Co-occurrence patterns of litter decomposing communities in mangroves indicate a robust community resistant to disturbances

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Background. Mangroves are important coastal ecosystems known for its high productivity, a significant part of that is exported to surrounding environments as dissolved or as particular organic matter. Most of the carbon found in mangroves is produced by its vegetation and is decomposed on its sediment. Nevertheless, this process involves a tight interaction between between microbial populations, litter chemical composition and environmental parameters. Therefore, this study was designed to study the complex interactions found during litter decomposition in mangroves by applying network analysis to metagenomic data.**Methods.** To achieve this, we have set leaves of the mangrove trees found in southest Brazil (*Rhizophora mangle, Laguncularia racemosa* and *Avicennia schaueriana*) in separate litter bags and left on three different mangroves for 60 days. These leaves were then used for metagenome sequencing using Ion Torrent technology. Sequences were annotated in MG-RAST and used for network construction using MENAp. **Results.** The most common phyla were Proteobacteria (classes Gamma and Alphaproteobacteria) followed by Firmicutes (Clostridia and Bacilli). The most abundant protein clusters were associated with the metabolism of carbohydrates, amino acids, proteins and mixed groups. Non-metric multidimensional scaling of the metagenomic data indicated that substrate (i.e. tree species) did not significantly select for a specific community. Both networks exhibited scale-free characteristics and small world structure due to the low mean shortest path length and high average clustering coefficient. These network also had low number of hub nodes most of which were module hubs.**Discussion.**The present study has shown that the community present in this decaying material is stable despite differences in the environment (i.e. plant species or mangrove location). These communities form a tight network that is robust and resistant to disturbances and therefore capable of withstanding this constantly changing environment hence maintaining the process despite these changes.

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Abstract

Background. Mangroves are important coastal ecosystems known for its high productivity. Part of this carbon is exported to surrounding environments as dissolved or as particular organic matter. Most of the carbon found in mangroves is produced by its vegetation and is decomposed on its sediment. Nevertheless, this process involves a tight interaction between microbial populations, litter chemical composition, and environmental parameters. Therefore, this study was designed to study the complex interactions found during litter decomposition in mangroves by applying network analysis to metagenomic data.

Methods. To achieve this, we have set leaves of the mangrove trees found in the southeast of Brazil (*Rhizophora mangle, Laguncularia racemosa,* and *Avicennia schaueriana*) in separate litter bags and left on three different mangroves for 60 days. These leaves were then used for metagenome sequencing using Ion Torrent technology. Sequences were annotated in MG-RAST and used for network construction using MENAp.

Results. The most common phyla were Proteobacteria (classes Gamma and Alphaproteobacteria) followed by Firmicutes (Clostridia and Bacilli). The most abundant protein clusters were associated with the metabolism of carbohydrates, amino acids, and proteins. Non-metric multidimensional scaling of the metagenomic data indicated that substrate (i.e., tree species) did not significantly select for a specific community. Both networks exhibited scale-free characteristics and small world structure due to the low mean shortest path length and high average clustering coefficient. These networks also had a low number of hub nodes most of which were module hubs.

Discussion. The present study has shown that the community present in this decaying material is stable despite differences in the environment (i.e., plant species or mangrove location). These communities form a tight network that is robust and resistant to disturbances and therefore capable of withstanding this constantly changing environment hence maintaining the degradation process despite these changes.

Introduction

Mangroves are coastal ecosystems known for its high productivity (Holguin, Vazquez & Bashan, 2001) contributing to 10-15% of the global coastal carbon storage (Alongi, 2014). Most of this organic matter (OM) is buried in its sediments (Alongi, Boto & Tirendi, 1989; Siikamäki, Sanchirico & Jardine, 2012). However, a significant part of that is exported to surrounding environments as dissolved or as particular OM (Alongi, Boto & Tirendi, 1989). Although there is a participation of water column and sediment organisms, most of the carbon found in mangroves is produced by its vegetation (Holguin, Vazquez & Bashan, 2001; Kristensen et al., 2008) and its processing of this OM happens on its sediment.

Litter degradation is a complex process that involves a dynamic community ruled by a tight interaction between litter chemical composition, environmental parameters and different populations of both macro and microorganisms (Schneider et al., 2012). These processes are triggered and mediated by microorganisms that colonize it during the degradation process (Heijden et al., 2016; Purahong et al., 2016). Thus, these microbes play an essential role in all biogeochemical cycling and in doing so they act as pools of both C and N (Prosser et al., 2007).
The changes through time in this process are tightly connected to how labile this organic matter is (Kristensen et al., 2008). This reflects in changes in the populations found and rate of decomposition (García-Palacios et al., 2016). Thus, these alterations lead to the formation of novel niches occupied by specific populations (Frossard et al., 2013).
This dynamic process of fluid niche composition and changing community composition leads to complex interactions between populations with different metabolic capabilities and therefore ecological functions (Dini-Andreote et al., 2014). These interactions can lead to the formation of

patterns of co-occurrence (and co-exclusion) between populations that could unveil ecological processes yet unknown (Green et al., 2017). Consequently, the use of network analysis has unveiled the relationships between populations and functions in the most diverse processes and habitats (Faust & Raes, 2012). The interactions between microorganisms happen in a variety of ways such as the flow of energy, matter, and signals leading to the formation of complex ecological networks (Montoya, Pimm & Sole, 2006). Understanding these complex structures and dynamics is essential to reveal the processes that rule biodiversity, and hence, ecological networks have received great attention in recent years (Zhou et al., 2011; Faust & Raes, 2012; Deng et al., 2016).

