A Robust Network Model for Studying Microbiomes in Precision Agriculture Applications

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Abstract. Recent rapid advancements in high-throughput sequencing technologies have made it possible for researchers to explore the microbial universe in high degrees of depth that were not possible even few years ago. Microbial communities occupy numerous environments everywhere and significantly impact the health of the living organisms in their environments. With the availability of microbiome data, advanced computational tools are critical to conduct the needed analysis and allow researchers to extract meaningful knowledge leading to actionable decisions. However, despite many attempts to develop tools to analyze the heterogeneous datasets associated with various microbiomes, such attempts lack the sophistication and robustness needed to efficiently analyze these complex heterogeneous datasets and produce accurate results. In addition, almost all current methods employ heuristic concepts that do not guarantee the robustness and reproducibility needed to provide the biomedical community with trusted analysis that lead to precise data-driven decisions. In this study, we present a network model that attempts to overcome these challenges by utilizing graph-theoretic concepts and employing multiple computational methods with the goal of conducting robust analysis and produce accurate results. To test the proposed model, we performed the analysis on plant microbiome datasets to obtain distinctive functional modules based on key microbial interrelationships in a given host environment. Our findings establish a framework for a new understanding of the association between functional modules based on microbial community structure.

Keywords: Precision agriculture, plant microbiomes, robust analysis, network models, graph algorithms

1 Introduction

Numerous studies have shown that the health of all living organism is underpinned by the many roles of microbiome in their environments. New technologies have revolutionized the way we understand these little microbes, encompassing

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interactions between the microbes, that perform vital functions, both individually and as a group. For the human host, many clinical conditions interact with microbes that impact developmental conditions for early childhood, quality of life in aging, and everything in between. Besides human microbiome research, understanding the impact of plant microbiomes on plant growth, health, and productivity have also gained significant attention recently. This is again due to the advancement in high-throughput technologies and the consequent availability of the data required to study such impact. Studying the impact of microbial composition and their properties in plants represent an opportunity to develop and improve proposed methodologies, considering that plant environments are relatively more accessible and easier to manage, as compared to those associated with humans. All living organisms in our ecosystems continue to evolve together. Such co-evolution is influenced by the intra-relationship among microbes and inter-relationship with their surrounding environment. Plants also host their own microbial communities, and they are influenced by a wide range of ecological interactions such as symbiotic, competitive, neutral, and mutualistic relationships [6], [17].

Several previous studies have identified microbial interactions that form important microbiomes and are essential for promoting plant growth and modulating disease outbreak [3], [4]. Considering the complexity of the nature of microbiome data, researchers have attempted to model and study the relationship of plant phenotype with their microbiome using various computational and statistical methods [15]. In accordance with a rapid advancement in technological capabilities, machine learning-based and deep learning-based methods have been applied in recent studies to study the impact of the microbiome on plant growth [7], [11].

Co-occurrence network-based analysis represents one of the powerful analyses. This approach explores these significant co-occurrence patterns of microorganisms. It has become a widely adopted method in ecological studies [2]. Such co-occurrence patterns are significant in the understanding of microbial community structure and are utilized for the potential prediction of species interactions in associated environments [5]. To measure these patterns, correlation coefficients or mutual information measures are often used to identify significant microbial abundance relationships. For example, an association network inference tool (CoNet) provides multiple types of network inference methods, and the ensemble approaches to network inference were proposed to increase the network accuracy [8]. Current computational and bioinformatics tools, including CoNet, are required to have their own parameters and, in many cases, specific thresholds to solve an each computational biology problem. However, it is a major challenge in Biomedical Informatics to find the optimal parameters for each case study. In order to minimize the accuracy concerns of the obtained results, it is critical to have a robust approach that limits the impact of the imperfections associated with heuristic steps and/or randomly selected thresholds.

