

Linking fungal–bacterial co-occurrences to soil ecosystem function

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Fungi and bacteria are major players in soil biogeochemical cycles, however, most studies linking soil processes to microbial function ignore the potential role of interactions between these groups. A small number of studies have used correlation network analyses to investigate fungal–bacterial co-occurrences in soil, and revealed differences, as well as overlaps, in the ecosystem roles of these groups. These results contradict the view that fungi and bacteria are two distinct functional groups which can be studied in isolation. A more comprehensive understanding of the interplay between soil properties, biogeochemical cycles and the interactions between fungi and bacteria will be an important step towards improving the prediction and management of soil ecosystem services.

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Introduction

Soils are home to some of the most diverse bacterial communities on earth [1,2], and fungi are often thought to dominate soil microbial biomass, especially under low disturbance, nutrient limiting conditions [3]. These two microbial groups are responsible for many of the biogeochemical processes that drive terrestrial ecological productivity [4], and considerable research effort is dedicated to characterisation of the diversity and roles of soil bacterial and fungal communities. Ultimately it is expected that a comprehensive picture of soil microbial diversity across different ecosystems and environments will facilitate the identification of key microbial drivers of soil ecosystem services. This in turn will improve the prediction of soil responses to disturbances and changes in

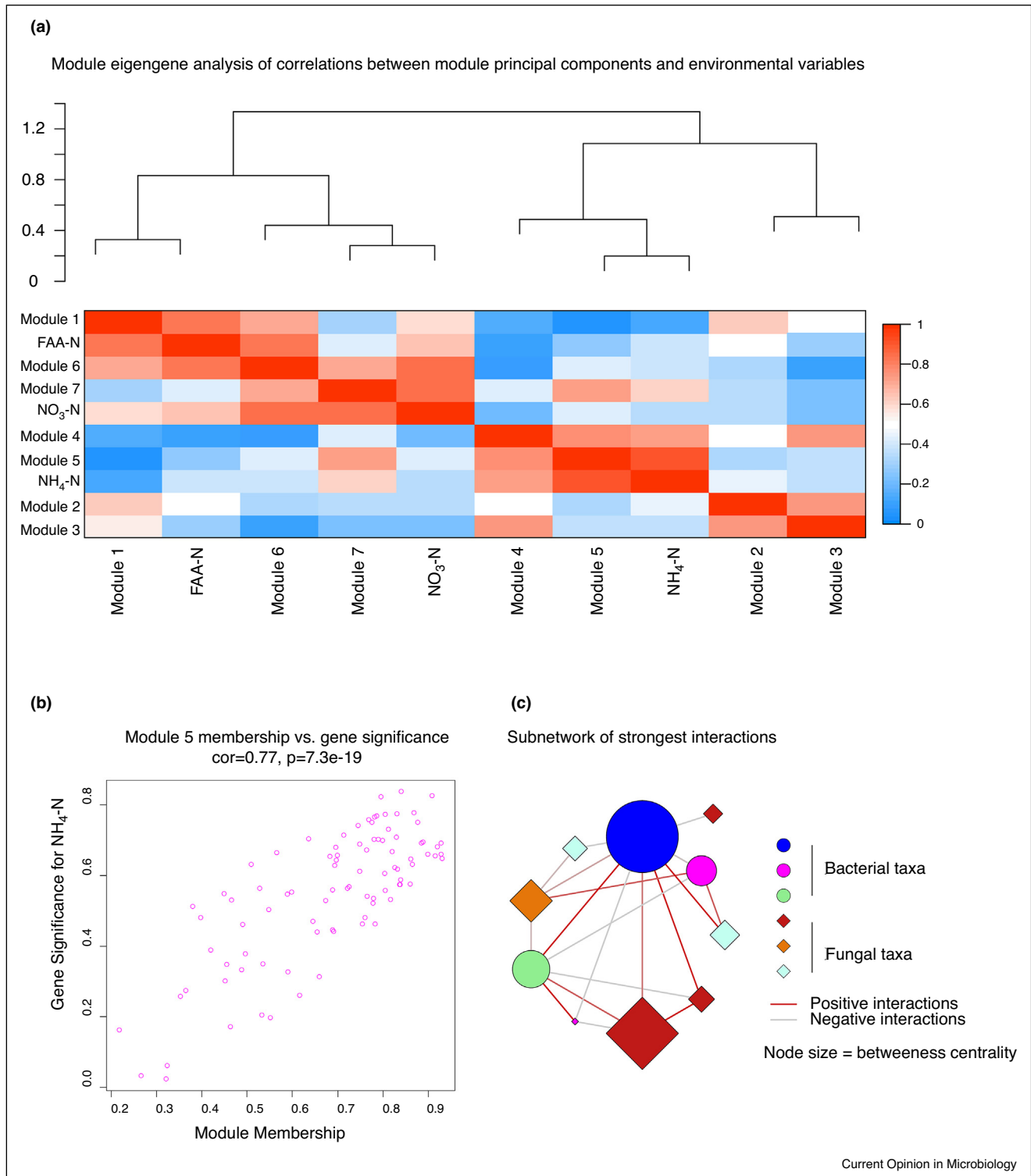
management practices (e.g. agricultural intensification, afforestation and reforestation programs, land restoration, among others). For example, the attribution of distinct ecological roles to fungi or bacteria is central to current understanding of soil ecosystem function, particularly organic matter decomposition and nutrient turnover. Soil fungi and bacteria are thought to have distinct substrate preferences and these metabolic differences (including differences in internal nutrient requirement and composition) have led to specific predictions regarding their ecological function in soil, with little consideration for their potential interactions [5,6**]. However, as reviewed by Strickland [7], most of the assumed distinctions between fungal and bacterial roles in soil have little empirical support.

Fungi and bacteria share the same habitats and are therefore almost certain to frequently interact in soil [8–10]. For example, changes in the gene expression and metabolism of both *Bacillus* and *Aspergillus* as interacting partners has been demonstrated [11]. Focusing on soil processes, the argument we put forward here is that interactions between co-occurring soil bacteria and fungi play a considerable part in determining their respective roles, and that explicit investigation of these interactions will lead to a more complete understanding of soil microbial ecology and other ecosystem interactions.

Fungal–bacterial co-occurrence in soil

Just as in plant and animal communities, a range of complex positive (commensalism, mutualism) and negative (amensalism, parasitism or predation and competition) interactions occur in the microbial world. As a consequence, microbial taxa that associate in nature are likely to show specific positive or negative co-occurrence patterns [12]. Methods that detect and characterise microbial co-occurrences can therefore not only reveal potential interacting microbial networks but also offer insights into modes of interaction. A range of correlation network analysis methods have been used to determine co-occurrence patterns in microbial communities, and each method can lead to substantially different results, particularly regarding their precision and sensitivity to detect interactions [13**]. Thus, an important consideration in choosing a network analysis method is whether the main interest lies in defining broad groups of non-randomly co-occurring microbes that may share a specific environmental niche or ecological function (Figure 1a,b), or whether the objective is to identify robust associations between a small number of microbial taxa, which may indicate physiological or ecological interdependence to

Figure 1



A suggested approach to help determining niche partitioning amongst bacteria and fungi OTUs would be to first characterise groups of co-occurring OTUs into modules using a method such as RMT [19]. Module eigengene analysis **(a)** allows the determination of the relationships between modules and between modules and environmental variables. Subsequently the importance of individual OTUs within a module and their correlation to specific environmental variables can be assessed **(b)**. Strong correlations can be used for further characterisation of identity of interacting partners and their potential ecological roles. A different and complementary approach would involve using methods such as LSA [17] or

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