In litter decomposition, the interaction between different populations is key to the decomposition of complex polymers such as cellulose and lignin (Purahong et al., 2016). The need for a variety of enzymes that take part in the degradation of these molecules often requires the association between different and complementary populations (Purahong et al., 2016). On the other hand, the absence of a population or enzyme could interfere with the rate of decomposition (Kaiser et al., 2014), thus requiring some degree of redundancy or alternative paths.

Therefore, this study was designed to study the complex interactions observed during litter decomposition in mangroves by applying network analysis to metagenomic data and to test the hypothesis that in such a complex environment the ecological network formed by these communities is responsible for the homeostasis of the process. The data was gathered using litterbags containing leaves of the three most abundant plant species in three different mangroves to obtain the relationships between different plant material and spatial scales.

Materials and Methods

Study site and field experiment

This study was conducted in three different mangrove sites in the State of São Paulo, Brazil. The first one, in the south of the state located in the city of Cananéia (Can) (25° 05'03" S–47° 57'75"W) and two in the city of Bertiga (Bert and BC) (23° 54'08"S-46°15' 06" W and 23° 43' 74" S-47° 57' 75" W, respectively) in the center of the state. The former (Can) is a preserved mangrove with no history of anthropogenic impact; the two later ones are located close to highly urbanized and industrial areas and therefore have high human influence (Andreote et al., 2012). Also, BC has had a major oil spill in 1983 from which is still in process of recovery (Andreote et al., 2012). In each of these mangroves, fresh and mature leaves (at the same phenological state) from the three main species of mangrove trees (*Rhizophora mangle, Laguncularia racemosa,* and *Avicennia schaueriana*) were sampled directly from the tree. The chemical composition of these leaves varies between species, *R. mangle* has the lowest hemicellulose and protein content and the highest lignin content, *L. racemosa* has the highest hemicellulose, and the lowest cellulose content while *A. schaueriana* has the highest cellulose and protein content (see Moitinho et al., 2018 for details). Field sampling was approved by the System of authorization and information in biodiversity (SISBIO #20366-3).

These leaves were added to sterile nylon litterbags (25 x 25cm, mash size 0.1mm) containing 300g of each plant material and left over the sediment for 60 days during the fall of 2014. For each plant species, four different litterbags were randomly distributed in a 30.0 m^2 area in each mangrove forest. After these, the bags were collected and 100 g of decomposed material was immediately frozen in liquid nitrogen for DNA extraction.

Nucleic acid extraction, processing, and sequencing.

105 The total DNA was extracted using RNA PowerSoil® Total RNA Isolation Kit and RNA
106 PowerSoil® DNA Elution Accessory Kit, respectively, following the manufacturer's protocol.
107 DNA quality and quantity were evaluated in Nanodrop 2000 and by agarose gel electrophoresis.
108 Metagenomic libraries were constructed using Ion Xpress Plus Fragment Library Kit with Ion
109 Xpress Barcode Adapters following the manufacturer's protocol. Sequencing templates were
110 constructed with Ion PGM Template OT2 400 Kit in an Ion torrent OneTouch 2 equipment.
111 Sequencing was performed using Ion PGM 400pb Sequencing Kit on an Ion Torrent Personal
112 Genome Machine. The sequencing of 21 libraries obtained a total of 9.317.861 reads with an
113 average of 233 bp.

114 *Sequencing processing and annotation*

115 Metagenomic sequences were uploaded to MG-RAST and were processed using the default
116 parameters and can be found under project number (mpg13300). All phylogenetic analysis
117 presented here is the result of the Best Hit Classification against the M5NR database using an E-
118 value cut-off of 10^{-5}, a minimum identity of 60% and a minimum alignment of 50 bp (Delmont
119 et al., 2011). The functional annotation was performed by Hierarchical Classification against the
120 Subsystems database using an E-value cut-off of 10^{-5}, a minimum identity of 60% and a
121 minimum alignment of 15 amino acids.

122 *Data analysis*

123 In order to reduce the sparsity of the data, low coverage samples (n<2000) were removed and the
124 obtained annotation tables were normalized using cumulative-sum scaling (CSS) (Paulson et al.,
125 2013) using Qiime 1.9.1 (Caporaso et al., 2010). In order to identify features (taxa or genes) that

126 could be considered as markers of a certain treatment, data were analyzed using MetagenomeSeq
127 (Paulson et al., 2013). Also, permutational multivariate analysis of variance (Adonis), Non-
128 metric Multidimensional Scaling and Mantel tests were performed within the Vegan package in
129 R (Oksanen, 2010). Mantel test was performed in Qiime (Caporaso et al., 2010).

