$ where p_{it} may be estimated by the proportion of observed individuals of taxon i on the detrital resource at time t, with $t = (1,..,T)$. Similarly, taxon j had proportion p_{jt}, and so on for each sampled taxon (S).

Thus, niche overlap between taxa i and j can be measured as $NO_{ij} = \sum_{t=1}^{T} \min(p_{it} p_{jt})$ [124]. Each measured overlap index represents the entry

of the community matrix $\mathbf{A} = [\alpha_{ij}]$, hereafter CM, that expresses the potential interferences among taxa[5].

4.2.3 Network approach

Mathematically, the eigenvector centrality (x_i) of a vertex *i,* is represented as:

$$x_i = \frac{1}{\lambda}\sum_{j=1} A_{ij}x_j \tag{23}$$

with λ constant.

The value of x_i depends on the centralities of neighboring nodes of node *i* so, if neighbors of *i* have high centralities, then *i* also has a high centrality

In vector notation this can be represented as $\mathbf{A}\vec{x} = \lambda\vec{x}$. This is an eigenvector equation, where $\vec{x}$ represents an eigenvector of the adjacency matrix of a weighted directed graph A_{ij} with the eigenvalue λ. In general, there can be many different eigenvalues λ for which an eigenvector solution exists. The largest eigenvalue produces a non-negative eigenvector, which represents the eigenvector centrality score of network nodes [14].

To sum up, eigenvector centrality is defined in a way that a node centrality depends on both the number of connections and their weight, i.e., the way in which the adjacency matrix A_{ij} was derived.

After, I measured the effect of each node on the whole community by the normalization of the summed difference between the maximum centrality and all nodes centrality with the minimum possible links observed for a network of nodes *S*, that is *S*-1.

[5] See Appendix A2

Thus, network eigenvector centralization $C(N)$ can be expressed as:

$$C(N) = \frac{\sum_{i \in N} [x_i \max - x_i]}{\max \sum_{i \in N} [x_i \max - x_i]} \quad (24)$$

where x_i is the eigenvector centrality score for node i in network N, and the maximum in the denominator is taken over all networks in a specified class that includes N. Network centralization ranged between 0 and 1, and will be 0 if all nodes achieve the same centrality score and 1 if one node dominates over all others.

As a measure of functionality, I chose to express the macrodetritivores activity by its coefficient of variation ($CV_m = \sigma_m / \mu_m$), the standard deviation of the monthly measured k_d 's above the mean, given a dimensionless measure of functional variability [145]. Since the mean annual salinity strongly differs from pool to pool, I measured the salinity by its coefficient of variation ($CV_s = \sigma_s / \mu_s$), to allow a comparison between sampling sites.

In order to explore the role of the whole network structure on the decomposition of leaf detritus, I correlated the measure of functional variability, CV_m, with the structural variability of observed communities, $C(N)$. This is because the different colonization ability of macroinvertebrates under different conditions of salinity variability (CV_s), i.e., the presence of the most widespread taxa with high abundances during the seasons, might influence the structural composition of communities. Here I show how the whole community assembly can reveal more about the relationship between communities structure and functioning.

4.3 Results

4.3.1 Decomposition of leaf detritus

I found a significant difference in the remaining dry weight of *P. australis* leaf detritus among the six sampling sites after 360 dd of field experiment, where a higher proportion was measured in hyperaline waters (Table 4.1).

In hyposaline waters (mean annual salinity 8.5 ± 2.45 gL^{-1}), the percentage of final dry weight in the coarse mesh bags was about 25%, while in hyperaline waters (mean annual salinity 115 ± 16.62 gL^{-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 (Fig. 4.1). The loss of leaf dry mass follows a negative exponential model in each sampled stations, according to Olson [136] (Table 4.1).

Table 4.1 - Remaining dry weight of *Phragmites australis* leaf detritus in coarse and fine mesh bags and statistical significance (Spearman's ρ correlation) of dry mass lost of leaf detritus at the end of field experiment (360 dd). Bold is for the statistical parameters derived from the fine mesh bags experiment. All leaf packs lost mass according to a negative exponential model (Olson 1963) with $P < 0.001$. Data are ordered from hyposaline (top) to high-hyperaline waters (bottom). Salinity is expressed as gL^{-1} (mean ± 2SE).

	Salinity	% dry weight (coarse)	% dry weight (fine)	ρ	d.f.	P - value
CM5	8.5 ± 2.45	25.43	47.89	-0.91**(-0.92)**	10	< 0.001
CM1	44.8 ± 2.63	31.88	60.12	-0.92**(-0.89)**	10	< 0.001
CM2	50 ± 2.84	34.38	62.14	-0.96**(-0.93)**	10	< 0.001
CM3	88 ± 5.60	56.53	71.57	-0.97**(-0.97)**	10	< 0.001
CM4	100 ± 7.09	49.60	79.77	-0.98**(-0.85)**	10	< 0.001
CM6	115 ± 16.62	78.70	78.20	-0.92**(-0.98)**	10	< 0.001

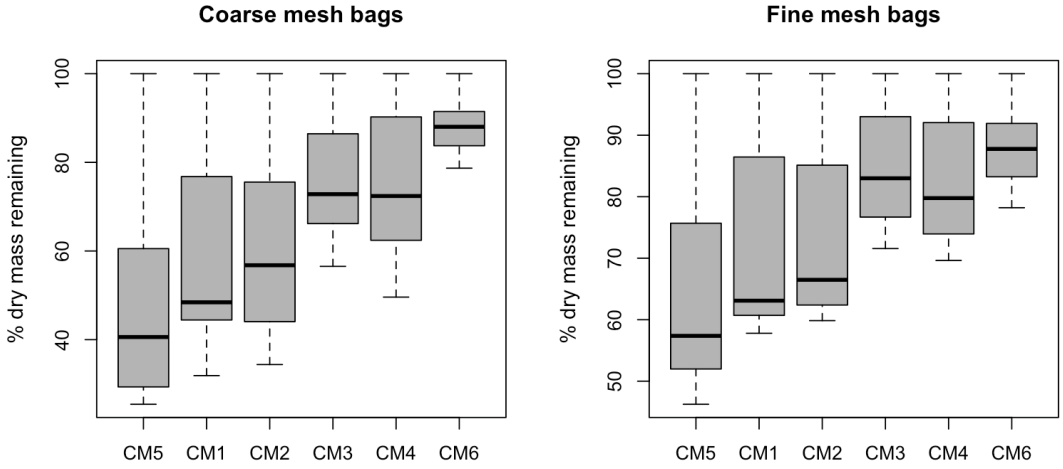

Figure 4.1 - Box plots showing the dry mass remaining (%) of *Phragmites australis* leaf detritus in coarse and fine mesh bags. The horizontal line dividing boxes in two indicates the median, box limits are the first and third quartiles of the distribution and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. Data are ordered from left to right following salinity gradient, from hyposaline (CM5, 8.5 ± 2.45 gL^{-1}) to highly hyperaline waters (CM6, 115 ± 16.62 gL^{-1}).

Decomposition rates of *P. australis* detritus decreased with the increase of salinity values (one-way ANOVA $F_{5,15} = 17.12$, $P < 0.001$), highlighting how the global decomposition rate (k_t), the leaching and conditioning rate (k_l), and the macrodetritivores activity (k_d) were faster in hyposaline waters than in hyperaline waters (Table 4.2).

Table 4.2 - Decay rates (mean ± 2SE) of leaf detritus: k_t = global decomposition rate; k_l = leaching rate + conditioning; k_d = macrodetritivores consumption rate. Salinity is expressed as mean (± 2SE).

	Salinity (gL^{-1})	k_t (dd^{-1})	k_l (dd^{-1})	k_d (dd^{-1})
CM5	8.5 ± 2.45	0.0058 ± 0.00070	0.0027 ± 0.00060	0.0031 ± 0.00040
CM1	44.8 ± 2.63	0.0038 ± 0.00080	0.0016 ± 0.00070	0.0022 ± 0.00060
CM2	50 ± 2.84	0.0035 ± 0.00060	0.0016 ± 0.00090	0.0019 ± 0.00030
CM3	88 ± 5.60	0.0022 ± 0.00090	0.0014 ± 0.00030	0.0008 ± 0.00040
CM4	100 ± 7.09	0.0016 ± 0.00070	0.0009 ± 0.00008	0.0007 ± 0.00030
CM6	115 ± 16.62	0.0007 ± 0.00002	0.0004 ± 0.00003	0.0003 ± 0.00001

4.3.2 Network structure

The increase of salinity conditions resulted in a decrease of the number of sampled taxa during the colonization process of leaf detritus; among sampled taxa, 10 were classified as detritivores and 8 as predators. In hyposaline waters it can be observed one central taxon at high value of centrality (0.596), the nymphae of Anisoptera, in dominance position with respect to other taxa (Table 4.3 and Fig. 4.2).

In a range of salinity between 44.8 ± 2.63 and 50 ± 2.84 gL^{-1}, the centrality scores highlighted the presence of the larvae of Coleoptera, *Cerithium rupestre* and *Gammarus aequicauda* in CM1 (0.522, 0.521 and 0.471, respectively), and four main taxa in CM2, Polichetae (0.465), *Idotea baltica* (0.466), *Corophium insidiosum* (0.466) and *Perinereis cultrifera* (0.421) (Table 4.3).

With the increase of the mean annual salinity, in a range between 88 ± 5.60 and 115 ± 16.62 gL^{-1} (CM3, CM4 and CM6), the most central taxon was represented by the larvae of *Chironomus* spp.. However, the differences among the centrality scores in CM3 and CM4 were lower than in CM6, where the presence of *Haliplus* sp. was only marginal (0.053).

Lower variations of k_d, that lead to a better efficiency in detritus consumption during the seasons, can be observed for high values of $C(N)$, that showed a negative correlation with CV_m (r = -0.89, P = 0.016) (Table 4.4). $C(N)$ was scale-invariant with respect to network size (r = 0.06, P = 0.897), allowing for a comparison among different size-structured communities, and increased with the increase of salinity variations (CV_s) (r = 0.92, P = 0.008), where the communities undergoing highest salinity variations (CM5 and CM6) were also characterized by highest values of centralization (Table 4.4).

Table 4.3 - Number of sampled taxa and eigenvector centrality scores. Mean annual salinity values (± 2SE): CM1 = 44.8 ± 2.63 gL^{-1}; CM2 = 50 ± 2.84 gL^{-1}; CM3 = 88 ± 5.60 gL^{-1}; CM4 = 100 ± 7.09 gL^{-1}; CM5 = 8.5 ± 2.45 gL^{-1}; CM6 = 115 ± 16.62 gL^{-1}.

		CENTRALITY SCORES					
		CM1	CM2	CM3	CM4	CM5	CM6
Detritivores	*Chironomus* spp. (larvae)	0.165	0.091	0.586	0.676	0.451	0.745
	Gammarus aequicauda	0.471	0.382	-	-	-	-
	Perinereis cultrifera	0.132	0.421	-	-	-	-
	Gordiidae	0.034	-	-	-	-	-
	Hydrobia acuta	0.337	0.001	0.530	0.316	-	-
	Cerastoderma glaucum	0.087	0.006	0.493	0.341	-	-
	Cerithium rupestre	0.521	-	-	-	-	-
	(other) Diptera (larvae)	-	0.009	-	-	0.272	-
	Corophium insidiosum	-	0.466	-	-	-	-
	Idotea baltica	-	0.466	-	-	-	-
Predators	Dytiscidae (larvae)	-	-	-	-	0.249	-
	Hydrophilidae	-	-	-	-	0.206	0.664
	(other) Coleoptera (larvae)	0.522	-	-	-	0.272	-
	Nereidae	0.257	0.093	-	-	-	-
	Polychaeta	-	0.466	-	-	-	-
	Haliplus sp	-	-	0.118	0.570	0.231	0.053
	Micronecta sp (larvae)	-	-	-	-	0.367	-
	Anisoptera (nymphae)	-	-	-	-	0.596	-

