Soil Biology and Biochemistry 177 (2023) 108913

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Responses of soil rare and abundant microorganisms to recurring biotic disturbances

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ARTICLE INFO

Keywords:
Rare taxa
Abundant taxa
Biotic disturbance
Temporal change
Inoculation
Soil microbiome

ABSTRACT

Periodic inoculations of soil-beneficial microbes can increase their populations, but they also act as recurring biotic disturbances on the native microbial community. Soil rare and abundant microorganisms disproportionally shape the community diversity and stability. Uncovering their dynamic responses to recurring biotic disturbances and the underlying driving factors helps improve our understanding of the inoculation effects. Here, we imposed temporally recurring biotic disturbances by inoculating soils with phosphate-solubilizing bacteria, nitrogen-fixing bacteria, and the combination of both, with the overall aim of studying the successive responses of bacterial and fungal subcommunities along a rarity index. Our results showed that, in both bacterial and fungal communities, the relatively rare taxa exhibited higher diversity than the abundant taxa, and the relative abundance of rare taxa increased with recurring disturbances. However, the responses of rare and abundant taxa to inoculations were different between bacteria and fungi and were related to time and inoculation frequency. The rarer bacteria and the more abundant fungi explained most of the effects of inoculations on the resident microbial community. About 20 percent of the microbes changed their rarity categories over time, and most of the changes and interactions occurred within the rarer taxa during the first 45 days. Modeling analyses and co-occurrence networks indicated that microbial interactions, soil biochemical factors, and inoculation time drove the shifts of subcommunities. In summary, relatively rare bacteria and relatively abundant fungi play major roles in understanding the impacts of recurring biotic disturbances, while the conditionality of microbial rarity is dependent on both biotic and abiotic factors.

1. Introduction

Soil microbial communities play a crucial role in maintaining ecosystem function and stability (Thiele-Bruhn et al., 2012; Zhong et al., 2020). Eco-evolutionary theory suggests that in most habitats, both bacterial and fungal communities comprise a few abundant species that dominate the community, and a large number of rare species coexist at very low abundance, often referred to as the "rare biosphere" (Pedrós-Alió, 2012; Jia et al., 2018). The abundant species represent a small fraction of microbial diversity (Pedrós-Alió, 2012), but rare species represent a large reservoir of taxonomic and functional diversity related to ecological functioning and stability (Reid and Buckley, 2011; Jiao et al., 2017). Despite the significance of rare species, many microbial studies have focused on the abundant species and routinely screened out rare species, thereby overlooking the potential role of rare species and their differences from abundant species (Jousset et al.,

Abbreviations: PSB, phosphate-solubilizing bacteria; NFB, nitrogen-fixing bacteria; RT, rare taxa; CRT, conditionally rare taxa; AT, abundant taxa; CAT, conditionally abundant taxa; MT, moderate taxa; CRAT, conditionally rare or abundant taxa; OT, other taxa except RT and CRT.

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https://doi.org/10.1016/j.soilbio.2022.108913
Received 23 June 2022; Received in revised form 15 November 2022; Accepted 9 December 2022
Available online 14 December 2022

2017).

In addition to the different roles of abundant and rare species in characterizing community structure and diversity (Dai et al., 2016; Nyirabuhoro et al., 2021), there is an increasing pool of literature indicating that rare and abundant species are unequal in response to environmental changes and disturbances (Jiao and Lu, 2020; Liang et al., 2020; Rocca et al., 2020). However, the underlying mechanisms may differ between bacteria and fungi. For instance, previous studies found that stochastic patterns such as ecological drift (i.e. random births and deaths in a population) were particularly pronounced for the assembly of rare plankton communities (Xue et al., 2018) and rare bacterial communities (Jiao et al., 2017; Liang et al., 2020), compared to the abundant ones, but an inverse pattern was found for fungal community (Jiao and Lu, 2020; Zheng et al., 2021). Therefore, an integrated study of the rare and abundant bacteria and fungi is needed to compare their differences and clarify how they respond to the same disturbance.

In response to a particular disturbance, some microbes may adapt to subsequent habitat changes or take over the functions of others that are unable to adapt to that change (Campbell et al., 2011; Kurm et al., 2019). To further elucidate the underlying mechanisms, many studies have examined the effects of abiotic disturbances on rare and abundant subcommunities, including a range of anthropogenic disturbances (i.e. organic input, glucose input, N input, heat shock, etc.) (Kurm et al., 2019) or natural climate change (Evans and Wallenstein, 2014; Zhao et al., 2017; Jiao et al., 2019; Liang et al., 2020). In contrast, despite the fact that the biotic disturbances are of common occurrence, such as the naturally occurring invasions of pathogens or deliberate introduction of beneficial microbes (van Elsas et al., 2012; Mallon et al., 2015), relatively little knowledge is available about the impact of biotic disturbances on the assembly of rare and abundant subcommunities.