130 Network analysis was performed on the CSS normalized data using Molecular Ecological
131 Network Analyses Pipeline (MENAp) (Deng et al., 2012). Networks were constructed based on
132 features that were present in at least 70% of the samples using Pearson correlation matrix.
133 Metagenomic NWs were constructed using a p-value cut-off of 0.01. The Gephi software
134 (Bastian, Heymann & Jacomy, 2009) was used to visualize the network graphs. To eventuate the
135 role of individual nodes we have applied edge degree, Betweenness, Zi and Pi (Zhou et al., 2010)
136 to describe the properties of each node and plots were produced using ggplot2 (Wickham, 2009).
137 Random networks were generated using the Maslov-Sneppen procedure (Maslov & Sneppen,
138 2002).

139 **Results**

140 *Site and leaf species effect on the function and composition*

141 The community found in the litter samples was homogeneous between plant species and sites
142 (Fig. 1). The most common phyla were Proteobacteria (classes Gamma and Alphaproteobacteria)
143 followed by Firmicutes (Clostridia and Bacilli) (Fig. 1A and B). Most of the reads detected in the
144 libraries belonged to Bacteria. Besides the bacterial phyla, the only phylum with normalized
145 relative abundance above 1% was the Euryarchaeota. The functional classification of the reads

146 was even more homogeneous than the taxonomic (Fig. 1C). The most abundant protein clusters
147 were associated with the metabolism of carbohydrates, amino acids, and proteins.

148 Non-metric multidimensional scaling (NMDS) of the metagenomic data indicated that substrate
149 (i.e., tree species) did not significantly select for a specific community (Fig. 2A and B). It also
150 showed that different mangroves had a large overlap between them. This pattern was more
151 pronounced in the NMDS based on the functional data (Fig. 2B) than the taxonomic (Fig. 2A).
152 Two-way Adonis ($p<0.05$) also confirmed these results. According to this test, neither site nor
153 plant species had a significant effect on the communities' functional profile, while there is a
154 significant effect of site (Pseudo-F=2.39424 R2=0.21981 p=0.020) on the taxonomic profile.
155 Despite this slightly different behaviors, the Mantel test indicates a strong (r= 0.86565) and
156 significant (p=0.001) correlation between functional and taxonomic data.
157 We have also attempted to identify differential features in the data set capable of identifying or
158 differentiating the treatments (i.e., substrate, site or substrate+site) using MetagenomeSeq
159 (Paulson et al., 2013). However, no feature was significantly different between treatments.

160 *Network Analysis*

161 The construction of ecological networks was applied to describe the interactions between
162 different features of a community (i.e., taxa or genes). The interactions do not represent close
163 contact between them but that their behaviors are significantly correlated. Nevertheless, these
164 correlations hold within them all different sorts of ecological interactions (e.g., competition,
165 mutualism, predation, environmental overlap). However, due to the complexity of microbial
166 communities and their diminished size, the true nature of such correlations is actually hard to
167 grasp.

168 The network based on the taxonomic classification of the metagenomic data has shown a
169 complex network with 2783 nodes and 5754 edges (Fig. 3). This network had a high degree of
170 modularity and several dual node subnetworks. Another feature of this NW is the high
171 association of populations of the same phyla.

172 The taxonomic and functional networks exhibited scale-free characteristics, as indicated by R^2 of
173 power-law fitting (0.83 for the functional network and 0.88 for the taxon network). Randomly
174 rewiring the network connections and calculation of network properties indicated that
175 associations observed deviate from a random association and that these networks exhibit small-
176 world structure due to the low mean shortest path length and average clustering coefficient (table
177 1).
178 The analysis of the centrality of individual nodes indicates that each phylum had a distinct role
179 within this network (Fig. S2). Bacterioidetes presented the highest average Betweenness
180 centrality (BwC) of all phyla, followed by Proteobacteria and Chloroflexi. Populations with high
181 BwC have central positions in an NW and cannot be easily removed, whereas low BwC
182 populations can be eliminated from the NW without disrupting the network. Another important
183 observation is the association between taxonomic affiliation, normalized abundance, and BwC.
184 Population with high abundance had the highest BwC and were affiliated with Bacteroidetes or
185 Proteobacteria.
186 The largest subnetwork was formed by Bactereoidetes. The remaining subnetworks were divided
187 between the other abundant phyla. Most of the subnetworks formed by Proteobacteria were
188 separated between the different classes Proteobacteria (Fig. 4A). The ZP plot (Fig. 4B) indicates
189 that all features present in the network are peripherals ($Zi \leq 2.5$, $Pi \leq 0.62$), with most of their
190 links inside their modules. Most of them had no links outside their own modules (i.e., Pi=0).

There was only one module hub (Zi > 2.5, Pi ≤ 0.62), no connectors (Zi ≤ 2.5, Pi > 0.62) or network hubs (Zi > 2.5, Pi > 0.62). This module hub was classified as a *Pseudomonas* closely related to *P. aeruginosa*. This result indicates low connectivity in the network.

The ecological network constructed from the functional assignment of the metagenomic sequences show a larger and more complex net of interconnected nodes (Fig. 5) with 4030 nodes and 12648 edges. The clustering by classification is not apparent in this network. Randomly rewiring the network connections and calculation of network properties indicate that associations observed deviate from a random association (table 1).