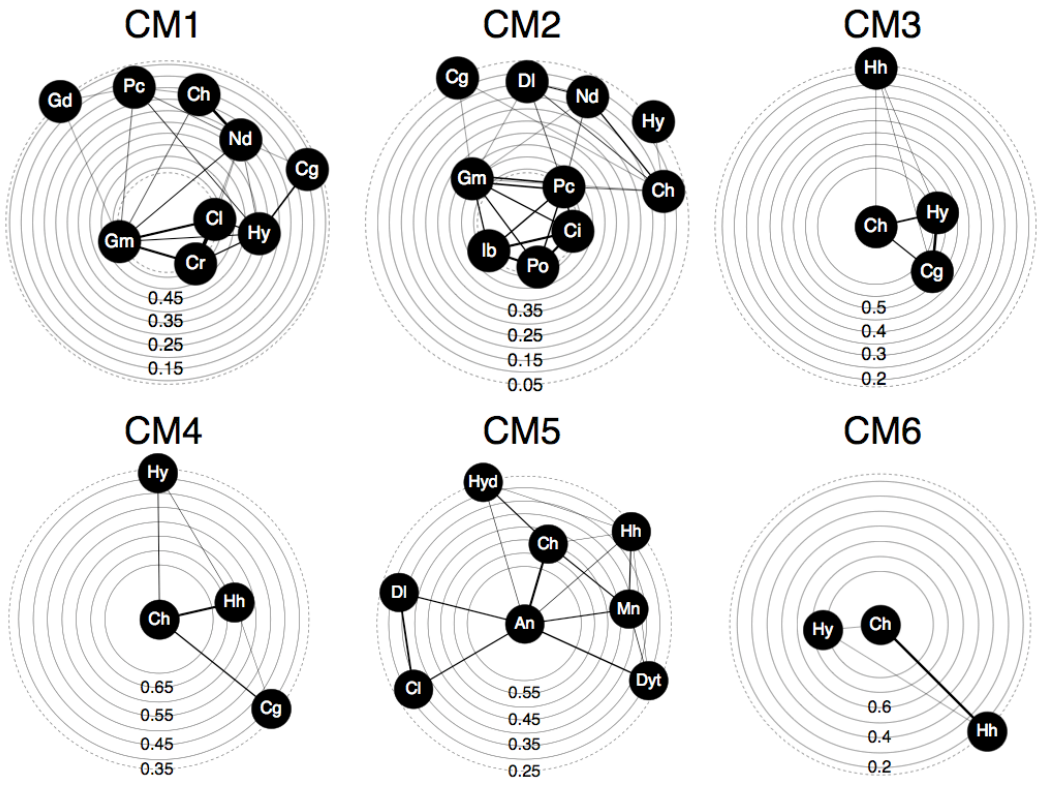

Figure 4.2 - Radial visualization of eigenvector centrality. Thickness of lines is proportional to the measured interferences Taxa legend: Ch = *Chironomus* spp. (larvae); Gm = *Gammarus aequicauda*; Pc = *Perinereis cultrifera*; Gd = Gordiidae; Hy = *Hydrobia* spp.; Cg = *Cerastoderma glaucum*; Cr = *Cerithium rupestre*; Dl = (other) Diptera larvae; Ci = *Corophium insidiosum*; Ib = *Idotea baltica*; Dyt = Dytisicidae (larvae); Hyd = Hydrophillidae; Cl = (other) Coleoptera (larvae); Nd = Nereidae; Po = Polichetae; Hh = *Haliplus* sp.; Mn = *Micronecta* sp.; An = Anisoptera (nymphae).

Table 4.4 - Correlation between network centralization $C(N)$, the environmental variability given by the coefficient of variation of salinity (CV_s), the variability of macrodetritivores activity (CV_m) and the number of sampled taxa (S).

	$C(N)$	CV_s	CV_m	S
CM1	0.241	0.110	0.633	9
CM2	0.212	0.100	0.642	10
CM3	0.220	0.120	0.648	4
CM4	0.207	0.130	0.700	4
CM5	0.302	0.518	0.277	8
CM6	0.267	0.260	0.500	3
r		0.92	-0.89	0.06
d.f.		4	4	4
P - value		0.008	0.016	0.897

4.4 Discussion

The influence of environmental conditions on the structuring process of ecological communities is of critical importance in order to understand the consequences of environmental change on ecosystems structure and functioning [30]. Results showed the influence of salinity on the structuring process of detritus-based communities and the decomposition process of *P. australis* leaf detritus, revealing how community structure and functionality is likely to change across salinity gradients. The distribution of macroinvertebrates showed how the colonization of leaf detritus was a process mainly driven by the salinity conditions under which the communities are structured. Increasing salinity reduced the number of sampled taxa, allowing high abundances of only a well-adapted group of taxa. Indeed, the communities subjected to highest salinity were characterized by the occurrence of taxa well suited and adapted to extreme salinity conditions and variations, as the larvae of *Chironomus* spp. [194]. From low to moderate salinity, the colonization process favoured the occurrence of predators, both in terms of richness and abundances, and this trend was particularly evident when a marked change in the salinity values occurs during the seasons. Minor variations (i.e., more stable salinity conditions during the seasons) led to an ecological adaptation of a narrow pool of taxa, placing some physiological limitations on the abundance and diversity of taxa, especially for predators [68], which may imply a reduction in predation activity [29]. The influence of salinity on the spread of potential interactions among taxa may be due to a differential response to the environmental conditions, which can be reflected in a temporal niche separation.

The increase of salinity involved a simplification of ecological communities, where less variable salinity conditions can result in a common pattern of colonization for only a small number of well-adapted taxa. Under these conditions, ecologically similar species might utilize the same temporal niche increasing the effect of inter and intraspecific competition. This could result in the homogenization of communities structure, involving the replacement of ecological specialists by the analogous widespread generalists [134]. The effect of homogenization may lead to intensified species-specific interactions, where ecologically and functionally similar species might enhance competition reducing

their functional activity.The salinity dependent variations in community structure were consistent with changes observed in decomposition activity, probably because salinity reduces the potential of predatory interactions that regulate competition among detritus consumers. Interferences among taxa have been suggested to regulate the dynamics between trophic levels [197], and the increased trophic complexity (i.e., the presence of predators) will potentially enhance the consumption rate by detritivores [120]. Therefore, changes in salinity might drive the structuring process of detritus-based communities, influencing the probability to observe trophic (i.e., predation) and non-trophic (i.e., competition) interactions, as a direct consequence of the life history phenologies of predators and preys that contribute to a temporal variation in network structure and function. Many laboratory and field studies suggest that species richness can be related to the rate at which leaf detritus is broken in stream ecosystems [78], showing a little redundancy among species in their effect on ecosystem process, on the contrary of what observed in marine environment [90], where the functional diversity among detritivores seems to be more correlated with the decomposition rate.

Results showed how the network analysis could be a useful tool to explain the relationship between diversity and abundance in relation to the decomposition process. In network analysis, node centrality provides insight into the individuals location in the network, and the relationship among the centrality values of all nodes can reveal more about the overall network structure [171]. High-centralized network corresponds to a structural configuration in which the entire network is focused around one or few central nodes (the so called star-shaped network), and the most central nodes are those that (on average) are more related to peripheral nodes. This is particularly evident for the community structured in hyposaline waters (CM5 in Fig. 4.2), characterized by the highest variation of salinity during the seasons. The central position observed for the nymphae of Anisoptera showed the complex structure of interactions of this central predator, given by the high number of well-distributed links with other taxa. This may reveal the role of the nymphae of Anisoptera in damping the potential interferences among other predators and their preys, regulating the feeding activity of detritivores. This is

also true for the community structured under high salinity conditions and variability (CM6 in Fig. 4.2). The high interference observed between the detritivore *Chironomus* spp. and the larvae of the predator *Haliplus* sp., and the peripherical position of this latter, reveal how the potential of predation occurs only in a small temporal scale, probably due to the well-suited environmental conditions for the individuals belonging to the Genus of Haliplus. However, the lower variation in decomposition activity during the seasons did not reflect a high consumption of leaf detritus. This is probably because the presence of one main taxon with high abundances (*Chironomus* spp.), and the small number of observed taxa, enhance the effect of intraspecific competition that can reflects in a reduced ability to process the leaf detritus of *P. australis*. By contrast, less centralized network (CM1 and CM2 in Fig. 4.2) showed more than one central node, observing how a high number of strong potential interactions occur mainly in the subgroup of nodes formed by the most central taxa. This finding reveals that the presence of keystone taxa [196] and their influence on the interactions structure within the network of interspecific interactions appear to be more important for decomposition than species diversity, suggesting that species richness *per se* could not be a necessary prerequisite to maintain ecosystem functioning.

Here I found how the use of network analysis may allow a more robust assessment of each species impact on its community, showing how high salinity variations increases the structural heterogeneity of ecological communities given by the different responses of species to varying environmental conditions, increasing the rate at which leaf detritus is broken. These findings revealed that studying important network positions might be a key to better understand the effect of the environment on communities composition. This suggests that structurally important species may need particular attention in conservation practice [79], because their protection through habitat conservation may have direct and indirect effects for the whole ecosystem integrity and functioning. This may be particularly important for artificial aquatic ecosystems (such as the salterns), where habitat conservation passes through the active water management, which represents the key to maintaining the whole system functionality.

PART

The small-world of detritus-based communities in Tarquinia saltern

5 MACROINVERTEBRATES ASSEMBLY IN A PATCHY ENVIRONMENT: CENTRALITY MEASURES FOR THE SPATIAL NETWORK OF DETRITUS-BASED COMMUNITES[†]

Spatial patterns influence the persistence of population and communities, giving useful insights on the mechanisms that confer robustness to ecological networks. The mechanisms that regulate the spatial distribution of species are strongly related to the ability of populations to respond to spatio-temporal variations of ecological conditions, contributing to network structure and dynamic of persisting communities. I applied the framework of complex network to study the colonization process of *Phragmites australis* leaf detritus in six different pools of the patchy aquatic environment of Tarquinia saltern (centre Italy). Colonization data on leaf detritus were used to find network partition and measure the positional importance of each identified taxon, based on betweenness and closeness centrality. Here I found how the topological characteristics of the network confer robustness against perturbations, showing the relationship between robustness and nodes synchronicity in network attachment dynamics.

5.1 Introduction

Several studies have shown how the structural characteristics of many complex networks are related to their stability and dynamic [4] [3], showing how some features in ecological networks and food webs followed well-defined patterns explained by network theory, as the degree distribution in food webs [38], or nestedness and modularity in plant-pollinator networks [11] [135]. Previous work have been suggested how the analysis of network topology can provide a new and straightforward way to quantify and identify keystone species [79] or to improve the keystone concept by differentiating species on the basis of the role they play in a network [52]. Network analysis also provides a robust way to study spatial networks [189], describing any network in which the links (or potential links) among nodes are constrained by their location in some kind of 'space'.

The topological structure of complex networks is mostly dependent on the structural arrangement of nodes and links; thus, defining the importance of each node is crucial to determine the dynamical properties and stability of networks [180]. In network analysis, the degree of importance of each node within a network is commonly quantified using the centrality indices [47] [80], where

[†] A slightly modified version of this chapter has been accepted for publication on **Transitional Waters Bullettin**. Bellisario B, Cerfolli F, Nascetti G (2010) MACROINVERTEBRATES ASSEMBLY IN A PATCHY ENVIRONMENT: CENTRALITY MEASURES FOR THE SPATIAL NETWORK OF DETRITUS-BASED COMMUNITES.

different indices measure different aspects of the positional importance of a node. The choice of using a particular index is a direct consequence of the type of information we want to extract from different types of networks (e.g., a spatial network of sites and plants, plants and their pollinators or species in a food webs) so, different indices reflect different aspects about the importance of a node within a network [79].

For instance, a node with many interactions is important as it can affect many different nodes or serves as a bridge among nodes, influencing some important characteristics, as colonization and migration [117] cascading effect in food webs [6], the spread of parasites and disease [43] or coevolutionary pattern in plants and their pollinators [13].

Most ecological networks seem to have a well-defined pattern of interactions where several subwebs are attached to a 'network core', that acts as the 'glue providing cohesion' [110] [12] and this core of potentially interacting species is often composed by generalist species [52]. Several studies suggest that the cohesive patterns of some ecological networks confer robustness, making them less vulnerable against species deletion and slightly compromising their ability to provide essential ecosystem functions (e.g., nutrient recycling, decomposition) [97].

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

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

5.2 Materials and methods

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

There are significant differences in the centrality measures, produced by the differences of scale used in the definition of centrality. Betweenness and closeness characterize the positional importance of a node at different scales, at local (i.e., the degree of influence a node has between pairs) and global (i.e., the sum of all distances separating a node from the rest), respectively. Since the use of a global measure, such as the Cc_i, is inappropriate in networks where distances are great [41], it must be account the distance among nodes, that is, measure the small-world properties of the network. A small-world network has short path length $\langle l \rangle$ (i.e., average node-to-node distance) and high clustering coefficient (*CC*), where nodes being tightly linked together and the network have high $CC/\langle l \rangle$ ratio than that observed in a random network [198].