Introducing beneficial microbes such as phosphate-solubilizing bacteria (PSB) and nitrogen-fixing bacteria (NFB) is a promising sustainable strategy for soil amendment and crop regulation (Wang et al., 2021b), but continuous inoculations can also act as a recurring biotic disturbance to the soil-resident microbial community through resource competition, synergism, or antagonism effects (Mawarda et al., 2020). In turn, the characteristics of the resident microbial community also determine the magnitude of the impact of intruders (van Elsas et al., 2012; da Costa et al., 2020). However, the causal-response relationship is generally temporally dynamic, and thus it is not conclusive to assess microbial response to disturbance at a single sampling time point (Nannipieri et al., 2019; Meisner et al., 2022). When studying rare microorganisms, the definition and conditionality of rare and abundant species may change over time, namely a species may be rare at a given time but may become more dominant as time evolves, and vice versa. For instance, rare species are expected to increase their abundance under different environmental conditions to maintain ecosystem function (Yachi and Loreau, 1999), while the temporal stability of abundant species is greater than that of rare species (Xue et al., 2018). Therefore, studying the community at multiple time points is extremely important to uncover the assembly processes of the rare and abundant subcommunities (Jia et al., 2018).

To quantify the ecological processes and potential factors driving the assembly of rare and abundant microbial communities, Stegen et al. (2013) proposed a quantitative framework that is widely used in recent microbial studies (Jiao and Lu, 2020; Santillan et al., 2020; Zheng et al., 2021). However, these studies focused on the effects of abiotic factors and defined the assembly processes as either stochastic or deterministic. So far, it is largely unknown how rare and abundant species change their abundance or temporal stability upon biotic disturbances. The underlying ecological theory and driving factors remain to be explored to explain (i) why some microbes turn to be more abundant and how they dynamically interact with other microbes in response to recurring biotic disturbances, and (ii) why the majority of microbes in soil are highly diverse but remain in low abundance.

In the present study, we examined the temporal responses of rare and abundant taxa in bacterial and fungal communities to recurring inoculations with three microbial consortia: PSB, NFB, and a combination with both PSB and NFB. We hypothesize that the rare microorganisms, at least some of them, would be more abundant under biotic disturbances, and the shifts of rare and abundant taxa would be strongly dependent on time and inoculation frequency during the succession of soil microbial community. We also hypothesize that rare and abundant taxa contribute unequally to community heterogeneity and diversity, and the imbalance between them would vary in bacterial and fungal communities. To address these hypotheses, we monitored the dynamic changes of rare and abundant taxa and calculated their contributions to community dissimilarity and diversity. We also attempted to uncover the major abiotic and biotic factors driving the inter-subcommunities shifts. Crucially, we incorporated the trait-similarity hypothesis (Wong et al., 2021), in which species possess the similar ecological niches or traits (e.g. functional traits related to biophysiochemical processes) compete intensely and eventually lead to a phase where co-existing species exhibit different traits or niches, to explain the shift and stability of rare species during the succession.

2. Materials and methods

2.1. Preparation of bacterial inoculants

Four beneficial strains, including two PSB: *Bacillus megaterium* W17 and *Pseudomonas fluorescens* W12, and two NFB: *Azotobacter chroococcum* HKN-5 and *Azospirillum brasilense* CW903, were applied in pairs as PSB inoculant and NFB inoculant, respectively, or in combination (PSB + NFB) in this study (Table S1). These bacteria have been documented to improve soil nutrient status and have no antagonistic effects on mutual growth (Wang et al., 2021a, 2021b). The detailed information on the preparation of inoculants has already been described (Wang et al., 2021a). Briefly, each strain was grown in lysogeny broth medium at 28 °C for 24–26 h to an optical density (OD) of 0.9 at 600 nm, corresponding to log phase. The bacterial population was assayed using the plate count serial dilution method while experimenting on building a standard curve between optical density and bacterial quantities. The suspensions were adjusted to a final concentration of 1×10^8 colony forming units (CFU)·mL^{-1} for each strain. Then, inoculant consortia were made by adding equal volume of each strain to final 50 mL (Table S1).