In this study, we focus on addressing two research questions: 1) How to capture the distinctive and impactful microbial interactions in the co-expression

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networks from raw microbial abundance data in a given environment. 2) How to develop a precise and robust approach for mining accurate microbial associations with relation to functional modules. To address these two issues, we present a new computational pipeline as the central component of a robust analysis in order to have a better understanding of the significant associations among functional modules and host plants based on microbial community structure. In addition, multiple computational methods or algorithms will be employed to model and solve such complex problems to avoid or limit the impact of selecting a computational approach on the outcome of the study. We argue that this will potentially lead to more trustworthy results that are less influenced by the characteristics as well as limitations associated with each computational tool.

2 Methods

2.1 Overview of Workflow

This pipeline takes in microbial abundance data together with phenotypical properties and returns 1) Highly associated bacteria in a given environment; 2) Operational taxonomic unit pairs (OTUs-pairs hereafter) specific to samples from higher and lower percentile of a phenotypic property (in this study 'total biomass'); and 3) Functional modules enriched in these groupings. The entire workflow of the proposed method is shown in Figure 1. It consists of four components: Identification of microbial association networks using multiple statistical methods, discovery of bacteria of interest based on phenotypical characteristics, functional enrichment analysis, and comparative analysis.

2.2 Data Description

In this study, we employed bacterial abundance data and associated metadata obtained from collaborators at the University of Nantes. The dataset comprised relative abundance of bacterial OTUs at the genus level across *Medicago truncatula* plant samples, along with metadata detailing 16 phenotypical parameters related to plant growth, such as estimated quantity of nitrogen and total biomass. Genus names were standardized using the NCBI taxonomy database [9]. Additionally, we acquired two sets of functional reference information for enrichment analysis based on the genus list derived from the abundance data. The first reference was generated using Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt) bioinformatics software, providing counts of KEGG Orthologs (KOs) for referenced taxa [13]. The second reference contained information on pathway modules, representing functional units of gene sets in metabolic pathways, retrieved using KEGG REST API in a Unix environment. This experimental dataset was employed as a case study to test the proposed methodology. All steps of the computational approach are designed and implemented to address similar scenarios in various applications. Hence, we suggest that our approach can be extended by incorporating additional datasets from diverse domains.

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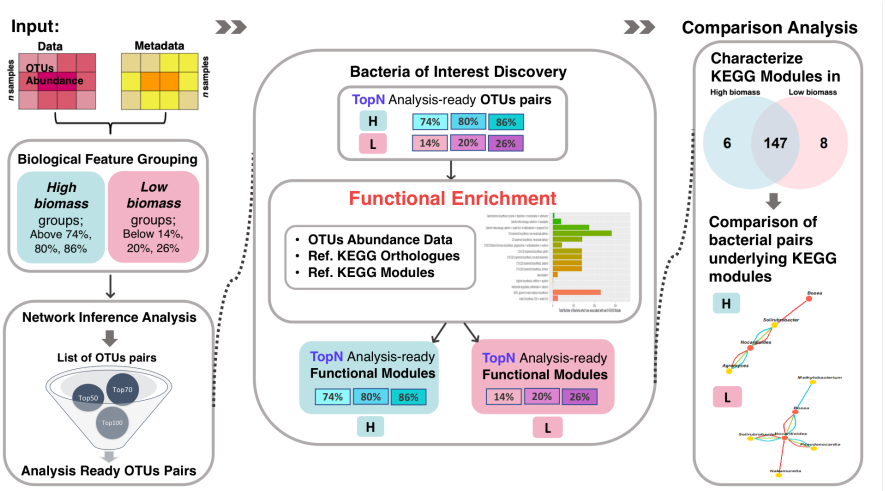

Fig. 1. Overview of the pipeline. The pipeline consists of four main components: 1) Construction of co-expression OTUs networks in a given environment; 2) Identification bacteria of interest; 3) Functional modules enrichment analysis; 4) Comparison analysis.