The functional network was highly connected, most nodes had a large value of degree. This indicated a strong redundancy of nodes. Hence, it was very difficult to identify among the most frequent functional groups one with higher BwC (Fig. S4).

Although the functional network has shown a clear relationship between abundance and BwC there is none with classification (Fig. 6A). However, nodes with higher BwC had a central role in the network (as module hub, connectors or network hubs) (Fig. 6B). The ZP plot (Fig. 6B) indicates that most of the features present in the network are peripherals (Zi ≤ 2.5, Pi ≤ 0.62), with most of their links inside their modules. However, links with high BwC held important positions in these networks as module hubs (Zi > 2.5, Pi ≤ 0.62) and connectors (Zi ≤ 2.5, Pi > 0.62). Additionally, no network hub (Zi > 2.5, Pi > 0.62) was present in these networks. This result also indicates a low connectivity in the network with a lot of small independent modules.

Discussion

The constant changes in environmental characteristics pose a challenge to the organisms that take part in the process of decomposition in estuarine environments (Holguin, Vazquez & Bashan, 2001). Sediments in which this process happens changes between fresh and marine characteristics and in the case of mangroves dry and submerged (Bouillon et al., 2004). These lead to a complex assemblage in which players from different sources interact among themselves and with the decomposing substrate (Freschet et al., 2013; Miura et al., 2015; Moitinho et al., 2018). In the present study, we have applied litterbag experiments to unravel the effects that plant species has on the microorganisms that colonize their decaying leaves and to identify how the environmental characteristics affect this process. Interestingly, the community composition did not present high variation when we looked at broader taxonomic ranks (such as phylum and class). This apparent stability was observed regardless of the factor analyzed (i.e., plant species or mangrove site). This effect was stronger in the functional than taxonomic classification. However, the contrasting pattern between functional and taxonomic classification relatively common and has been observed in many environments (Costello et al., 2012; Delmont et al., 2012; Taketani et al., 2014). Furthermore, the communities found in the decaying leaves were different from those usually found in mangrove sediments that have a high abundance of sulfur reducing Deltaproteobacteria (Andreote et al., 2012; Varon-Lopez et al., 2014) while leaves were dominated by Gamma and Alphaproteobacteria. This must be determined by the fact that the environment in which the decomposition takes place is not suitable for this organisms due to the higher concentration of O_2 which also prevents the presence of methanogenic archaeal populations (Dias et al., 2011; Mendes et al., 2012). This suggests that these organisms may come from aerobic sources such as air, water, and leaf.

233 This small variation in the composition also reflected in NMDS and Adonis patterns which were
234 found to be not significant. This is indicative that despite the variation in environmental
235 characteristics that the community profile is quite stable. Alternatively, we can propose that the
236 populations that inhabit this material might be selected to withstand this variation.

237 Estuarine aquatic communities, due to the mix between fresh and marine waters, present spatial
238 and temporal variation driven mostly by the movement of the tides (Guo et al., 2017). Thus
239 mangrove litter subjected to large variation in environmental characteristics or a tight
240 relationship between the populations and the substrate. Additionally, plant material with different
241 chemical properties has been shown to have only a minor effect on the bacterial community
242 composition (Tláskal et al., 2018). This explanation is supported by the fact that we did not find
243 any functional feature or taxonomic group that was differentially abundant in any leaf species,
244 mangrove site or both.

245 The functional and taxonomic networks presented a great number of co-occurring nodes. The
246 network constructed based on these data presented scale-free characteristics, this type of network
247 is considered very resistant to disturbances and the removal of nodes, hence it is a very robust
248 network (Green et al., 2017). This structure also indicates a relatively stable structure of the
249 community since it would be able to withstand the constant changes this environment endures.
250 These networks also exhibit small-world structure, which indicates that nodes are accessible to
251 every other node through a short path (Layeghifard, Hwang & Guttman, 2017). These networks
252 are believed to be highly coordinated while allowing for a high degree of functional
253 specialization into clustered units (Watts & Strogatz, 1998; Green et al., 2017). However, a
254 small-world structure is common in large networks (Green et al., 2017).

The taxonomy based network formation indicates that there is a tight link between phylogeny and lifestyle since the co-occurrence patterns indicate a preference for similar environmental conditions (Fig. 4A). The correlations between nodes of the same taxonomic groups might be related to similar lifestyles shared by closely related taxa (Philippot et al., 2010). Despite the possibility that minor differences between such taxa might lead to distinct ecological strategies or lifestyles (Fraser et al., 2009; Denef et al., 2010). It can be speculated that there is some degree of redundancy in this networks which would aid in the stability of the process.

The Bacteroides are recognized as consumers of complex polysaccharides in marine environments and its genomes have a large number of genes related to glycoside hydrolases (GH) families (Bauer et al., 2006). Hence, this nodes might have an important role in the leaf degradation despite the expected role of fungi in this process (Hu et al., 2017; Tláskal et al., 2018). This result indicates that, at least on mangrove sediments, bacteria (specially Bacteroidetes) might have an important role in the decomposition, possibly due to the lower cost of reproduction of this bacterial taxa, that are considered r-strategists (Hu et al., 2017), in the energy limited anaerobic sediments (Taketani et al., 2010b).