2.2. Experimental design

A pot experiment was set up in a three-block pattern based on a randomized complete block designed with three inoculation treatments (PSB, NFB, PSBNFB) and one control-check treatment (CK). The soils for the pot experiment were collected from a degraded low-fertility land on which a native medicinal plant, *Cyclocarya paliurus*, was grown (Wang et al., 2022). The detailed information on the experimental design was previously described (Wang et al., 2021a). Briefly, there were 3 blocks and 80 pots were established in each block (4 treatments × 20 pots). This is to make sure there are enough pots for each sampling time. (Fig. 1a). Each pot (top diameter, 25 cm; bottom diameter, 20 cm; height, 30 cm) contained 5 kg soil as the growth medium.

Inoculations were carried out periodically four times at an interval of 45 days (April 4, May 19, July 6, and August 19, 2018), and each time with the same dose (5×10^9 cells per pot). Specifically, we dug a 5-cm deep circle around the rim for all pots (including CK) before each inoculation. Then, 50 mL of inoculum was injected into each circle, which was subsequently covered with soil. As a control, the same amount of sterilized water was added.

For each treatment, five bulk soil samples (0–10 cm, 10 g) were randomly collected from three inoculated pots and mixed evenly into one composite sample in each block, resulting in three replicate samples (3 blocks × 50 g) and a total of 12 samples (i.e. 4 treatments × 3 blocks)

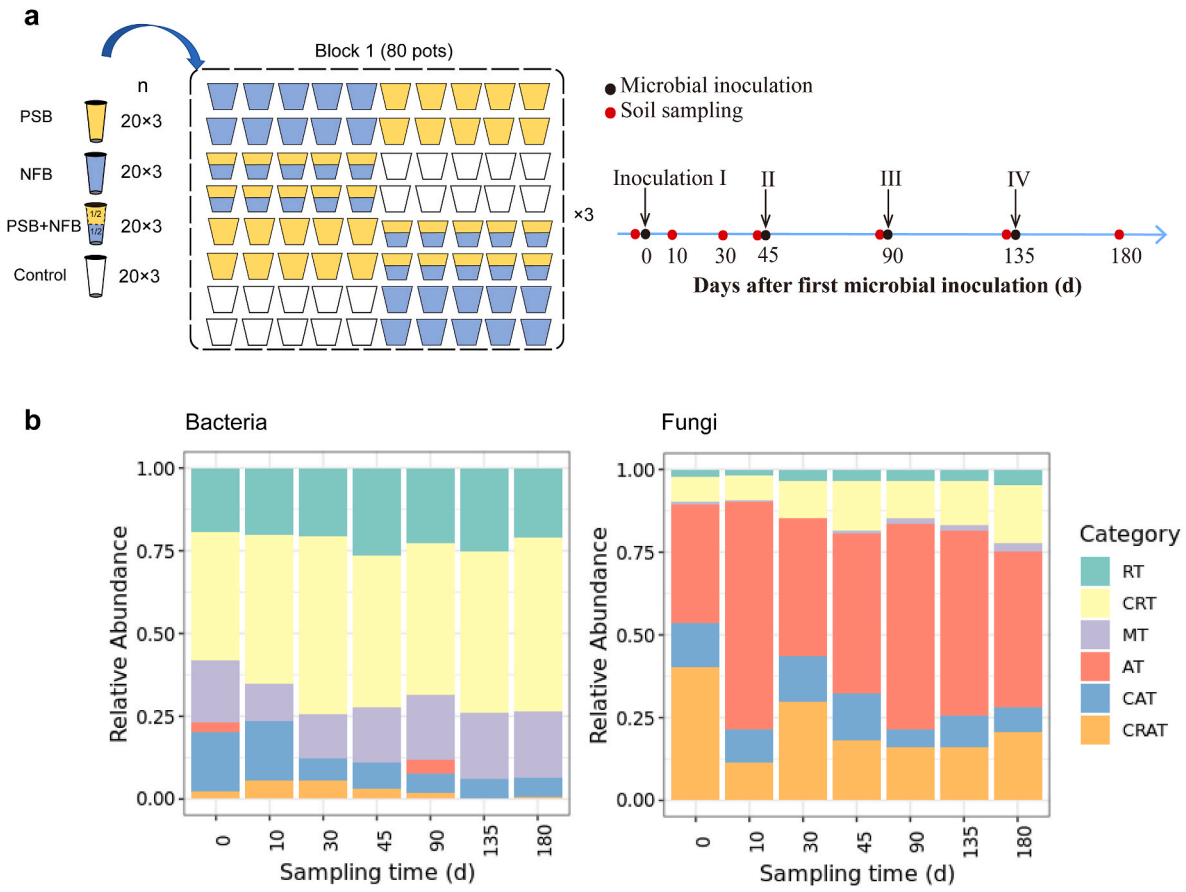

Fig. 1. Experimental design and microbial subcommunities identified in this study. Illustrations of treatments, inoculation frequency, and sampling time (**a**). Relative abundance of all categories in bacterial and fungal community across all sampling time points (**b**). PSB: phosphate-solubilizing bacteria. NFB: nitrogen-fixing bacteria. RT: rare taxa. AT: abundant taxa. CRT: conditionally rare taxa. CAT: conditionally abundant taxa. MT: moderate taxa. CRAT: conditionally rare or abundant taxa.