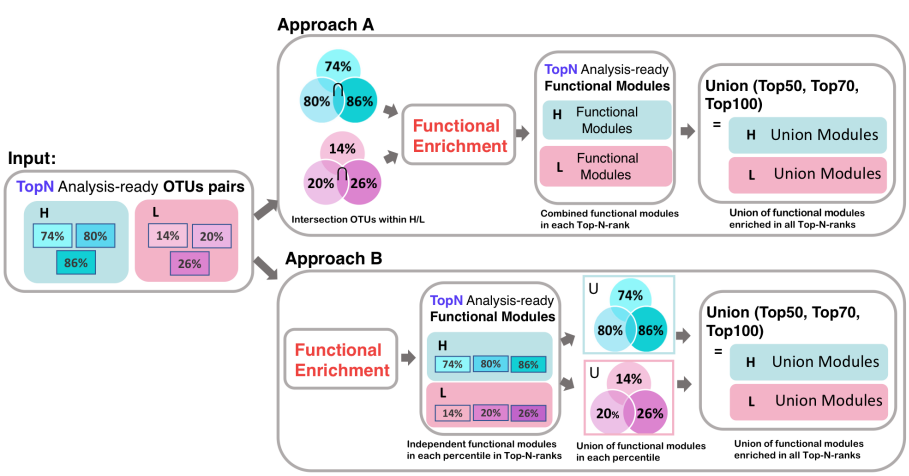

Fig. 2. Detection of distinctive OTUs pairs through Approaches A and B.

2.3 Biological Feature Grouping

Given that the input attributes of each plant included the total biomass, we observed differences in the total biomass across plant samples, presuming it reflects plant health. Also, assuming that each percentile point of the total biomass may

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indicate the host phenotypical conditions, the microbial abundance data were grouped into 49 percentile points of the total biomass. Six percentile points were selected for data subset, ensuring statistical robustness. Therefore, samples above the 74th, 80th, and 86th percentiles were categorized as high biomass, while those below 14th, 20th, and 26th percentiles were categorized as low biomass.

2.4 Co-expression Network Analysis

Microbial co-expression networks were constructed from the OTUs abundance data, considering the association between each pair of OTUs within both sample groups. We employed two established co-expression measures: rank correlation coefficients and mutual information. These analyses were conducted using R.

Spearman Rank Correlation-Based Network
The Spearman rank correlation matrices were computed from the OTUs abundance data within each sample group, utilizing the *'corr.test'* function in the *psych* package with Bonferroni correction applied. The correlation coefficient rank values, ranging from -1 to 1, were sorted from positive to negative for subsequent analysis.

Mutual Information-Based Network
For the Mutual Information-based network, the shared information between OTUs was estimated using mutual information (MI). Prior to MI calculation, the relative abundance data of OTUs were discretized using the *'discretize'* function. MI was then computed using the *'mutinformation()'* function. These analyses relied on the *infotheo* package. Following computation, all co-expression pairs in each analysis were filtered based on Top-N-ranking (Top 50, 70, and 100). This resulted in dataframes of 50, 70, and 100 bacterial pairs, respectively, prepared for further analysis.

2.5 Characterizing Robust Biological Functions

The proposed pipeline consists of two component workflows designed to characterize the biological functions of Top-N-ranking OTUs pairs using KEGG modules (see Figure 2).

In the first component (shown in Approach A), for each of the Top-N-ranking OTUs pairs, we identify an intersection of microbial associations across high biomass groups (74%, 80%, and 86%) and low biomass groups (14%, 20%, and 26%), respectively. The microbial communities based on these common microbial associations were considered bacteria of interest for functional enrichment analysis. The union of functional modules enriched in all Top-N-ranking defined as the high and low biomass functional features. In the second component (shown in Approach B), beginning with each Top-N-ranking OTUs pairs, we analyzed each of the OTUs pairs in the individual percentile group of the high and low biomass. Subsequently, the high and low biomass functional features sets at each Top-N ranking were obtained by the union of functional modules enriched in all three percentiles of the high and low biomass groups.

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2.6 Comparison of OTUs Pairs Underlying KEGG modules

For each co-expression method, we compared the union modules from the high and low biomass groups and identified distinctive functional modules in each group. The intersection of these unique functional modules derived from two co-expression methods are used for further analysis. The OTUs annotated with these common distinctive functional modules are labeled as driver OTUs. OTUs associated with the driver OTUs were captured from both high and low biomass groups and were represented as networks. To visualize the networks, R package *igraph* was used. Next, we compared the dynamic change of relationships between driver OTUs in the high and low biomass group networks.