The second phylum with the highest BwC was the Proteobacteria which is a very versatile group (Cobo-Simón & Tamames, 2017) and very abundant in marine environments and mangroves (Taketani et al., 2010a; Andreote et al., 2012; Varon-Lopez et al., 2014). Also, in terrestrial ecosystems, Alpha-, Beta- and Gammaproteobacteria were found to be prevalent in the initial phases of litter degradation due to their fast growth (DeAngelis et al., 2013) and arrive during succession to replace the initial colonization by phyllospheric communities (Vojtěch, Voríškivá & Baldrian, 2016). This wide range of lifestyles contributed to the broad dispersal of BwC observed in figure 4.

The topological role of individual nodes (Zi-Pi plot) indicated that a Pseudomonas (Gammaproteobacteria) is the only taxon that has an important position in this network as module hub. Hubs have a central role in a network and/or module (Jiang et al., 2015). Hence, this Pseudomonas is a key node within a module despite its low abundance and BwC. However, scale-free networks usually display only a small portion of hubs (Green et al., 2017) which contributes to its robustness.

However, the role of individual nodes in the functional network was slightly different than observed in the taxonomic. All of the broad functional groups had a similar average BwC which indicates that they have similar importance within the network. Besides, nodes with higher BwC were identified as Hubs (module hubs and connectors) which indicates that the removal of these would affect the structure of the network (Deng et al., 2012). However, since within these nodes there is a mixture of different taxa that would respond differently to perturbation, there is a chance that the higher robustness of the taxonomic network would aid the community to endure stresses. Hence, there might be an important role of functional redundancy to the stability of the community present in mangrove litter (Strickland et al., 2009; Banerjee et al., 2016) which would aid in the efficient decomposition of litter by maintaining the process balance (Kaiser et al., 2014)

Conclusions

The present study has shown that the community present in mangrove plant's decaying material is stable despite differences in plant species or mangrove location. These communities form a tight network that is robust and resistant to disturbances and therefore capable of withstanding this constantly changing environment.

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Figure 1

Classification of metagenomic sequences from samples of litterbags left on mangrove sediments.

A - classification of sequences to the level of phylum; B – classification of sequences from Proteobacteria to the level of class; C - classification of sequences in functional SEED subsystems.

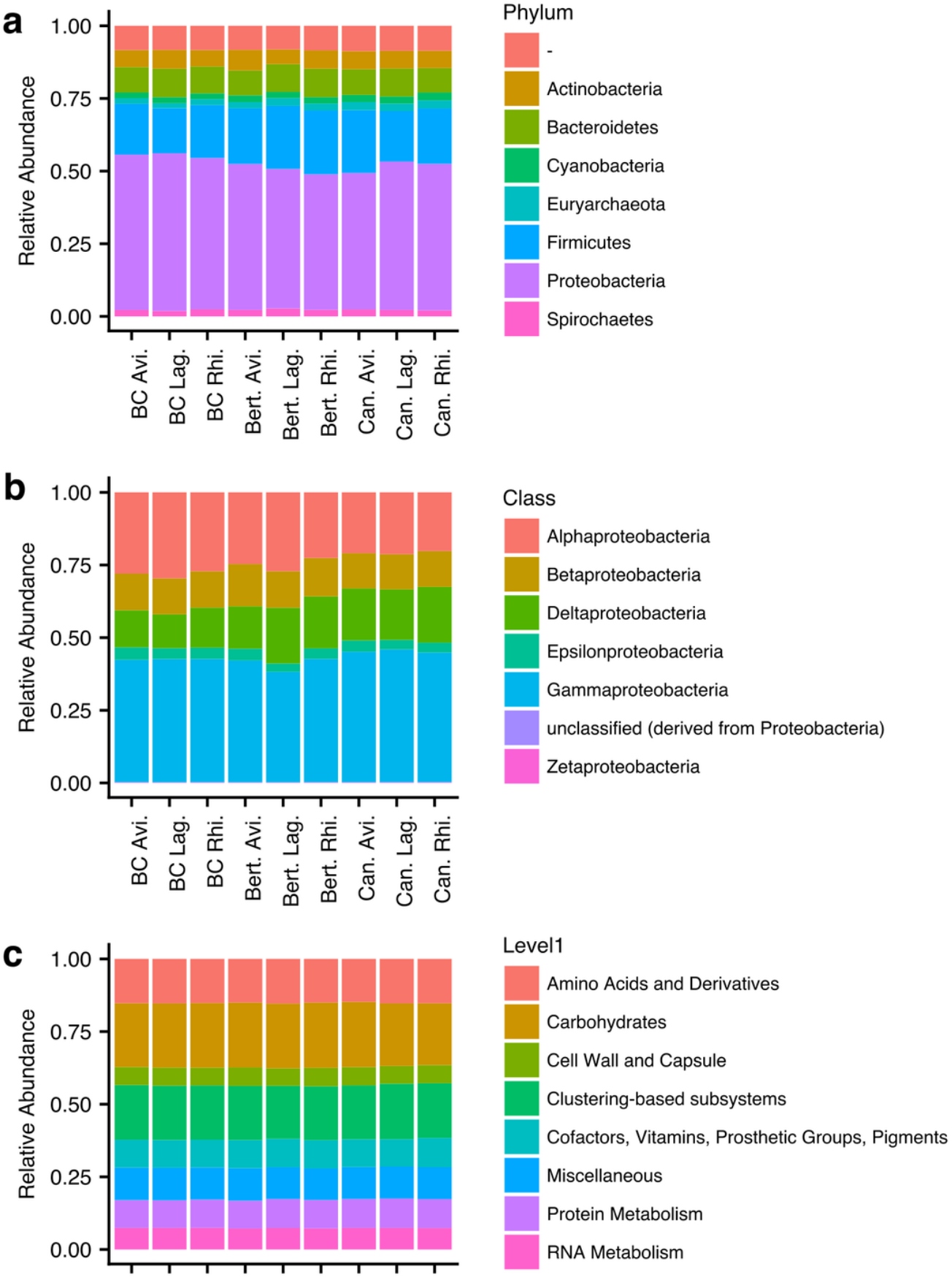
a
Relative Abundance
1.00
0.75
0.50
0.25
0.00
BC Avi.
BC Lag.
BC Rhi.
Bert. Avi.
Bert. Lag.
Bert. Rhi.
Can. Avi.
Can. Lag.
Can. Rhi.
Phylum
-
Actinobacteria
Bacteroidetes
Cyanobacteria
Euryarchaeota
Firmicutes
Proteobacteria
Spirochaetes
b
Relative Abundance
1.00
0.75
0.50
0.25
0.00
BC Avi.
BC Lag.
BC Rhi.
Bert. Avi.
Bert. Lag.
Bert. Rhi.
Can. Avi.
Can. Lag.
Can. Rhi.
Class
Alphaproteobacteria
Betaproteobacteria
Deltaproteobacteria
Epsilonproteobacteria
Gammaproteobacteria
unclassified (derived from Proteobacteria)
Zetaproteobacteria
c
Relative Abundance
1.00
0.75
0.50
0.25
0.00
BC Avi.
BC Lag.
BC Rhi.
Bert. Avi.
Bert. Lag.
Bert. Rhi.
Can. Avi.
Can. Lag.
Can. Rhi.
Level1
Amino Acids and Derivatives
Carbohydrates
Cell Wall and Capsule
Clustering-based subsystems
Cofactors, Vitamins, Prosthetic Groups, Pigments
Miscellaneous
Protein Metabolism
RNA Metabolism