The consequences of a small world pattern can be of great importance in recognizing evolutionary paths, the stability and the sensibility to perturbations in ecological networks, suggesting that such architecture would play a relevant role in enhancing nodes synchronization [199] and a strong robustness and fast response to perturbations [180]. In ecological networks, synchronization is often related to a correlation between changes in the abundances of different populations in different patches, documented with reference to many taxa [89]. Synchronization may arise from migration (or dispersal) of populations among patches and from the dependence of all population dynamics on some common environmental noise (e.g., salinity, water temperature). Therefore, in this work,

synchronization among nodes might be given by the co-occurrence of macroinvertebrates (i.e., synchronicity in abundances and frequencies of colonization) in all the pools of the saltern. Since estuaries, salt marsh, and almost all natural habitats where environmental conditions are temporally variable (including solar salterns) are dynamical habitats in which the resident species are tolerant of a range of conditions, I would expect generalists to dominate [184] [36] and the presence of a small world pattern in network topology.

To measure the occurrence of a small world pattern and the centrality of nodes in the spatial network of Tarquinia saltern I first deconstructed the two-mode matrix, that expresses the bipartite network of taxa and pools, into a one-mode matrix (namely unipartite projection) of taxa, establishing a link between two taxa if they share a common pool. Generally, from a bipartite network it is possible to derive a uni-modal network for each set of nodes, in this case taxa and pools. Since I was interested on the colonization process of macroinvertebrates on leaf detritus, in this work I do not consider the pools one-mode network.

Another interesting measure in network topology is the *k*-core decomposition, a measure able to identify particular subsets of the graph, called *k*-cores, each one obtained by recursively removing all the vertices of degree smaller than *k*, until the degree of all remaining vertices is larger than or equal to *k*. Larger values of 'coreness' clearly correspond to vertices with larger degree and more central position in the network structure.

To test the significance of the short path length $\langle l \rangle$ and clustering coefficient (*CC*) measured in real network I compared these measures with those of 1000 random networks with the same degree distribution as the empirical one [11], and examined whether the empirical values of $\langle l \rangle$ were significantly lower and *CC* significantly higher than the random ones. As a measure of centrality, I chose to use the betweenness (Bc_i) and closeness centrality (Cc_i). I followed the rationale that: i) a taxon with $Bc_i > 0$ may be defined a connector, linking areas of the network that would be not connected at all [129], since a large number of links passing through it and ii) a taxon with high Cc_i is the one more closely related to each other and can quickly influences or be influenced by other taxa. Betweenness centrality is defined as [47]:

$$Bc_i = \frac{1}{(S-1)(S-2)} \sum_{j,k \in V, j \neq k \neq i} l_{jk}(i)/l_{jk} \quad (25)$$

where S is the number of taxa, l_{jk} is the number of shortest paths l connecting two taxa and $l_{jk}(i)$ is the number of shortest paths between taxa i and j that pass through i. Closeness centrality measures how close a taxon is to other taxa, and is defined as [47]:

$$Cc_i = \sum_{j=1; i \neq j} \frac{d_{ij}}{S-1} \quad (26)$$

where, S is the number of taxa and d_{ij} measure the shortest distance (i.e., the number of links) between i and j. The topological parameters were compared among themselves and with the normalized abundances (n_i) and frequencies of colonization, defined as the proportion (f_i) of how many times a taxon colonized the detrital substrates in the pools during the field experiment (see Eq. 22, Chapter 3.3).

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

5.3 Results

I sampled a total of 2406 individuals belonging to S = 18 taxa of macroinvertebrates on P = 6 pools, resulting in a total of L = 38 potential links in the two mode projection (Fig. 5.1A) and L = 95 potential links among taxa in the unipartite projection (Fig. 5.1B). Among sampled taxa, 10 taxa were classified as detritivores and 8 as predators, according to the available literature [106] [17].

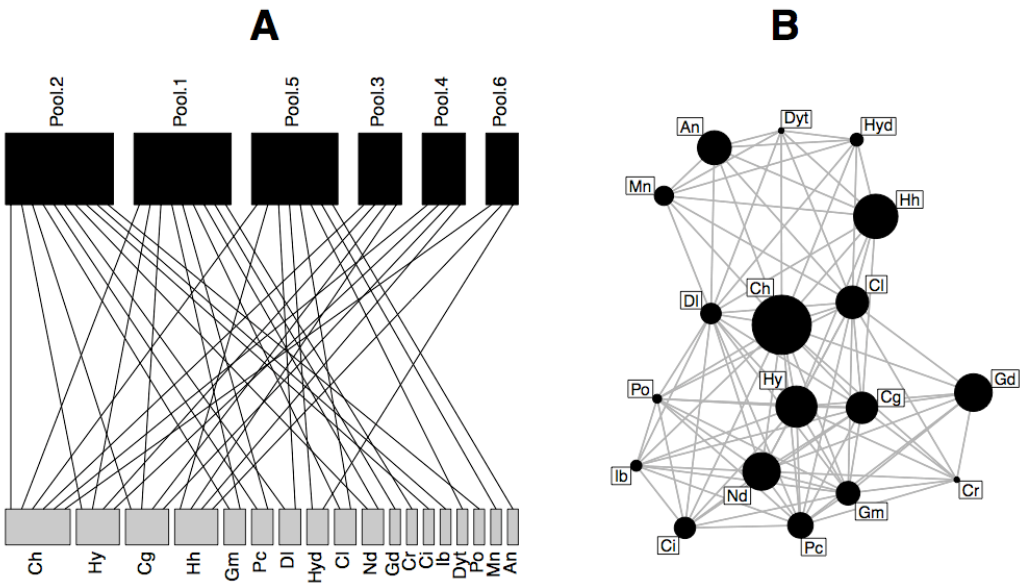

Figure 5.1 - A bipartite network (A) where links are established between two different sets of nodes, taxa and pools. Width of a box follows a decreasing order of colonization, from left to right. The unipartite projection is showed (B), where the (potential) links are established between two taxa if they shared a common pool. Width of a node is proportional to the log-transformed value of abundances. Taxa legend: Ch = *Chironomus* spp. (larvae); Gm = *Gammarus aequicauda*; Pc = *Perinereis cultrifera*; Gd = Gordiidae; Hy = *Hydrobia acuta*; Cg = *Cerastoderma glaucum*; Cr = *Cerithium rupestre*; Dl = (other) Diptera (larvae); Ci = *Corophium insidiosum*; Ib = *Idotea baltica*; Dyt = Dytisicidae (larvae); Hyd = Hydrophilidae; Cl = (other) Coleoptera (larvae); Nd = Nereidae; Po = Polychaeta; Hh = *Haliplus* sp.; Mn = *Micronecta* sp. (larvae); An = Anisoptera (nymphae).

The *k*-core partition of unipartite projection revealed $k = 3$ main sub-graphs, observing how a large amount of predators (62.5%) was comprised in the most peripheral subgroup (black nodes in Fig. 5.2A and Table 5.1), while 70% of detritivores in the main core of the network (white nodes in Fig. 5.2A and Table 5.1). Only few taxa (the predators larvae of Coleoptera and the detritivores *Cerithium rupestre* and the larvae of dipterans) belong in the core at the middle of a central and peripheral position within the network (grey nodes in Fig. 5.2A and Table 5.1).

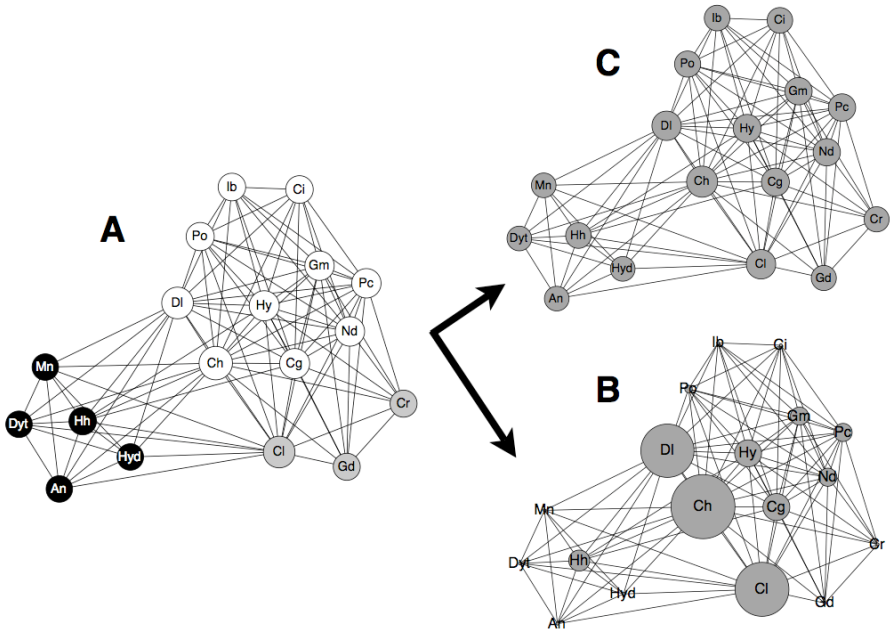

Figure 5.2 - The *k*-core partition (A) of the unipartite projection of macroinvertebrates on leaf detritus shows three well-defined sub-networks (black nodes = peripheral taxa, white nodes = central taxa, grey nodes = low-peripheral to central taxa). Closeness centrality (C) is almost equal for all taxa while betweenness centrality (B) reveals the role of environmental generalist in the cohesion of the network. Id's are given in Figure 5.1.

Table 5.1 - Network parameters for each identified taxon. Bc_i is the betweenness centrality, Cc_i the closeness centrality and k the number of identified sub-graphs, from the most peripheral (1) to the most central (3). Id's are given in Figure 5.1.

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

The spatial network of macroinvertebrates in Tarquinia saltern showed a small world pattern, as revealed by the high clustering coefficient and the small mean-shortest path length among taxa (Table 5.2). The CC/$\langle l \rangle$ ratio was significantly higher (11.32) than that given by a random association between taxa and sites (4.25 ± 0.0003, $P < 0.001$). Centrality showed as 50% of sampled taxa had a $Bc_i > 0$, observing a high percentage of detritivores with a higher betweenness centrality than that of predators (60% and 37.5%, respectively).

Table 5.2 - Mean shortest path length $\langle l \rangle$ and clustering coefficient (CC). r*N* corresponds to the values given by the null model with the same degree distribution of original network (*N*). All parameters are significantly different ($P < 0.001$) from the random ones, showing the small world pattern of the network.

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

Among detritivores, *Chironomus* spp. showed the highest Bc_i (0.32), while the larvae of Coleoptera showed the highest betweenness centrality for predators (0.23). The frequencies of colonization and the abundances of sampled macroinvertebrates showed a significant correlation (Spearman's ρ correlation) ($\rho = 0.77$, $P < 0.001$) (Fig. 5.3), revealing how the most abundant taxa were also the most widespread, as the larvae of *Chironomus* spp., a species well-suited and adapted to changing salinity conditions [194]. The frequencies of colonization showed a non-significant correlation neither with betweenness ($\rho = 0.29$, $P = 0.24$) nor with closeness centrality ($\rho = 0.22$, $P = 0.39$), while the abundances of sampled macroinvertebrates showed a significant correlation with Bc_i ($\rho = 0.57$, $P = 0.013$).