2.7 Bacterial Functional Enrichment Analysis

To identify functional pathways that are over-represented in any given OTUs list of interest, we performed an enrichment analysis. A fisher's exact test (*'phyper'* function in R environment) was used to identify pathways enriched in the OTUs list of interest from Top-N-ranking OTUs pairs. Table 1 illustrates a contingency table with a KEGG module (M00001 Glycolysis) as an example. In this case, the 40 OTUs of interest have been analyzed. A total count of known KEGG modules and the total count of background OTUs are also required for this comparison.

Table 1. An example contingency table for enrichment analysis.

	Present	Absent	Total
Present in KEGG module	40	0	40 (OTUs of interest)
Absent in KEGG module	320	1	321
Total OTUs in KEGG module	360	1	361 (Total OTUs)

For all enriched functional modules in high and low biomass groups, we identified the overlapping of these modules using a Venn diagram. The *'venn.diagram()'* function in R was implemented for this analysis.

3 Results and Discussion

3.1 A Comparison of Networks in High and Low Biomass Groups

We collected the Jaccard similarity index (J.I) for comparing Top-N-rank analysis-ready OTUs pairs at each percentile point (see Table 2). The Jaccard similarity index was computed based on the edges, and Table 2 presents a summary of the similarity between networks within and between high and low biomass groups. Notably, within high biomass (74th, 80th, and 86th percentiles) and low biomass groups (14th, 20th, and 26th percentiles), we observed high degrees of similarity.

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Despite the relatively homogeneous microbial abundance data, distinct similarity patterns emerged between high and low biomass groups of OTU pairs in the Top-N rankings. These findings suggest that the thresholds for high or low biomass groups minimally affect the overall results, indicating a high level of robustness in our approach.

Table 2. Jaccard similarity index (*J.I*) for comparison of network in high and low biomass groups.

Network comparison within high biomass group			
Range of high (H) biomass groups	*J.I* in Top50	*J.I* in Top70	*J.I* in Top100
74th and 80th percentile	0.79	0.75	0.83
80th and 86th percentile	0.56	0.59	0.60
74th and 86th percentile	0.52	0.51	0.57
Network comparison within low biomass group			
Range of low (L) biomass groups	*J.I* in Top50	*J.I* in Top70	*J.I* in Top100
14th and 20th percentile	0.75	0.73	0.74
20th and 26th percentile	0.61	0.63	0.60
14th and 26th percentile	0.64	0.71	0.67
Network comparison between groups			
Range of H and L biomass group	*J.I* in Top50	*J.I* in Top70	*J.I* in Top100
74th and 26th percentile	0.45	0.41	0.38
80th and 20th percentile	0.47	0.41	0.42
86th and 14th percentile	0.39	0.33	0.29

3.2 Co-expression Networks Analysis

Table 3 provides an overview of the obtained networks, including their size parameters and densities. It reports the total count of vertices and edges present in our co-expression networks. The edges in these networks are undirected and represent associations between vertices, which signify bacterial communities. Edge density reflects the ratio of actual edges in the network to the total possible edges, calculated as n(n-1)/2. Here, we present the network descriptions of Spearman rank correlation-based networks in Top 50, 70, and 100.

3.3 Characterization of Distinctive KEGG Modules in High and Low Biomass Groups

We begin with each of the Top-N-ranking OTUs pairs derived from co-expression networks to implement our proposed methods (Approach A and B). The two approaches are independent of one another, each having its own benefits and limitations. The Approach A consists of common OTUs pairs from different

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Table 3. Summary of the spearman correlation-based networks at different percentile of the total biomass (V= Vertices, E= Edges, *D*= Edge density).