Figure 2

Non-metric multidimensional scaling plots (NMDS) of metagenomic data based on MG-RAST classification of sequences obtained from litterbags left on mangrove sediments.

A – NMDS of the taxonomic classification of metagenomic data; B – NMDS of functional classification of the metagenomic data. Samples are colored as displayed on the legend.

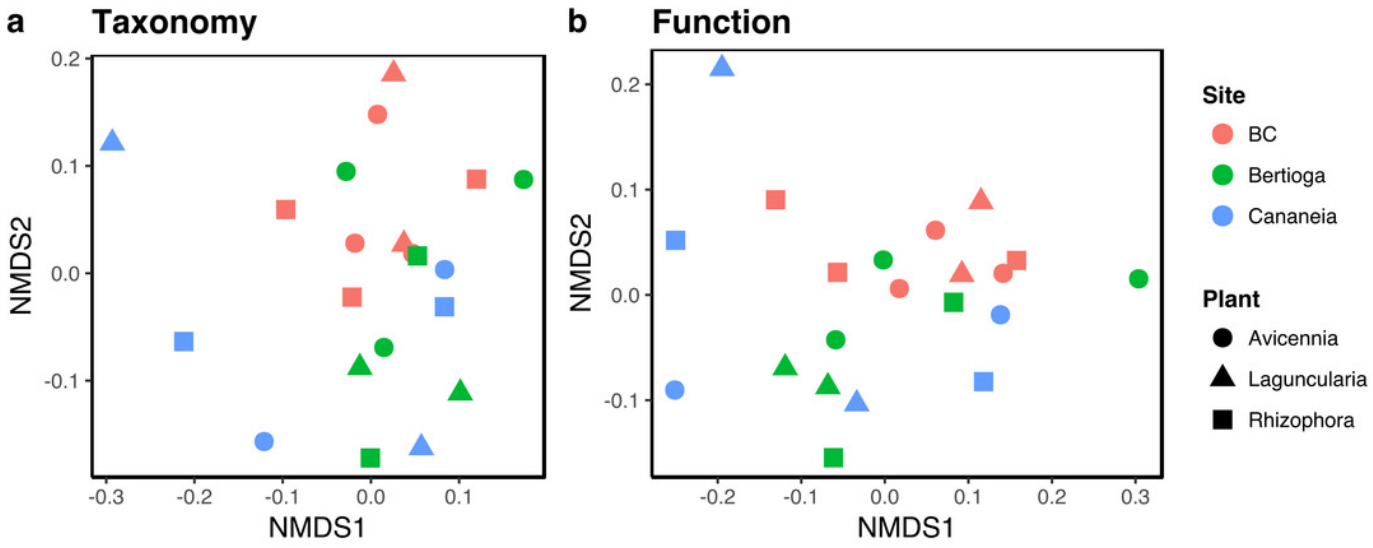

Figure 3

Ecological network based on the taxonomic classification of the mangrove trees litter decomposition metagenomic samples.