Results also showed a significant correlation between Bc_i and Cc_i ($\rho = 1$, $P < 0.001$) revealing a general coincidence in the rankings produced by betweenness and closeness centrality, which in some way give certain regularity to the network. This might indicate homogeneity in network topology related to nodes synchronicity in network attachment dynamics (e.g., a correlation between

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

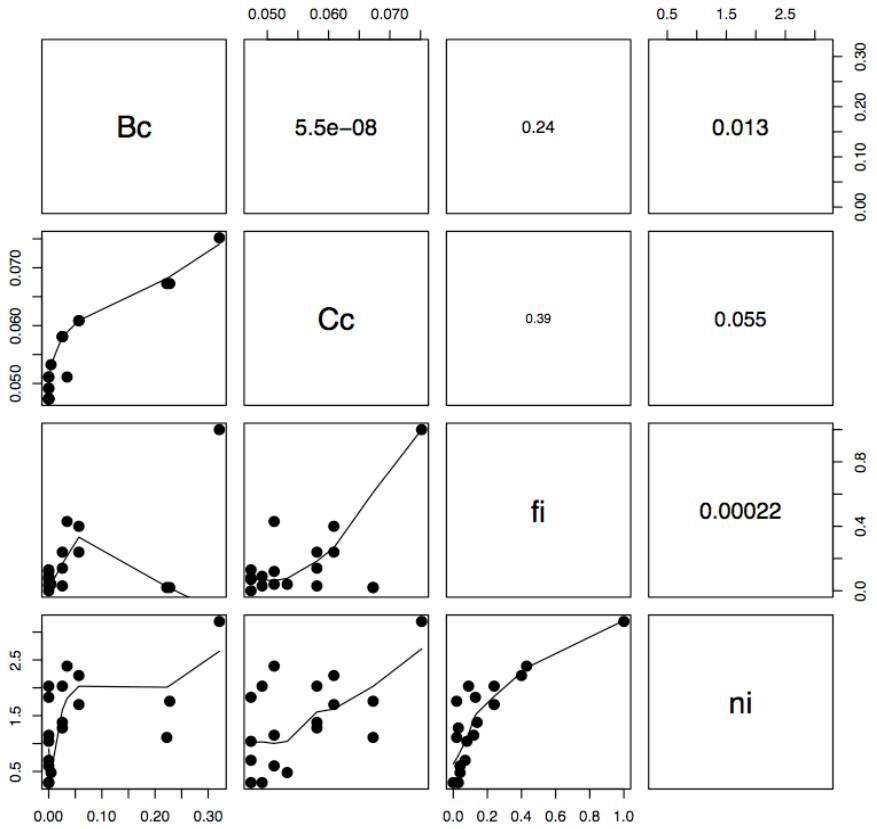

Figure 5.3 - Relationships among centrality values and normalized abundances and frequencies of colonization of macroinvertebrates on leaf detritus. *Bc* = betweenness centrality, *Cc* = closeness centrality, f_i = frequencies of colonization, n_i = normalized abundances. Upper panels show the significance of a correlation (Spearman's ρ correlation) and width of a correlation is proportional to the level of significance. Smooth lines in lower panels show the best curve describing the correlation.

5.4 Discussion

The one-mode network of colonizers on leaf detritus reveals high clustering and small path-lengths values, that is, a small world pattern where all taxa are closely linked together [199]. The small world topology reveals strong robustness and fast response to perturbations [3], and its prevalence in many biological systems may reflect an evolutionary advantage of such an architecture [9]. In most ecological systems, a disturbance can be an external signal like invasions by alien species, extinctions or changes in the behavioural or ecology of species already present in the network. For instance, changes in local ecological conditions might affect the colonization ability of macroinvertebrates, and this may result in increasing opportunities for invaders, if they have an advantage over residents in some places or times *via* different environmental responses, or *via* differences in life-history trait.

Here, I have found how the local ecological conditions of the pools in Tarquinia saltern influence the spatial distribution and colonization ability of macroinvertebrates (i.e., abundances and frequencies of colonization), and the ability of populations to respond to spatio-temporal variations in stochastic environment and to regulate network dynamic.

This suggests the influence of different array of ecological processes that may operate at different spatio-temporal scales [67]. It has been noticed [41] how a general correlation among centrality values in networks may exist, since nodes with large degrees show in general short average distance to the other nodes in the network. This produces high correlations between node degrees and various measures of centrality, given by a general coincidence in the rankings produced by the different centralities. This result may be a signal of a behavioural synchronicity of nodes, given by a convergent similarity in the traits of taxa and by the co-occurrence of macroinvertebrates on leaf detritus.

The differences in spatial distribution reveal some important characteristics of species traits, such as dispersal limitation or spatial variation in the strength of interspecific interactions. Centralities provide an evaluation of how rich the interaction pattern of a particular taxon is, and this is particularly important in systems where indirect effects (i.e., competition for resource) dominate [79]. The

k-core partition of the unipartite projection of macroinvertebrates shows three well-defined sub-graphs of taxa, revealing the peripheral position of predators in network topology. This might reflect an ecological adaptation to local environmental conditions able to influence their life history and phenologies, placing some physiological limitations on the abundances and frequencies of colonization, which may imply a reduction in predation activity over space and time [68].

The most dense network sub-graph is mainly composed by detritivores, observing the prevalence in this sub-network of those nodes characterized by the highest betweenness centrality, indicating how this dense core of environmental generalist may be crucial for the exchange of 'information' within the network (i.e., the spread of potential interactions). Generalism for a species have been defined in a variety of ways [108]: i) a species that maintain a variety of specialist genotypes that can be expressed depending upon the environmental conditions, ii) species in which each genotype has the ability to express various phenotypes depending upon environmental conditions (the so-called phenotypic plasticity), and iii) the *jack-of-all-trades*, a species with phenotypes intermediate to the range of environmental conditions experienced. This trade-off can influence the performance of species, predicting that a generalist will outperform a specialist under fluctuating and non-optimal environmental conditions [159] in which the costs of being a generalist are small relative to the benefits of the increased behavioural reduction in performance of the specialist [51].

Comparisons under natural conditions are confounded by the multitude of biotic and abiotic interactions [87]. In this context, the network analysis has shown how it is possible to identify the role of species within a community based on their position within the network, revealing the importance of generalists in maintaining network structure and resilience [52]. However, it can be noticed how the effect of the sub-core of extremely peripheral taxa may be important in maintaining network functioning, since an increased trophic complexity (i.e., the presence of predators) will potentially enhance the consumption rate by detritivores [120] able to regulate the competition among detritus consumers.

The characteristics of the spatial network of macroinvertebrates on leaf

detritus in the patchy environment of Tarquinia saltern reveal a well-defined pattern of colonization, which confer to this network robustness against random perturbations.

PART

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

6 SPATIAL NETWORK STRUCTURE AND ROBUSTNESS OF DETRITUS-BASED COMMUNITIES IN A PATCHY ENVIRONMENT[†]

The mechanisms that regulate the spatial distribution of species are an essential aid to understand the effects of environment on the persistence of populations and communities. The effect of the spatial structure on the persistence and robustness of ecological communities can also give useful insights about their functioning, such as the ability to process the detrital substrates. Here I apply the framework of complex networks to assess how the spatial network structure influences the colonization patterns of leaf detritus. The study area was the artificial aquatic ecosystem of Tarquinia saltern (Italy), whose spatial network is composed by 6 pools with different salinity. I 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 within links and minimize the number of links between modules, showing the presence of a strong site-specific association. This finding suggests that random perturbations, such as flooding or heavy rains, slightly affect the robustness of the whole system, but localized perturbations on the most connected nodes could have a negative effect on network connectivity. The consequences could lead to a structural and functional simplification, with possible effects for the whole trophic chain. Here I discuss the topological properties of the network in relation to the spatial distribution of pools, showing how the use of network approach could yield valuable insight to for conservation and management of these particular ecosystems.

6.1 Introduction

Network analysis represents a useful tool in the analysis and description of many complex systems [4] [130] [59]. Its extensive use in recent years has been applied to the complex network of food webs [139] [145], plant–animal mutualistic networks [11] [88], and spatial ecological networks [189] [45] [43]. In 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 which represent some kind of association among nodes, such as interspecific interactions [101] [151] or dispersal movements [63] [115].

In network analysis, the structural characteristics of the networks are related to their robustness against disturbances [59], as the ability to regulate the spread of information (e.g., the spread of parasites or diseases, [43]) or the effect of alien species invasion [140]. The use of network analysis can also give useful information about the effects of spatial structure on migration, colonization, species distributions, and species persistence [117]. The rationale behind this view is that the mechanisms that generate the spatial distributions of organisms are of

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greater importance for our understanding of the consequences of environmental change on ecosystems structure and functioning [30].

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 of sites, that reflects the "costs" associated with the formation of links between nodes [10]. In aquatic ecosystems, the decomposition of leaf detritus involves three main mechanisms: i) the rapid weight loss of soluble constituents; ii) the modification of detrital matrix by microorganisms and iii) the feeding activity of macroinvertebrates, whose activity regulates the rate of detritus processing [143]. 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 [60], stabilizing the dynamics of consumers populations and food webs that would be otherwise unstable (for a complete review see [120]). Moreover, the spatial characteristics (e.g., the spatial extent) were found to influence the decomposition dynamic [163], showing how the control of decomposition process may vary across spatial scales [185].

Here I 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. I used the network analysis to answer some specific questions about: i) the role of the spatial arrangement of the pools and the environmental constraints on the colonization process of leaf detritus in aquatic environment, and ii) the consequences of spatial pattern for robustness against perturbations. In order to answer these questions I first analysed 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. Then, I explored the individual use of substrates by macroinvertebrates by applying a nested analysis, which might reveal an asymmetric use of pools by taxa.

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 in compartmentalized systems disturbances are more easily countered [102]. On the other hand, nestedness measures the order in which species is related to area [8] or the extent to which specialized species interact with increasingly large subset of generalists [11] [135] [56]. Nestedness has been shown to increase network robustness, since nested networks appear less prone to the detrimental effects of habitat loss [44]. Therefore, modularity and nestedness can be viewed as two complementary measures of network complexity [135], playing a critical role in both functioning and stability of the networks.

Here I focused on the spatial characteristic of the network, suggesting the importance of habitat heterogeneity in community structure and dynamics, yielding valuable insight for conservation and management.

6.2 Materials and Methods

6.2.1 Study area and field experiment

I studied six different detritus-based communities which structuring process was made under 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, given by the seasonal variations of salinity conditions.

The study area is the artificial aquatic ecosystem of the Biological Reserve of Tarquinia saltern (Italy) (42°12 N, 11°43' E), whose spatial network is composed by 36 pools characterized by a wide salinity gradient (Fig. 6.1), from hyposaline (mean annual salinity 8.5 gL^{-1}) to hyperaline waters (mean annual salinity up to 100 gL^{-1}). The pools are shallow basins, whose connectivity is given by the inflow of seawater or by accidental events like flooding or heavy rains. The input of seawater occurs through a single opening, which connects the saltern with the sea, located north of the area.

To measure the decomposition and colonization process of leaf detritus, I placed 48 mesh bags in six sampling sites, covering the full spectrum of salinity variation (Fig. 6.1). Mesh bags were filled with *P. australis* leaf fragments weighed to the nearest mg after drying at 60 °C for at least 72 h (leaf pack: 2.000

± 0.004 g dry mass). The mesh bags had dimension of 10 x 10 cm with a coarse mesh of 5 x 5 mm, to allow the colonization of substrates by macroinvertebrates. I also used 48 bags with a fine mesh (0.5 x 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 number of $r = 4$ replicates for each type (coarse and fine) for each site, with a time step t of one month for a total of twelve months, measuring: i) the loss of leaf detritus weight in both the fine and coarse mesh bags; ii) the number of taxa colonizing the detrital substrates and iii) the number of individuals for each sampled taxon, averaged out the r replicates.

Decomposition rate was measured following 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 (dd). 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) by the loss of detritus weight in the fine mesh bags. Thus, the macrodetritivores activity can be measured as $k_d = k_t - k_l$. I 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 experiment.

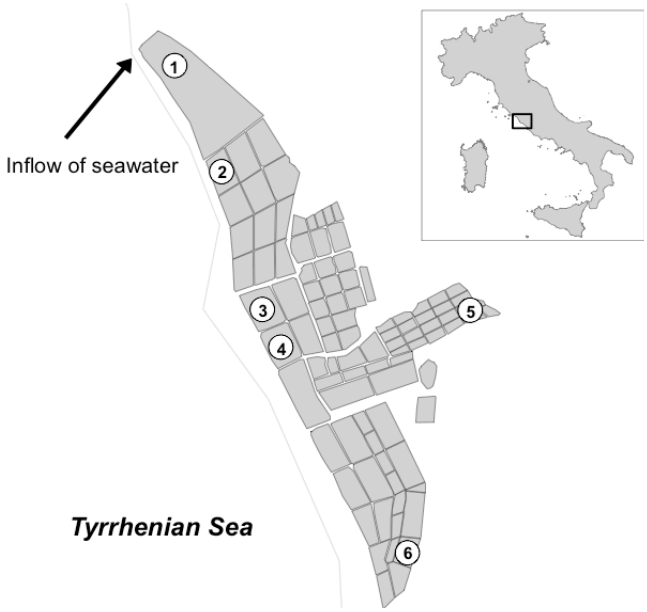

Figure 6.1 - Spatial location of sampled pools in the Biological Reserve of Tarquinia saltern. In figure, the inflow of seawater is the point of water refill located north of the area. Circles correspond to the sampled pools; the salinity gradient increases from north to the south of the area Mean annual salinity values: **1** = 44.8 ± 2.63 gL^{-1}; **2** = 50 ± 2.84 gL^{-1}; **3** = 88 ± 5.60 gL^{-1}; **4** = 100 ± 7.09 gL^{-1}; **5** = 8.5 ± 2.45 gL^{-1}; **6** = 115 ± 16.62 gL^{-1}.