	Top50			**Top70**			**Top100**		
Percentile	V	E	*D*	V	E	*D*	V	E	*D*
74th	54	50	0.03	63	70	0.04	76	100	0.04
80th	52	50	0.04	64	70	0.03	75	100	0.04
86th	55	50	0.03	72	70	0.03	79	100	0.03
14th	53	50	0.04	69	70	0.03	88	100	0.03
20th	51	50	0.04	65	70	0.03	80	100	0.03
26th	53	50	0.04	61	70	0.04	78	100	0.03

percentiles followed by the union of functional modules enriched in Top-N-ranks. On the other hand, the Approach B includes functional modules enriched in all percentiles with Top-N-ranks.

Through each approach, we first compared the number of distinctive significant functional modules underlying both high and low biomass groups shown in a Venn diagram (see Figure 3). Figure 3 effectively illustrates the number of unique functional modules for both high (blue) and low (pink) biomass groups obtained from the usage of two approaches (Approach A and B) and two co-expression analyses. The first row of Figure 3 is the result of the comparison between Spearman analysis (left) and mutual information (right) through the Approach A. In a similar manner, the second row depicts the comparison result from the Approach B.

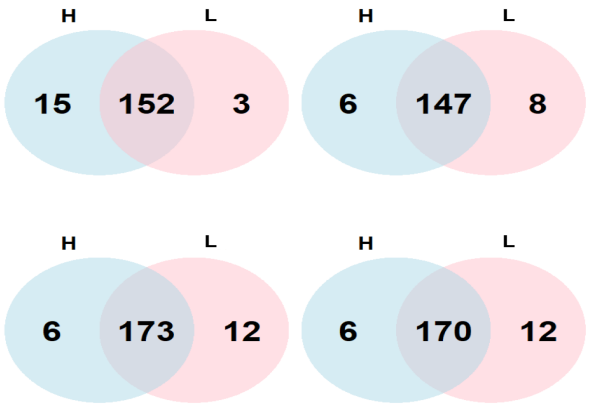

Fig. 3. KEGG modules are identified in high (H) and low (L) biomass groups. First row is the Venn diagram results in Spearman analysis on the left and mutual information on the right from Approach A. Second row has the same order of information as the first row, but from Approach B.

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Table 4. List of distinctive KEGG functional modules in High (H) and Low (L) Biomass groups.

Approach A	
High	M00159 V-type ATPase, prokaryotes M00529 Denitrification, nitrate ⇒ nitrogen M00567 Methanogenesis, CO2 ⇒ methane M00736 Nocardicin A biosynthesis, L-pHPG + arginine + serine ⇒ nocardicin A M00804 Complete nitrification, comammox, ammonia ⇒ nitrite ⇒ nitrate
Low	M00091 Phosphatidylcholine (PC) biosynthesis, PE ⇒ PC M00745 Imipenem resistance, repression of porin OprD
Approach B	
High	M00754 Nisin resistance, phage shock protein homolog LiaH
Low	M00152 Cytochrome bc1 complex M00555 Betaine biosynthesis, choline ⇒ betaine M00564 Helicobacter pylori pathogenicity signature, cagA pathogenicity island M00721 Cationic antimicrobial peptide (CAMP) resistance, arnBCADTEF operon

Incorporating both approaches serves the dual purpose of ensuring highly confident results and retaining significant information. Approach A reveals five distinctive functional modules in the high biomass group, whereas only two distinctive modules are observed in the low biomass group. Likewise, in Approach B, only one functional module was identified in the high biomass group, whereas four exclusive functional modules were represented in the low biomass group (refer to Table 4). Notably, upon comparing these two approaches, no overlapping distinctive functional modules were observed.

In Table 4, the denitrification process (M00529), an exclusive functional module of high biomass group, is a known primary pathway for nitrogen (NO) production by bacteria, which promotes energy to the cell under low oxygen conditions [19],[12]. On the other hand, Phosphatidylcholine (PC) biosynthesis is a pathway exclusive to the low biomass group. The significance of phosphatidylcholine (PC) in bacteria with an emphasis on multiple ecological microbe-host plant interactions have been revealed in a number of studies [1].