Node size is proportional to the Node Betweenness. For a high-resolution version of the figure check figure S1.

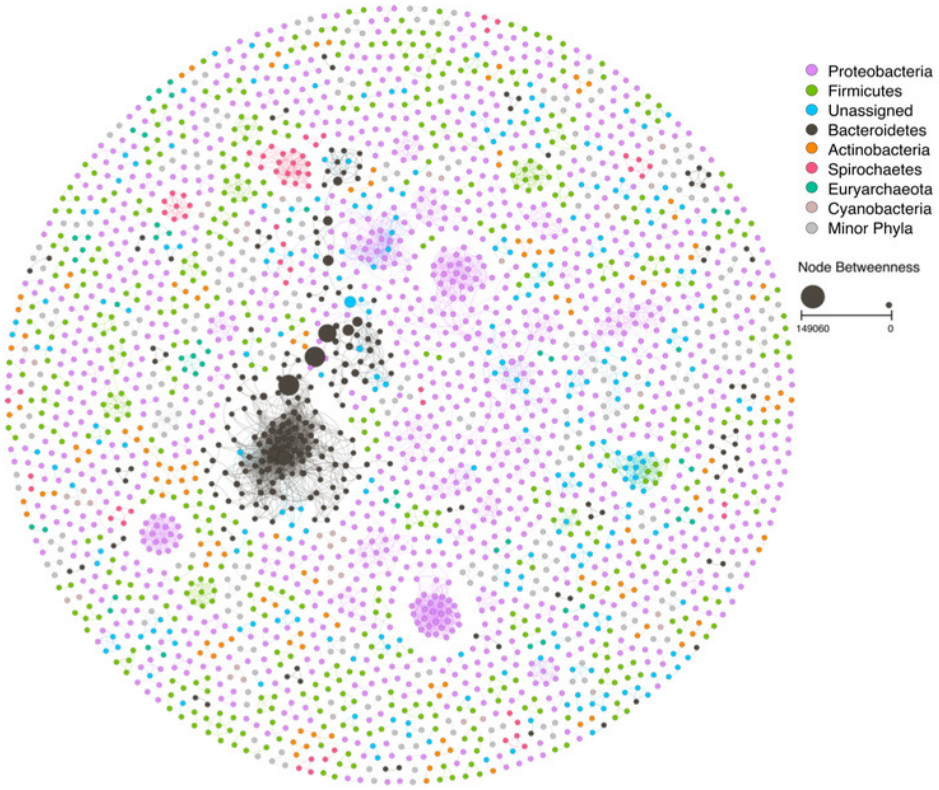

Figure 4

Properties of each node as represented by their role within the network.

A – relationship between node betweeness, abundance and taxonomic assignment; B –relationship between within-module connectivity (Zi) and among-module connectivity (Pi), node betweeness, and taxonomic assignment.

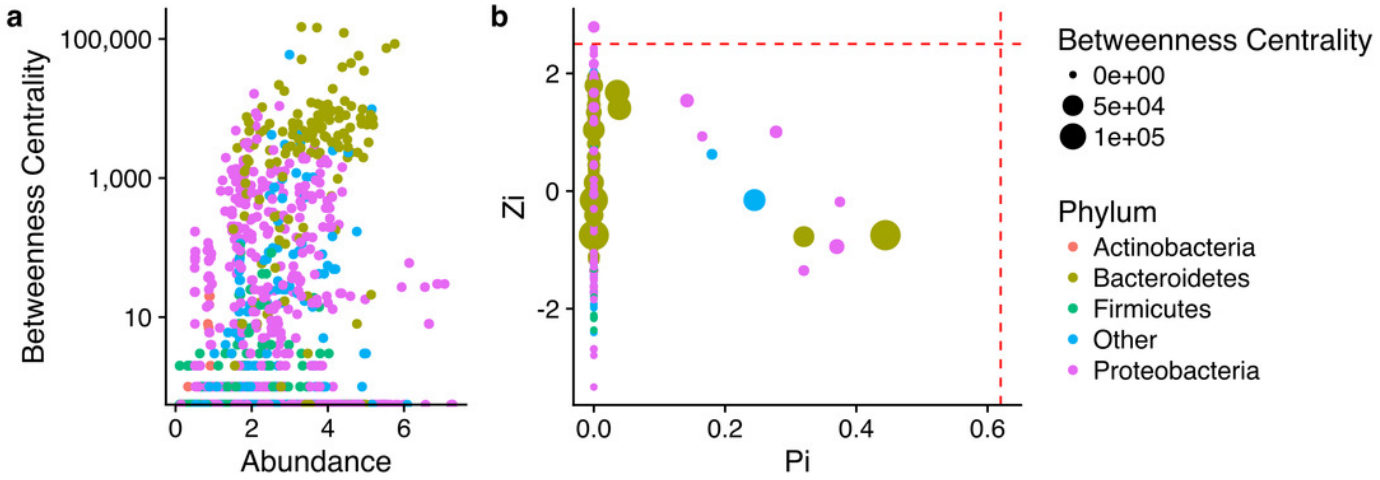

Figure 5

Ecological network based on the functional classification of the mangrove trees litter decomposition metagenomic samples.