6.2.2 Network analysis

I 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. I first compiled the incidence matrix (Table 6.1), whose values express the presence of a particular taxon *S* (row) in a given pool *P* (column). The incidence matrix was then converted in a bipartite graph, in which a single edge is created for every non-zero element. I used only presence/absence data to standardize the dataset for modularity and nestedness, since the chosen algorithm for nestedness works only with binary data. Therefore I 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 network, where the links are not homogeneously distributed, and the density of links inside modules is higher than among modules [128].

Table 6.1 - Incidence matrix in which each entry represents the associations between taxa (rows) and pools (columns). 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.

		Pool1	Pool2	Pool3	Pool4	Pool5	Pool6	$\sum_{i=1}^{P} x_i$
Detritivores	*Chironomus* spp.	1	1	1	1	1	1	6
	Gammarus aequicauda	1	1					2
	Perinereis cultrifera	1	1					2
	Gordiidae	1						1
	Hydrobia acuta	1	1	1	1			4
	Cerastoderma glaucum	1	1	1	1			4
	Cerithium rupestre	1						1
	(other) Diptera (larvae)		1			1		2
	Corophium insidiosum		1					1
	Idotea baltica		1					1
Predators	Dytiscidae					1		1
	Hydrophillidae					1	1	2
	(other) Coleoptera (larvae)	1				1		2
	Nereidae	1	1					2
	Polichetae		1					1
	Haliplus sp.			1	1	1	1	4
	Micronecta sp. (larvae)					1		1
	Anisoptera (nimphae)					1		1
	$\sum_{j=1}^{S} x_j$	9	10	4	4	8	3	

There are several algorithms to detect community structure in networks [131] [58]. In this work I used an algorithm implemented in R [154] to find communities in a graph via a spin-glass model based on simulated annealing, SA [85]. 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 [131] (for more details see [157]).

The algorithm requires some specific parameters, 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 [157]. I chose six spin states, because in the 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), gradually decreased during the process towards deep minima (i.e., low-cost configuration) of network partition [85]. To test the significance of the modular structure I compared the measured modularity with those of 100 random networks with the same degree distribution as the 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 to its maximum when the bulk of links occurs within the same module, and the probability of a random association among different sets of nodes is small. Therefore, in my 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.

I 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 [58]. If we define l_{im} the number of links l of node i to other nodes in its own module m and $\bar{l}_m$ and σ_{lm} the average and standard deviation of within module l of all nodes in m, the within-module degree is simply defined as:

$$z = \frac{l_{im} - \bar{l}_m}{\sigma_{l_m}} \tag{27}$$

The among-module connectivity (*sensu* [135], identical to the participation coefficient of [58]) expresses the position of node *i* with respect to other modules, and is defined as:

$$c = 1 - \sum_{k=1}^{M} \left(\frac{l_{ik}}{l_i} \right) \quad (28)$$

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). Once the modules were identified, the role of a taxon can be identified in the *zc*-parameter space (see [58] and [135] for references).

Nestedness - I quantified nestedness *N*, a complementary measure of modularity [135], by using the matrix temperature T^*. Matrix temperature is calculated 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 [8]. Nestedness temperature (T^*) was estimated from the BINMATNEST algorithm [161] implemented in the "bipartite" package of R [154]. I followed [11] 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 the null model 3 implemented in BINMATNEST. This null model assigns 1's 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 [11]) and, since this is a conservative model, it is less prone to type I and II error [188].

6.3 Results

6.3.1 The structure of detritus-based communities

During the field experiment I sampled a total of 2406 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, 10 were classified as detritivores and 8 as predators, according to the available literature [106] [17] (see Table 6.1 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. 6.2A).

The mean abundances (n_i) and the mean frequencies of colonization (f_i) of macroinvertebrates have been normalized to the maximum measured value (n_i max and f_i 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 ρ 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. 6.2B). The most abundant and widespread taxa were the larvae of *Chironomus* spp., *Gammarus aequicauda*, *Hydrobia acuta* and *Haliplus* sp. .

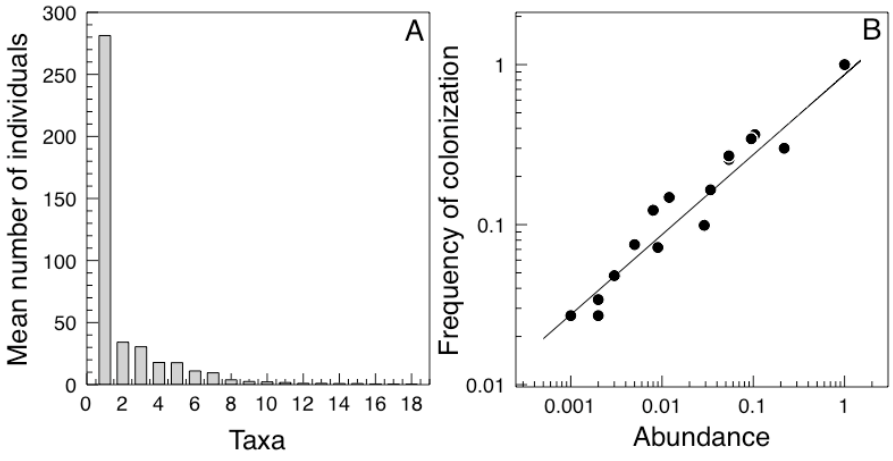

Figure 6.2 - The frequency distribution shows the asymmetry in the mean number of individuals *per* taxa in the detritus-based communities of Tarquinia saltern (A). The abundances (n_i) and frequencies of colonization (f_i) show a positive correlation. In the log-log graph (B), the best fit is given by a power law ($y = 0.866x^{0.5}$, $R^2 = 0.867$). n_i and f_i are expressed by their means normalized over their maximum. Notice how the measured values of abundance and frequency of some points in (B) are similar and, therefore, superimposed in figure.

6.3.2 Network analysis

Results on modularity showed how the network structure was significantly modular (M = 0.360) than expected by a random colonization of leaf detritus by macroinvertebrates (M_{null} = 0.220 ± 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, I found a different, yet specular, modular distribution of predators and detritivores, where the bulk of predators (75%) and detritivores (80%) have been assigned to only one module (Module 3 and Module 1 in Fig. 6.3, respectively). The modular structure of the network maximized the number of links inside 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. 6.3), 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 occurred only in one module (Module 2 in Fig. 6.3), revealing an asymmetric use of pools by macroinvertebrates, that 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_{null} = 0.674 ± 0.0023, P < 0.001). This finding revealed a heterogeneous pattern in the use of pools by macroinvertebrates, since the bulk of pools have been colonized by few taxa and a few pools were much more used than expected by chance (Fig. 6.4A). 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 specialist), with most of their links inside their module (i.e., both low c and z) and 61% of these had connections only with pools in their own module (c = 0, ultraperipheral sensu [58]) (Fig. 6.4B). The remaining 11% (2 taxa) were generalists, equally distributed between module (the predator *Haliplus* sp.) and network hub (the larvae of detritivore *Chironomus* spp.), important for the coherence and cohesion of the module and the whole network, respectively.

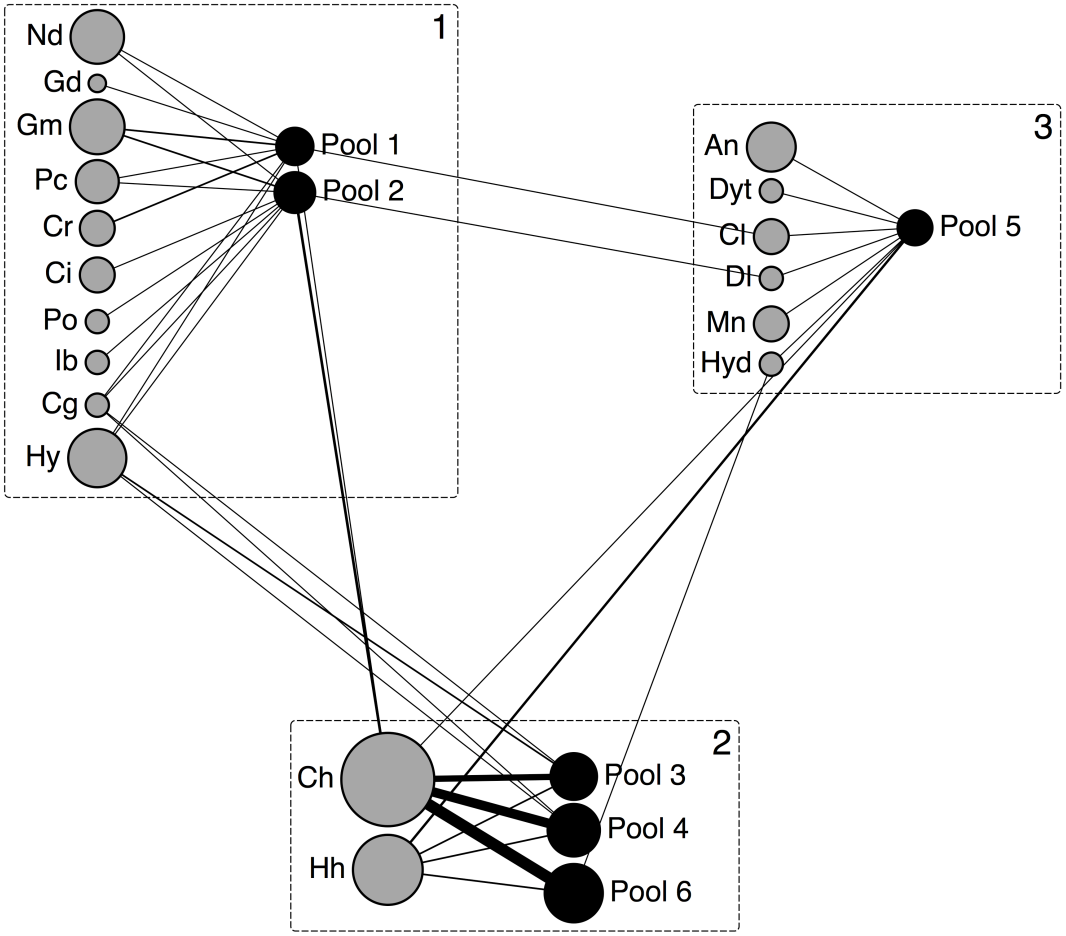

Figure 6.3 - Modular structure of the bipartite spatial network. Light gray nodes represent taxa and black nodes pools, dashed numbered boxes are the identified modules. The size of nodes is proportional to the mean log-transformed abundances of taxa and the mean annual salinity value of the pools. The thickness of a link represents the mean normalized frequency of colonization and indicates a proportion of how many times a taxon colonized the detrital substrates in the pool during the field experiment. Taxa legend: Ch = *Chironomus* spp. (larvae); Gm = *Gammarus aequicauda*; Pc = *Perinereis cultrifera*; Gd = Gordiidae; Hy = *Hydrobia acuta*; Cg = *Cerastoderma glaucum*; Cr = *Cerithium rupestre*; Dl = (other) Diptera (larvae); Ci = *Corophium insidiosum*; Ib = *Idotea baltica*; Dyt = Dytisicidae (larvae); Hyd = Hydrophilidae; Cl = (other) Coleoptera (larvae); Nd = Nereidae; Po = Polychaeta; Hh = *Haliplus* sp.; Mn = *Micronecta* sp. (larvae); An = Anisoptera (nymphae).

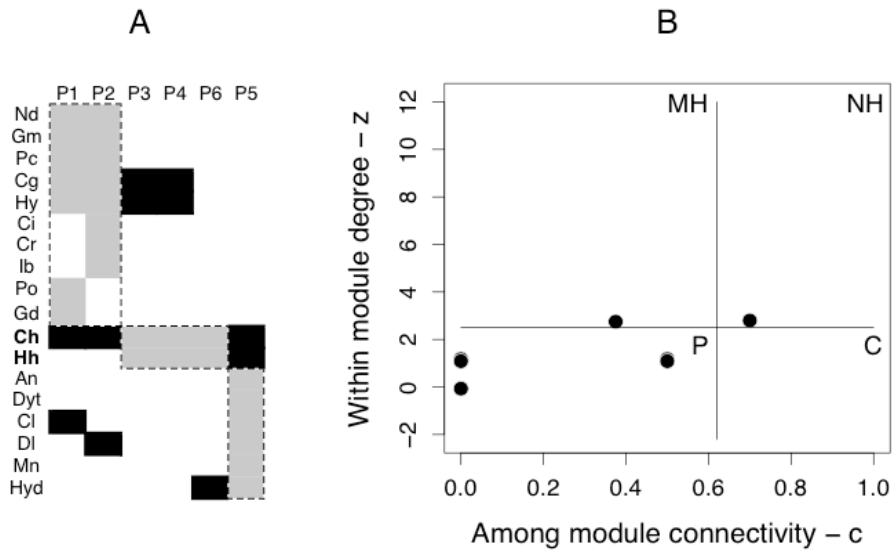

Figure 6.4 - The modular matrix (A) of the network (with nodes sorted according to their modular affinity as in Fig. 3) shows the differences in the colonization of detrital substrates in the different pools. Dashed boxes are the identified modules and black cells represent links between taxa and pools connecting the modules. Almost all sampled macroinvertebrates are peripheral nodes (B) with one module hub and one network hub, bolded in (A). Id's for each taxon are the same as in Fig. 6.3. *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 ($z \leq 2.5$, $c > 0.62$).