This evidence suggests that distinctive functional modules are associated with specific plant health groups. However, this work presents preliminary results characterizing functional modules of high and low biomass groups. The biological association between these groups may be more complex than initially observed. It's possible that these functional modules may occasionally contribute to opposite health conditions.

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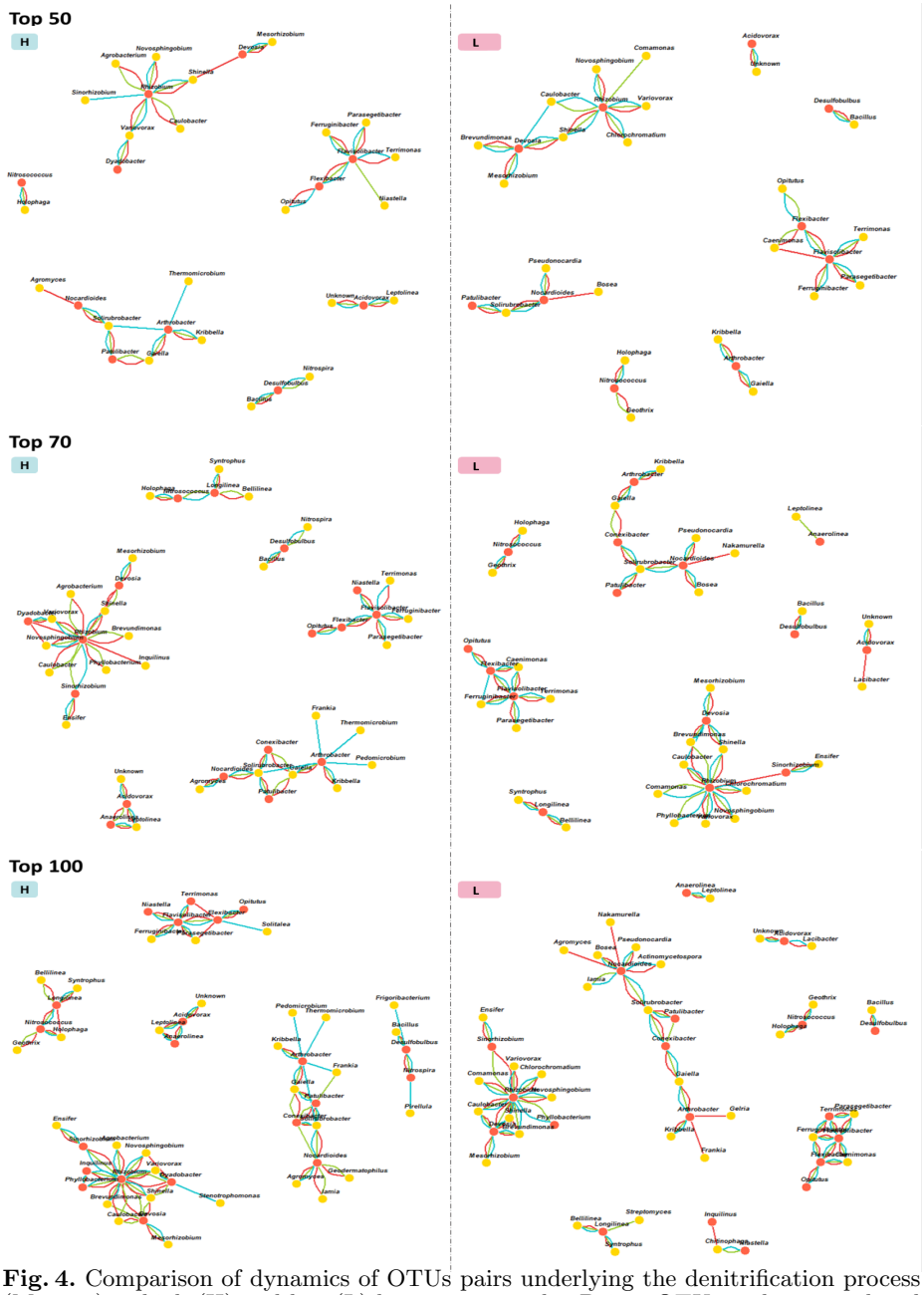

Fig. 4. Comparison of dynamics of OTUs pairs underlying the denitrification process (M00529) in high (H) and low (L) biomass networks. Driver OTUs nodes are red and their neighbor nodes are yellow. Edges are colored by percentile of samples: 74th and 14th percentile (red), 80th and 20th percentile(green), and 86th and 26th percentile (turquoise).