Node size is proportional to the Edge Betweenness. For a high-resolution version of the figure check figure S3.


Carbohydrates
Clustering-based subsystems
Amino Acids and Derivatives
Miscellaneous
Cofactors, Vitamins*
RNA Metabolism
Protein Metabolism
Cell Wall and Capsule
Minor groups
Node Betweenness
76599
0

Figure 6

Properties of each node as represented by their role within the network.

A – relationship between node betweeness, abundance and functional assignment; B –relationship between within-module connectivity (Zi) and among-module connectivity (Pi), node betweenness, and functional assignment.

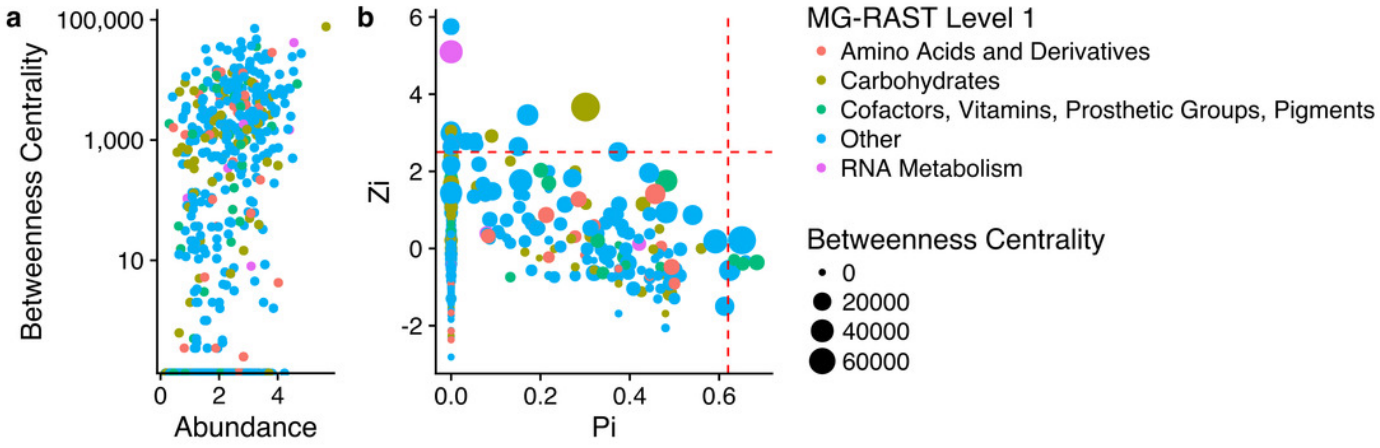

Table 1(on next page)

Indexes based on ecological network analysis of metagenomic data from decomposing leaves of mangrove trees and random trees constructed based on this data.

Table 1: Indexes based on ecological network analysis of metagenomic data from decomposing leaves of mangrove trees and random trees constructed based on this data

Network Indexes	Taxonomic		Functional	
	Empirical Network	100 Random Networks	Empirical Network	100 Random Networks
Modularity(fast_greedy)	0.927	0.490 ± 0.003	0.781	0.363 ± 0.002
Lubness	1.000	1.000 ± 0.000	1.000	1.000 ± 0.000
Hierarchy	0.000	0.000 ± 0.000	0.000	0.000 ± 0.000
Efficiency	0.827	0.999 ± 0.000	0.985	0.999 ± 0.000
Connectedness (Con)	0.007	0.851 ± 0.011	0.093	0.902 ± 0.008
Transitivity (Trans)	0.723	0.028 ± 0.002	0.453	0.018 ± 0.001
Reciprocity	1.000	1.000 ± 0.000	1.000	1.000 ± 0.000
Density (D)	0.001	0.001 ± 0.000	0.002	0.002 ± 0.000
Centralization of eigenvector centrality (CE)	0.171	0.160 ± 0.011	0.174	0.141 ± 0.011
Centralization of stress centrality (CS)	0.038	0.214 ± 0.014	18.19	0.220 ± 0.013
Centralization of betweenness (CB)	0.002	0.035 ± 0.002	0.009	0.029 ± 0.002
Centralization of degree (CD)	0.019	0.019 ± 0.000	0.021	0.021 ± 0.000
Harmonic geodesic distance (HD)	320.933	4.864 ± 0.059	45.375	4.251 ± 0.031
Geodesic efficiency (E)	0.003	0.206 ± 0.002	0.022	0.235 ± 0.002
Average path distance (GD)	0.03	3.784 ± 0.061	0.464	3.662 ± 0.036
Average clustering coefficient (avgCC)	0.524	0.012 ± 0.002	0.636	0.012 ± 0.001