Thus, the network of Tarquinia saltern was characterized by a clear subdivision in 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, the network analysis has been revealed a useful tool for characterizing the spatial pattern of species distributions, producing predictions about robustness against perturbations and their consequences.

6.4 Discussion

The present distribution of macroinvertebrates on leaf detritus reveals as the colonization pattern is a process mainly driven by the environmental conditions under which the communities are structured, influencing the abundance, richness and the 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 the salinity conditions during the seasons due to the highest evapotranspiration, and the colonization process seems to favor the occurrence of predators when a marked change in the salinity conditions occurs during the 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 [68], which may imply a reduction in predation activity [29], with possible consequences on the feeding activity of macrodetritivores. Indeed, interferences among taxa, such as competition among the 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 [197].

Modularity analysis shows a dense core of within module connections and sparse connections between 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 linking the modules. The taxon acting as a connector among modules in the network (i.e., network hub) is the most abundant and widespread, the larvae of *Chironomus* spp., a species well adapted to changing and extreme salinity conditions [194]. 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” [8], given by the presence of ecologically distinctive taxa that creates 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 *Haliplus* sp.) are also the ones 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. I also observed an association between modularity and the spatial proximity of the pools; the pools located near the point of water refill (Pool 1 and 2 in Fig. 6.1), and the pools far away this point (Pool 5 and Pool 3, 4 and 6 in Fig. 6.1) belong to different modules. The modularity of the network may thus reflect habitat heterogeneity [149] [21], driven by the different environmental conditions of the pools, and the clustering of closely ecologically related species (as observed in plant-pollinator networks by [94]).

Therefore, habitat heterogeneity and the ecological adaptation of taxa to the salinity conditions involve a non-random pattern of colonization, which contributes to network complexity. The spatial structure of the network can also favour the formation of clusters among spatially close nodes (as in communication and transportation networks, [58]), and I observe the same trend in the spatial network of Tarquinia saltern (Fig. 6.3). These results may have far-reaching conservational implications, because in modular network, disturbances are expected to spread more slowly than a non-modular structure, due to the strong within module connections and the few number of links among modules.

As well noticed in ecological literature, decomposition is a key process in regulating the regeneration of carbon and nutrients, being an important link between primary and secondary production [42]. 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 [60]. 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 [120]). Thus, any kind of alteration in the network structure of detritus-based

communities could have implications for the highest levels of trophic chain (e.g., migratory birds).

I notice as the network seems to be less sensitive to random removal of nodes but high sensitive to the removal of the most connected ones, and I suggest that the gradually loss of these latter could be a signal of growing system fragmentation. The distance among 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, which measures the "costs" associated with the formation of links (such as social distance measured by salary or socio-professional category differences, see [10]). This can produce the clustering of spatially closed pools, characterized by the occurrence of ecologically related species. Network topology tells that random events, as floods or heavy rains, slightly affect network connectivity. 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 strongly depend on the role a node has in the network, since the selective removal of nodes may cause fragmentation of modules or the whole network [135].

The spatial structure of the detritus-based communities in Tarquinia saltern shows a greater structural and functional heterogeneity than expected by chance. Results reveal how the increased functionality (i.e., the higher consumption of leaf detritus) is observed in the presence of a higher site-specific association (Pool 5, Table 4.2 and Fig. 6.3). 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 [134], and this may cause fusion of modules with long-term effects on network functioning.

What are the effects of the alteration in system connectivity at higher trophic levels deserves further investigation. It can be assumed that an 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 enhancing competition). Since saline ecosystems are artificial aquatic environments, the need for a constant maintenance, which involves the water management inside the pools, should take into account these findings for conservation practices.

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

SYNOPSIS

A The network structure of detritus-based communities

Network analysis has been a useful tool to identify and quantify the effect of environmental conditions on network structure and persistence of detritus-based communities in Tarqunia saltern.

Here I found how the network structure of macroinvertebrates on leaf detritus follows some specific patterns, related to changing environmental conditions, especially of salinity. Salinity influences the diversity and abundance of macroinvertebrates on leaf detritus, revealing its secondary effect on the spread of potential interactions among taxa. In particular, the variation of salinity during the seasons could affect the degree of network homogeneity/heterogeneity of detritus-based communities. Communities structured under variable conditions of salinity tend to be more heterogeneous, exhibiting a high degree of centralization. This may be given by the life history phenologies of predators and preys that contribute to a temporal variation in network structure. The star shaped-like configuration of these networks showed the presence of one or few keystone taxa, defined as those taxa occupying a central position in the space of interspecific interactions. Under more stable conditions of salinity, communities tend to be more homogeneous, indicating how the extreme and constant environmental conditions allow the colonization and persistence of only a narrow number of interacting taxa. Results showed how the salinity seems to impose some physiological limitations on the persistence of predators populations [68], simplifying the network structure of detritus-based communities.

Therefore, the temporal niche available for colonization is reduced, and the networks show a more even distribution of taxa during the seasons, enhancing the effect of (potential) competition.

From local to global, the spatial analysis of network structure showed other interesting patterns: i) a strong modular structure and nestedness, ii) high cohesion and small world-like properties, such as high clustering and mean shortest path length among nodes. All these properties reveal interesting patterns in the colonization of leaf detritus, and confer to the network high robustness against perturbations. The small world topology means that informations (e.g., disturbances) spreads rapidly through the network [118]. The prevalence of small world networks in many biological systems may reflect an evolutionary advantage of such architecture, since it is more robust to perturbations than other network architectures.

In most ecological systems, a disturbance can be an external signal like invasions by alien species, extinctions or changes in the behavioral or ecology of species already present in the network [140]. Therefore, the topological properties of the network indicate strong robustness, but a high sensitivity to the spread of disturbances (if these occur) within the network [119]. For instance, changes in local ecological conditions might affect the colonization ability of macroinvertebrates, and this may result in increasing opportunities for invaders, if they have an advantage over residents in some places or times *via* different

environmental responses, or *via* differences in life-history traits [68]. Here, I found how the colonization ability of macroinvertebrates (i.e., abundances and frequencies of colonization) might be important traits, which can regulate the ability of populations to respond to spatio-temporal variations in stochastic environment and to regulate network dynamic.

Therefore, the effect of disturbances could result in a homogenization of both structure and function of the system, involving the replacement of ecological specialists (peripherals taxa) by the same widespread generalists. The topological characteristics of this network has far reaching implications for conservation. Since the Tarquinia saltern is an artificial aquatic environment, the need for a constant maintenance, which involves the water management inside the pools, should take into account these findings for the conservation of this area.

B The effect of network structure on detritus decomposition

The decomposition of detritus plays important role in the processes of energy flow and nutrient cycling. Decomposition of plant litter is among the most fundamental processes in many ecosystems, both terrestrial and aquatic, including forested streams [143].

The field experiment carried out in the six pools of Tarquinia saltern allowed to understand and quantify the role of the complex network of potential interactions among taxa for decomposition [26]. Results did not highlight a correlation between the number (and abundances) of identified detritivores, and the rate at which detritus is consumed. By contrast, including detritivores and their predators allowed a more robust assessment of the relationship between communities structure and functioning.

Species interactions are found to be of greater influence on decomposition dynamics, suggesting how the relationship between species richness and functioning may be driven by the abundances of detritivores organisms and the effect of predation and competition. Which species are important, and how they interact to create and maintain species diversity patterns represents a key issue to understand the mechanisms of decomposition processes.

Results seem to confirm how, including multiple type of interactions (i.e., predation and competition) in network analysis may allow a more robust assessment of each species impact on its community. These findings confirm how the decomposition may be only weakly correlated with species richness and the total abundance of detritivores organisms, because some species are far more important than others, supporting the idea that the presence of keystone taxa (i.e., topological keystone species) may be more important for decomposition than species diversity *per se*.

Therefore, an increased structural heterogeneity may allow a better efficiency in detritus consumption, since interferences among taxa may regulate the dynamics between trophic levels, increasing trophic complexity that, in turn, will potentially enhance the consumption rate by detritivores.

The effect of environment on the decomposition of leaf detritus revealed the inhibitory effect of salinity, allowing the persistence of high percentage of leaf detritus that accumulates in sediments. This is particularly evident under high and stable conditions of salinity during the seasons, where salinity constraints the

decomposition process *via* direct (e.g., decreasing enzymatic activity on decaying leaves) and indirect (e.g., altering communities composition and network structure) mechanisms. The role of salinity on the leaching and conditioning rates might involve some changes related to decreases in enzymatic activity of microfungi and bacteria on the decaying leaves. The quality of detritus is tied to the degree of microbial and microfungi colonization, such that it may be more useful in some cases to consider them as grouped entities, as higher consumers in the detrital branch may not distinguish between the consumption of detritus and the microorganisms that feed on it. This means that the rate of colonization of detrital substrate by macroinvertebrates could be influenced indirectly through changes in salinity to which cascaded to other elements of the biota.

Finally, I want to point out how the explicit consideration of the factors that determine the structures and govern processes in space are a key aspects of comprehending ecosystem structure and processes.

Scaling theory predicts that variance increases when critical thresholds are approached in a system. The consequences of such scale relations in the analyses of ecological communities are an increased heterogeneity in spatial structure. The spatial distribution of pools in the area of Tarquinia saltern showed as the 'costs' associate with links formation between taxa and pools are driven by the local environmental conditions under which communities are structured. These differences in local conditions confer to the network a high functional variability, which might be the cause of increased species diversity at high levels of trophic chain.

C Perspectives

This work is one of the first that explictly use the framework of complex networks in the study of colonization pattern of leaf detritus and the consequences of network structure for stability and functioning.

However, some issues remain outstanding and worthy of a deeper understanding:

i) The temporal variation of network structure in relation to changing environmental conditions and the consequences for system functionality could be an interesting starting point in understanding the effects of changes in ecological conditions (also in the face of global changes), and how the detritus-based communities respond on short spatio-temporal scales;

ii) The influence of multiple determinants in the structuring of detritus-based communities from a network perspective. The different responses to environmental changes (i.e., the number of species, abundances, frequencies of colonization), the degree of palatability of detrital resource, or the influence of interspecific interactions (i.e., predation and competition) could be considered a *continuum* of determinants.

Future works linking the topological structure and attachment dynamics of macroinvertebrates on leaf detritus on multiple resources and in different ecosystems (e.g., lakes, rivers, forested stream) will provide insight on the variation in network structure and topology, bringing us closer to the understanding of the ecological processes behind network dynamical processes and its consequences on functional processes.

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APPENDICES

Appendix A1

Glossary

Average path length: the mean shortest path between all nodes in the network.

Betweenness: the number of shortest paths that the focal node lies on.

Bipartite graph: a network with two distinct types of node.

Closeness: the mean shortest path between a focal node and all other nodes in the network.

Complexity: the product of the number of species, S, and connectance, C, within a food web [$SC=S(L/S^2)=L/S$]. Once thought to be destabilizing, complexity is now believed to enhance stability if most links are weak (i.e. low interaction strength) (see after).

Component: a group of nodes mutually interconnected.

Consumer: an organism that uses a given food resource.

Clustering coefficient: a measure of the proportion of neighboring nodes that can be reached through the nodes other neighbors; calculated as the proportion of a focal nodes neighbors who are themselves neighbors.

Degree/**Connectivity**: the number of edges that connect the focal node to other nodes.

Degree distribution: the frequency distribution of the individual node degree for an entire network.

Directed graph: nodes in a directed graph are connected by an asymmetric relationship, such as predation.

Ecological network: a set of nodes (usually species) that are connected to one another *via* pairwise interactions (represented by links). Food webs are the most familiar ecological networks, with the links between species representing trophic interactions (i.e., fluxes of matter and energy).