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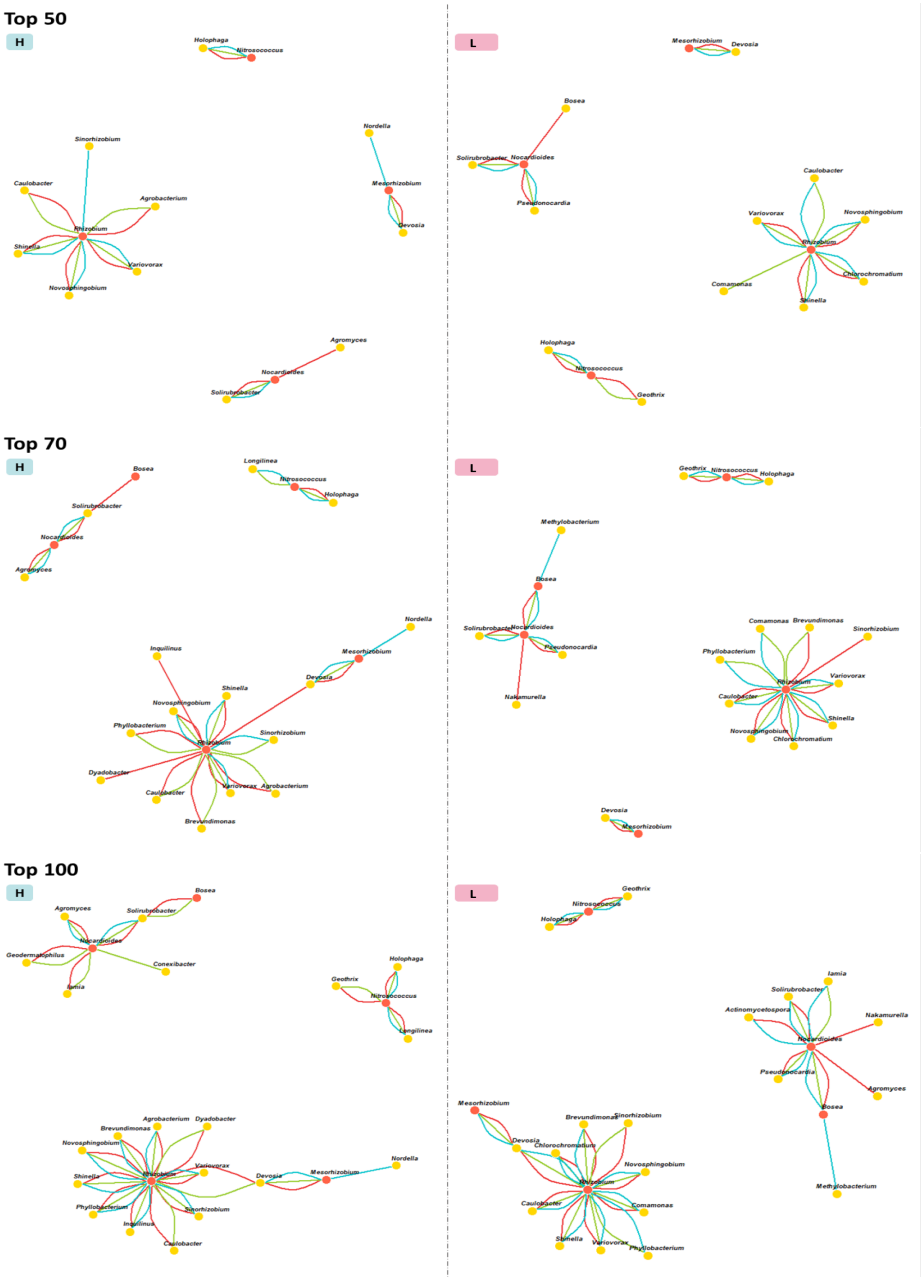

Fig. 5. Comparison of dynamics of OTUs pairs underlying the dhosphatidylcholine(PC) biosynthesis (M00091) in high biomass (H) and low biomass (L) networks.

3.4 Comparison of Dynamics of OTUs Pairs Underlying KEGG Modules

To comprehend the biological significance of identifying distinctive functional modules in OTU pairs, we examined how the dynamics of association between

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driver OTUs, derived from functional modules, varied in high and low biomass networks. Specifically, we compared the representation of association dynamics between driver OTUs involved in the denitrification process (M00529) across Top-N-ranking high and low biomass groups (see Figure 4). We hypothesized that these driver OTUs' relationships might serve as key OTU pairs within functional modules related to host environmental conditions. The differing representation of association dynamics between driver OTUs across Top-N-ranking networks in high and low biomass groups is illustrated in different rows of Figure 4. We posited that the relationship between driver OTUs could serve as crucial pairs within functional modules associated with host environmental conditions. The representation of this relationship differs across Top-N-ranking networks between high and low biomass group networks, as depicted in different rows of Figure 5.

In addition, the microbiome community among *Flexibacter*, *Flavisolibacter*, *Opitutus*, and *Terrimonas* are commonly represented in both high and low biomass networks across Top-N-ranks. However, these microbes are consistently associated with *Niastella* only in a high biomass group network. Moreover, each of following pairs, the group of *Longilinea* and *Nitrosococcus*, the group of *Acidovorax* and *Anaerolinea*, the group of *Desulfobulbus* and *Nitrospira*, have shown strong correlations in high biomass group networks whereas the relationship of these pairs are not represented in low biomass group networks. In particular, the *Dyadobacter* has shown exclusive associations with *Rhizobium* in high biomass group networks. *Rhizobium* is one kind of rhizosphere bacteria, which is also known as plant beneficial microbes, and can establish a symbiotic relationship with legumes species [10]. It can fix atmospheric nitrogen to help plant growth and improve soil fertility. The *Dyadobacter* is also known as core rhizosphere bacteria [18]. Therefore, it could be inferred that these driver OTUs pairs may have the potential to facilitate plant health and disease suppression.

Figure 5 illustrates the network comparisons of the association between driver OTUs derived from phosphatidylcholine (PC) biosynthesis (M00091) in high and low biomass groups. The M00091 module was commonly enriched in both Spearman analysis and mutual information and was distinctive to low biomass groups. The relationship between *Bosea* and *Nocardioides* is depicted differently in high and low biomass group networks. This OTUs pair constantly appears in low biomass group networks, while this pair has shown an indirect relationship through *Solirubrobacter* in the high biomass group (See Figure 5). The *Bosea* belongs to non-rhizobial endophytes (NRE), which were also detected in nodules of legume species, although it does not have a similar function like the rhizosphere bacteria group [14]. This suggests that they might cause the rhizobial infection when co-inoculated with rhizosphere microbial communities [14], [16].

4 Conclusion

In this study, we introduced a new approach for modeling and analyzing heterogeneous datasets associated with microbiome. Our proposed pipeline aims to

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mine microbial associations in relation to functional modules in a given environment. The pipeline is designed with robustness in mind in order to achieve a high degree of accuracy and trustworthiness. Our proposed approach facilitated the identification of distinct functional modules based on key OTUs pairs in a given health condition. The result produced by this pipeline highlighted the association between distinctive functional modules and legume species on the basis of key OTUs pairs in both high and low biomass samples. The obtained findings are consistent with previous relevant results reported in the literature. There is a great potential to further develop the proposed approach to analyze microbiome in different environments in future studies. The model presented in the reported study can serve as a framework within which future modifications, in line with choosing percentiles based on given phenotypical factors with different types of microbiome data, can be easily incorporated.

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