Edge: interacting nodes are connected by edges.

Food chain: the sequence of transfers of matter and energy from organism to organism in the form of food. Food chains intertwine locally into a food web because most organisms consume more than one type of animal or plant (see after).

Food web: a set of species linked by predator/prey relationships. A food web depicts who eat whom in a given community.

Graph theory: a branch of mathematics dealing primarily with the statistical description of static networks.

Hamiltonian: In quantum mechanics, the Hamiltonian H is the operator corresponding to the total energy of the system. Its spectrum is the set of possible outcomes when one measures the total energy of a system. It is of fundamental importance in most formulations of quantum theory because of its close relation to the time-evolution of a system. In statistical mechanics, is a function of temperature or other parameters, such as the volume enclosing a gas or the number of microstates and modules in a network. It also represents the quality function that minimizes the energy states during the network partitioning.

Interaction strength: measure to quantify the direct and indirect effects of species on each other. Interaction coefficients (as ‘‘*per capita interaction strengths*’’) are the most useful empirical metric quantifying the impact of one species on another. This metric underlies various other measures of interaction strength used in theory (e.g., elements of the community matrix, the Jacobian matrix, or the inverse Jacobian matrix). Many empirical studies have estimated interaction coefficients by directly measuring consumption rates or from time series of population densities.

Keystone species: species that exert disproportionately strong effects within a community or ecosystem. Perturbations (e.g., changes in abundance) that affect keystone species typically propagate rapidly throughout the network. It can be also defined as a species in key position in the topological space of interactions (see Jordan et al. [80]).

Stability: there are three main definitions of stability in common use, all of which refer to the ability of a system to maintain its structure (e.g., the species complement within a food web) over time: i) response to temporary (pulse) perturbations: ability to recover from small (local stability) and large (global stability) perturbations; rate of recovery (resilience); ability of non-equilibrium systems to recover (permanence); ii) response to permanent (press) perturbations: resistance (degree of change in structure; for example, if the loss of a species does not result in secondary extinctions, the system is resistant with respect to species composition); iii) internal stability (no perturbations): inverse of variability in population densities over time (variability can be internally and/or externally driven).
In network analysis, the stability of a network is also defined as the ability to resist to system fragmentation after removal (random or non-random) of nodes. This definition is strictly related to the degree distribution of links *per* nodes.

Trophic level: main step in a nutritive series, or food chain, of an ecosystem. The organisms of a chain are classified into these levels on the basis of their feeding behavior.

Trophospecies: aggregations of biological species on the basis of trophic similarity.

Appendix A2

Measuring the potential interactions

Measuring the interactions among species can be a hard work, especially under non-manipulative experimental conditions. The measured interaction strengths available in ecological literature often refer to the effect a species has above another, as regards the influence on population dynamics, and the relationships that link these species are often of predator/prey type.

This is because it is easily to detect the influence of predators removal on the population density of their preys (Paine 1966). One of the elements of controversy in the study of food webs is that these are often represented as composed only by one type of interaction at time (e.g., predation). Melián et al. (2009) showed as including multiple type of interactions in network analysis may allow a more robust assessment of each species impact on its community and a greater understanding of the relationship between community structure and functioning.

The partitioning of available resources within ecological communities has been suggested as contributing towards the determination of community structure (Pianka 1974). As such, quantifying the degree of species overlap in the utilization of resources such as food or space has become a valuable approach in studies of both community structure and species coexistence. Traditionally, overlap in resource use has been quantified as the degree of niche overlap between species, where niche overlap is simply the joint use of a resource (or resources) by two or more species (Hutchinson 1957, Colwell and Futuyma 1971).

Niche overlap between species may be viewed as the volume in multidimensional hyperspace in which two or more species maintain a viable population(s) in the presence of one another (Mouillot et al. 2005). Depending upon the organisms in question, a number of discrete or continuous biotic or abiotic variables may be considered as hypervolume axes. These may include i) environmental conditions (e.g., altitude, temperature, salinity, soil type), ii) resource use (e.g., prey type, refuge type, host identity), iii) a physical trait which indicates the type of resource used (e.g., for fish, gut length may be indicative of diet), or iv) a measure of resource usage (e.g. habitat selection or food preference). Furthermore, a single study may incorporate a number of different types of variables, including categorical, continuous count or binary data, as well as electivity scores (on a 0-1 range); however, incorporating axes described by different data types into a single measure of niche space is potentially problematic because, statistically, different data types cannot be dealt with in the same way.

Using appropriate transformations and density estimation techniques, each data type gives rise to a standard measure of niche overlap ranging from 0 (no overlap) to 1 (complete overlap). The use of a standard measure of niche overlap ensures that the geometric interpretation of the overlapping density functions or probability is the same for each data type. Once estimated, probability distributions are available for each data type, the overlap statistic between two species is simply the overlapping area between the distributions for each species. It is then possible to blend measurements derived from different types of data into a single multivariate analysis of niche overlap by averaging over multiple axes.

A single study may incorporate one or more axes of hypervolume space. Some axes are measured on each individual (e.g., physical traits), while others are site-specific (e.g., the environmental conditions above). A measure of resource usage is based on individual usage, but becomes site-specific when the electivity is calculated.

Traditionally, niche overlap was calculated using categorical data (e.g., presence or absence of a particular predator, or level of availability of a certain type of food, low, medium or high) (Ludwig and Reynolds 1988, Chapter 10). Because continuous data is seldom normally distributed, continuous variables were converted to categorical data (e.g., maximum daily temperature to low, medium and high categories); however, there is a loss of information when continuous data is replaced with ordered categories.

Mouillot et al. (2005) provided a breakthrough, describing an approach based on kernel distribution estimators that models niche overlap from continuous data independently of the underlying distribution of the data. Their approach extended niche overlap studies to allow the construction of broad, multivariate indices of niche overlap based on probability distributions of continuous measurements constructed using density estimation that were, therefore, comparable across different axes. The traditional binary and categorical measures may be combined with the continuous-variable quantitative functional traits of Mouillot et al. (2005), and other measures such as ratios, count data, and electivity scores on a scale of 0-1, using transformations and density estimates appropriate for each particular data type.

Consider the restriction to a single axis, namely t. For each data type, a probability distribution may be estimated for each species, and the overlap of species i and j is defined as the overlap of the probability distributions. This generic measure of niche overlap along axis t will lie between 0 and 1 (inclusive). Data may be collected at a single site, or over multiple sites. At a single site, individual-based data are used to provide niche overlap measures. Over multiple sites, site-based data (e.g. environmental variables) may also be incorporated.

I considered that, if in a given period of time t, S species colonized with n individuals the food traps of *P. australis* leaf detritus, these species may potentially interact. The type of interaction derived from their feeding habits, and the "strength" of these interactions are a function of their abundances. This is obviously a "simplification" and does not account the reciprocal effect on population dynamic. However, in ecological literature, indices that use information about some surrogate properties in network connectivity as body size [208] or the frequency of pollinator visit on flowers [193] are not new. Here I show how it is possible to measure the potential of interaction between pairs starting from the feeding habits of sampled taxa, their abundances and temporal niche partition.

Suppose we have K categories all assumed to be equally available to species i.

The proportional use of category k (with $k \in K$) by species i is written as p_{ik}, assuming $\sum_{k=1}^{K} p_{ik} = 1$.

With respect to the aim of this work, let me call the category k the time step t of colonization on the detrital substrates of *Phragmites australis*, with $t = (1,..,T)$. p_{ik} might be estimated by the proportion of observed individuals of species i on the detrital substrates at time k. Similarly species j has proportions p_{jk}, and so on for each sampled taxon. In an extension from binary data (two categories) to K categories, the niche overlap between species i and j on axis t is defined as:

$$NO_{ijt} = \sum_{t=1}^{T} \min(p_{it} p_{jt})$$

An example of data and calculation with $T = 4$ follows:

Category (t)	t_1	t_2	t_3	t_4	Tot
Specie i	0.10	0.35	0.40	0.15	1
Species j	0.45	0.25	0.20	0.10	1
min(i, j)	0.10	0.25	0.20	0.10	0.65

This example, with niche overlap 0.65, is illustrated in Fig. A2.1. Species *i* and *j* are represented by bar charts with light and dark gray bars, respectively.

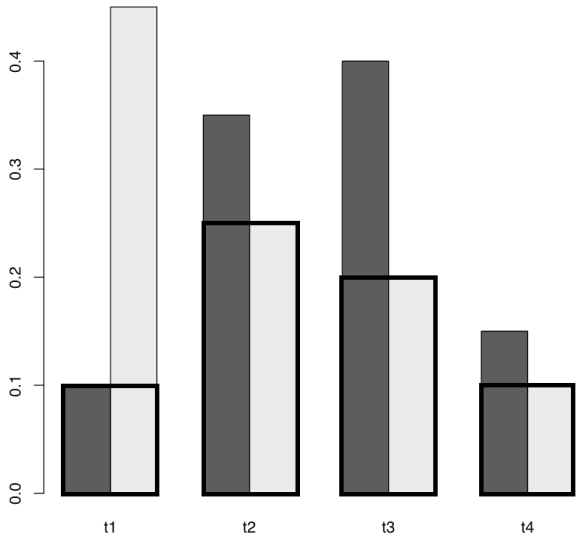

Figure A2.1 – Niche overlap from categorical data (t_1, t_2, t_3, t_4). Species *i* has light gray bars, and species *j* has dark gray. The summed widths of the bars are one and the niche overlap is the crossing area common to both species, represented by the black boxes. In this figure, $NO = 0.65$.

Therefore, it is possible to derive all the pairwise potential interferences (i.e., interactions) among the S taxa during the total time of experiment T. Each measured overlap represents the entry of a community matrix $\mathbf{A} = [\alpha_{ij}]$, that represents the matrix of potential interactions among taxa in a community.

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Appendix A3

Matrices of potential interferences

Table A3 1 –Matrix 1

	Ch	Gm	Pc	Gd	Hy	Cg	Cr	Cl	Nd
Ch		0.190	0.134	0.000	0.000	0.000	0.000	0.000	0.702
Gm	0.190		0.174	0.098	0.275	0.000	0.576	0.576	0.267
Pc	0.134	0.174		0.100	0.233	0.000	0.000	0.000	0.169
Gd	0.000	0.098	0.100		0.000	0.000	0.000	0.000	0.000
Hy	0.000	0.275	0.233	0.000		0.433	0.333	0.333	0.157
Cg	0.000	0.000	0.000	0.000	0.433		0.000	0.000	0.022
Cr	0.000	0.576	0.000	0.000	0.333	0.000		0.944	0.124
Cl	0.000	0.576	0.000	0.000	0.333	0.000	0.944		0.124
Nd	0.702	0.267	0.169	0.000	0.157	0.022	0.124	0.124	

Table A3 2 - Matrix 2

	Ch	Dl	Gm	Ci	Ib	Pc	Cg	Hy	Nd	Po
Ch		0.376	0.133	0.000	0.000	0.333	0.013	0.049	0.611	0.000
Dl	0.376		0.133	0.000	0.000	0.333	0.000	0.000	0.471	0.000
Gm	0.133	0.133		0.600	0.600	0.733	0.049	0.000	0.133	0.600
Ci	0.000	0.000	0.600		1.000	0.667	0.000	0.000	0.000	1.000
Ib	0.000	0.000	0.600	1.000		0.667	0.000	0.000	0.000	1.000
Pc	0.333	0.333	0.733	0.667	0.667		0.000	0.000	0.333	0.667
Cg	0.013	0.000	0.049	0.000	0.000	0.000		0.000	0.000	0.000
Hy	0.049	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000
Nd	0.611	0.471	0.133	0.000	0.000	0.333	0.000	0.000		0.000
Po	0.000	0.000	0.600	1.000	1.000	0.667	0.000	0.000	0.000	

Table A3 3 – Matrix 3

	Ch	Hy	Hh	Cg
Ch		0.65	0.121	0.47
Hy	0.65		0.101	0.982
Hh	0.121	0.101		0.083
Cg	0.47	0.982	0.083	

Table A3 4 – Matrix 4

	Ch	Cg	Hy	Hh
Ch		0.261	0.175	0.412
Cg	0.261		0.000	0.026
Hy	0.175	0.000		0.103
Hh	0.412	0.026	0.103	

Table A3 5 – Matrix 5

	Ch	Dyt	Hyd	Hh	Cl	Mn	Dl	An
Ch		0.000	0.333	0.118	0.000	0.333	0.000	0.590
Dyt	0.000		0.000	0.010	0.000	0.200	0.000	0.400
Hyd	0.333	0.000		0.042	0.000	0.000	0.000	0.167
Hh	0.118	0.010	0.042		0.000	0.314	0.000	0.187
Cl	0.000	0.000	0.000	0.000		0.000	0.500	0.348
Mn	0.333	0.200	0.000	0.314	0.000		0.000	0.321
Dl	0.000	0.000	0.000	0.000	0.500	0.000		0.348
An	0.590	0.400	0.167	0.187	0.348	0.321	0.348	

Table A3 6 – Matrix 6

	Ch	Hy	Hh
Ch		0.050	0.670
Hy	0.050		0.100
Hh	0.670	0.100	

Taxa legend

- ✓ Ch = *Chironomus* spp. (larvae)
- ✓ Gm = *Gammarus aequicauda*
- ✓ Pc = *Perinereis cultrifera*
- ✓ Gd = Gordiidae
- ✓ Hy = *Hydrobia acuta*
- ✓ Cg = *Cerastoderma glaucum*
- ✓ Cr = *Cerithium rupestre*
- ✓ Dl = (other) Diptera (larvae)
- ✓ Ci = *Corophium insidiosum*
- ✓ Ib = *Idotea baltica*
- ✓ Dyt = Dytisicidae (larvae)
- ✓ Hyd = Hydrophilidae
- ✓ Cl = (other) Coleoptera (larvae)
- ✓ Nd = Nereidae
- ✓ Po = Polychaeta
- ✓ Hh = *Haliplus* sp.
- ✓ Mn = *Micronecta* sp. (larvae)
- ✓ An = Anisoptera (nymphae)

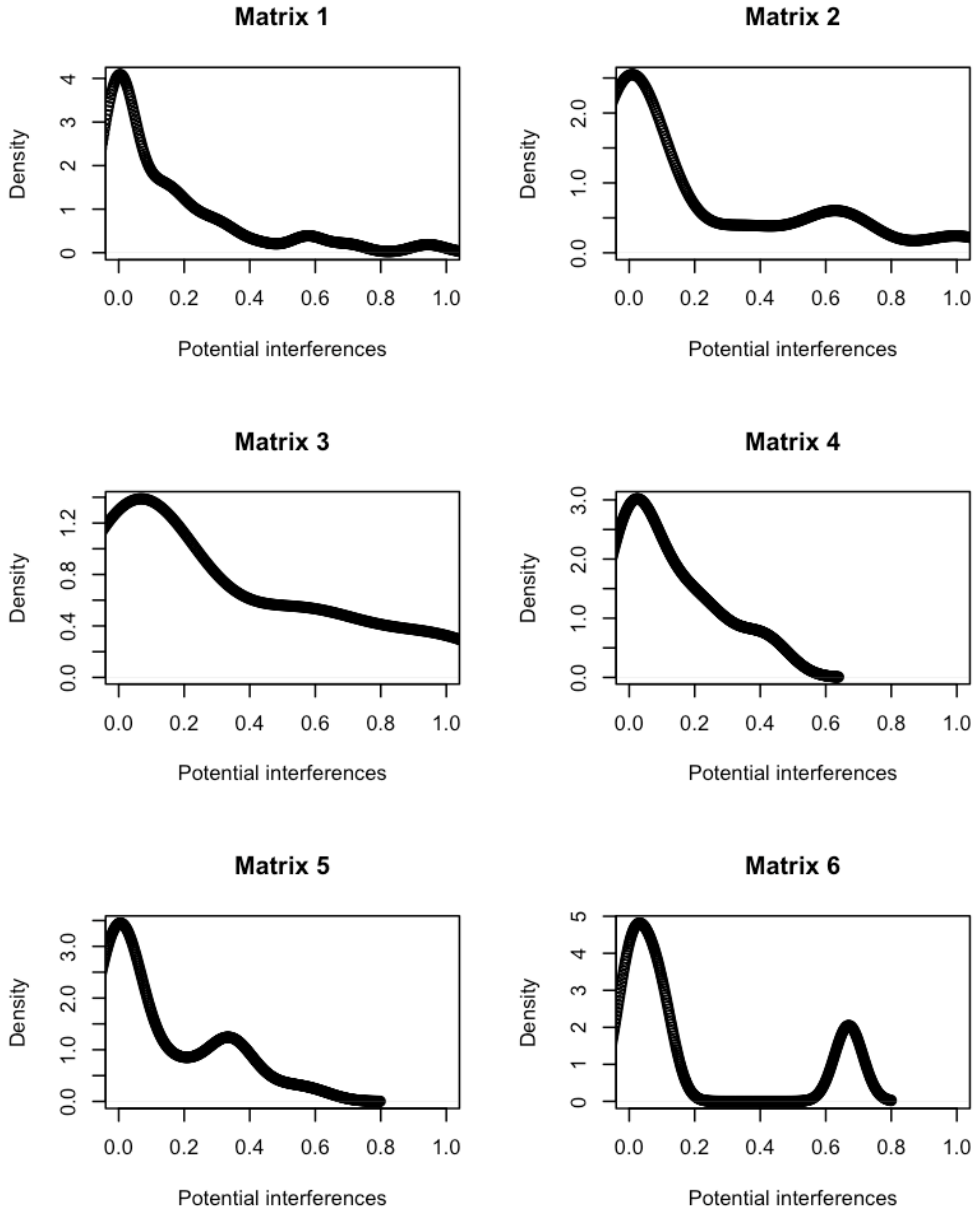

Figure A3. 1 – Kernel density profile of potential interactions (α) for analyzed community matrices. Zero values are non-found interactions among taxa; intraspecific interactions (the main diagonal in community matrix) were excluded. Kernel density (K) disperses the mass of the empirical distribution function over a regular grid of at least 512 points and then uses the fast Fourier transform to convolve this approximation with a discretized version of the kernel and uses a linear approximation to evaluate the density at the specified points. The statistical properties of a kernel are determined by $\sigma^2(K) = \text{int}(t^2 K(\alpha) d\alpha)$ which is always 1 (and hence the smoothing factor is the standard deviation of the kernel) and $R(K) = \text{int}(K^2(\alpha) d\alpha)$. The smoothed profiles of potential interferences show a skewed distribution, where the bulk of taxa have no or, at least, low interferences, except for Matrix 5 and Matrix 6 that show two well-defined peaks. This might indicate the presence of strong interactors within the communities.

Appendix A4

R codes

To use these codes, simply copy and paste on the **R** console and substitute the "YOUR_FILE.csv" with the name of your database.

Remember to put codes and data into the same directory!

Network analysis I: Eigenvector centrality and centralization

```
#Load libraries#
library(network) #Tool for network analysis#
library(nettheory) #Tool for network analysis#
library(sna) #Tool for social network analysis#

#Import community matrix#
#Change sep="" and dec="" if CSV separator is not ; and decimal places are given by , #
read <- read.csv("YOUR_FILE.csv", header = TRUE, sep = ";", dec=",")
#Transform CSV in matrix#
C <- data.matrix(read)

#Calculate network size#
ns <- network.size(network(C))
#Eigenvector centrality#
ev <- evcent(C)
#Eigenvector network centralization (see Chapter 5)#
N <- sum(max(ev)-ev)/(ns-1)
```

Network analysis II: Centralities and small-world

```
#Load libraries#
library(bipartite)
library(igraph)
library(sna)
library(inetwork)
library(scatterplot3d)
library(Hmisc)
#Read data#
readCSV1 <- read.csv("YOUR FILE.csv", header = TRUE, sep = ";", dec=".") #Read one-mode matrix#
Dat1 <- read.csv("YOUR FILE.csv", header = TRUE, sep = ";", dec=".") #Read colonization parameters#
M1 <-(data.matrix(readCSV1))
M1[is.na(M1)]=0#Replace NA (not available) values with 0
NN1 <- t(M1)
MM1 <-((M1+NN1)>0)*1#Create a binary matrix from weighted data

AF1 <- data.matrix(Dat1)
Dc <- degree(MM1,ignore.eval=FALSE, gmode="undirected",rescale=TRUE) #Calculate degree centrality#
Bc <- betweenness(MM1,ignore.eval=FALSE,gmode="undirected", rescale=TRUE) ) #Calculate betweenness centrality#
Cc <- closeness(MM1,ignore.eval=FALSE,gmode="undirected", rescale=TRUE) ) #Calculate closeness centrality#
DATA <- data.frame(Bc,Cc,AF1) #Merge centralities in a data frame
DataMatrix <- as.matrix(DATA) #Convert the data frame into a matrix
corr<-rcorr(DataMatrix, type=c("spearman"))
print(corr)
#Small-world#
#Calculate from random graph with the same degree distribution#
library(brainwaver)
library(Matrix)
edges1 <- nnzero(MM1)/2
sw1<-rand.sw(100,18,edges1,dist.mat=MM1) #Random network generator with 100 replicates
#Calculate from a given graph#
library(igraph)
```

```
g1 <- graph.adjacency(MM1)
sp1 <- average.path.length(g1)/18
clust1 <- transitivity(g1,type=c("average"))
shortestpaths1 <- c(sw1$Lp.rand,sp1)
clustering1 <-c(sw1$Cp.rand,clust1)
SWratio1 <- clust1/sp1#Small worl for a given network
SWratio_rnd <- sw1$Cp.rand/sw1$Lp.rand#Small worl from a random network
#Compare centrality measures with the abundances and frequencies of colonizations#
pdf("Fig.2.pdf")
panel.cor <- function(x, y, digits=2, prefix="", cex.cor, ...)
{
   usr <- par("usr"); on.exit(par(usr))
   par(usr = c(0, 1, 0, 1))
   r <-c((rcorr(x, y,type=c("spearman"))$P[1,2]))
   txt <- format(c(r, 0.123456789), digits=digits)[1]
   txt <- paste(prefix, txt, sep="")
   if(missing(cex.cor)) cex.cor <- 0.6/strwidth(txt)
   text(0.5, 0.5, txt, cex = cex.cor*(1-r))
}
pairs(DATA,lower.panel=panel.smooth,upper.panel=panel.cor,pch=19,col.smooth="black",cex=1.
5,main="")#This function gives a figure of correlations and the statistical significance (Spearman's
rho) in the upper panel
dev.off()
```

Network analysis II: Modularity and nestedness

```
#Load libraries#
library(bipartite)
library(igraph)
library(fields)
#Import, transform and sort web#
#Change sep=”” and dec=”” if CSV separator is not ; and decimal places are given by , #
readCSV <- read.csv("YOUR_FILE.csv", header = TRUE, sep = ";", dec=".")
Matrix <- data.matrix(readCSV)
#Sort data matrix in increasing (sort.orde=”inc”) or decreasing order (sort.order=”dec”)#
M1 <- sortweb(Matrix,sort.order="dec")
#Total connectance#
TC <- sum(M1>0)/(ncol(M1)*nrow(M1))
#Linkage levels#
#LSites <- sum(M1>0)/ncol(M1)
#LSpecies <- sum(M1>0)/nrow(M1)
#NESTEDNESS#
x <- nestedness((M1))
y<-nestedtemp(M1)
temp <- (100-x$temperature)/100
#Plot options#
tiff(filename = "nested.tiff", width = 1000, height = 1000, units = "px", pointsize = 12, bg =
"white", res = 150, compression="jpeg")
par(mfrow=c(1,2))
plot(y,names=TRUE,col=0:8,kind=c("incidendce"))
plot(y,names=TRUE,col=gray(8:0 / 8),kind=c("temperature"))
dev.off()
#Null model for modularity#
#Transform data matrix in a TRUE/FALSE web#
binweb <- M1>0
pweb<-outer(rowSums(binweb)/sum(binweb),colSums(binweb)/sum(binweb),
FUN="*")#Probability function based on constrained marginal totals
#Make a new, emtpy matrix with 0#
rbinweb <- matrix(0, nrow=nrow(binweb), ncol=ncol(binweb))
#Put the links into random places, with probability as given by the same degree distribution#
rbinweb[sample(1:prod(dim(binweb)), size=sum(binweb), prob=pweb)] <- 1
M1random <- rbinweb*M1
```

```
#Transform random matrix in a graph object#
gi1 <- graph.incidence(M1random)
MOD1<-
spinglass.community(gi1,spins=6,start.temp=0.995,stop.temp=0.01,update.rule=c("config"),gamma=1) #Modularity for random web (start.temp is the starting temeprature for annealing, in this case T = 0.995) - the number of spins has been setted as the maximum number of communities that would be expected...in this case are equal to the six sampled pools#
MOD<-
spinglass.community(gi,spins=6,start.temp=0.995,stop.temp=0.01,update.rule=c("config"),gamma=1)#Modularity for observed web#
```