at each sampling time. The sampling procedure has already been described (Wang et al., 2019). Briefly, for each treatment, five vertical holes (5 × 10 g soil) were implemented with a sampling tube in each block to lessen the disturbance of sampling on microbes. Soil sampling procedures were performed on the day before the first inoculation (0d), 10 days (I-10), 30 days (I-30) and 45 days (I-45) after the first inoculation, and 45 days after the second (II-45), third (III-45), and fourth inoculation (IV-45) (Fig. 1a). All soil samples were stored at −20 °C prior to DNA extraction.

2.3. DNA extraction and Illumina MiSeq sequencing

Total soil DNA (0.5 g soil) was extracted using the NucleoSpin® Soil DNA Kit (Macherey-Nagel GmbH & Co.KG, Düren, Germany) according to the manufacturer's protocols. Final DNA concentration and purity were determined using a NanoDrop 2000 UV–Vis spectrophotometer (Thermo Scientific, Wilmington, USA), and DNA quality was checked by 1% agarose gel electrophoresis. The primer pair of 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′) was used to amplify the V4 hypervariable region of bacterial 16S rRNA gene. The primer pair of ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′) was used to amplify the internal transcribed spacer (ITS) region of fungal rRNA genes. PCR was performed in triplicate in a 20-μL mixture containing 2 μL of 10 × FastPfu buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase and 10 ng template DNA. PCR were carried out following procedure: initial denaturation at 95 °C for 5 min; 25 cycles of 95 °C for 30 s, 56 °C for 30 s, and 72 °C for 90 s; and a final extension at 72 °C for 7 min. The PCR products were extracted from a 2% agarose gel, purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified using QuantiFluor™-ST (Promega, USA) according to the manufacturer's protocol. The purified amplicons were pooled in equimolar ratios and paired-end sequenced on an Illumina MiSeq platform (Illumina, San Diego, California, USA) according to the standard protocols of Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). CRA007288

2.4. Sequence data processing

Raw DNA sequences were processed with the DADA2 (Divisive Amplicon Denoising Algorithm 2) pipeline (Callahan et al., 2016) using the "dada2" package (v.1.7) in R 4.0.1 (R Core Team 2019). DADA2 infers true biological sequences of reads (i.e. amplicon sequence variants [ASVs]) from Illumina sequence data and does not involve sequence clustering (Callahan et al., 2017). Briefly, primers and adapters were screened and removed using the "cutadapt" package (v.2.10). Raw sequences were first demultiplexed by comparing index reads with a key and then quality-filtered using the filterAndTrim function. Error rates were subsequently derived from a set of subsampled reads (i.e. 1 million random reads). Sequences were dereplicated, and unique sequence pairs were denoised using the "dada" function. Finally, paired-end sequences were merged, and chimeras were removed. After filtering and trimming the sequence data, a total of 13735 denoised ASVs for bacteria and 4393 ASVs for fungi were recovered from the 76 soil samples, including 4 treatments in 6 sampling time points (72 samples) and 1 control treatment from the day before inoculation (4 samples). Taxonomy group

information was then assigned using the SILVA databases (v.138) (Quast et al., 2013) for bacteria and archaea and UNITE databases (Release 8.2 http://unite.ut.ee/index.php) for fungi.

2.5. Definition of rare and abundant subcommunities

To distinguish the role of rare and abundant taxa in community assembly and succession, we classified the bacterial and fungal taxa according to the method reported by Dai et al. (2016). As shown in Fig. S1, we set relative abundance thresholds at ≤0.1% for rare ASVs and ≥1% for abundant ASVs. Considering the relative abundance of the same ASV may vary with samples across sampling time, we further classified all ASVs into six categories at each sampling time point: (i) rare taxa (RT), ASVs with abundance ≤0.1% in all samples; (ii) abundant taxa (AT), ASVs with abundance ≥1% in all samples; (iii) moderate taxa (MT), ASVs with abundance between 0.1 and 1% in all samples; (iv) conditionally rare taxa (CRT), taxa with abundance of less than 1% in all samples and ≤0.1% in some samples; (v) conditionally abundant taxa (CAT), taxa with abundance greater than 0.1% in all samples and ≥1% in some samples but never rare (≤0.1%); and (vi) conditionally rare or abundant taxa (CRAT), taxa with abundance varying from rare (≤0.1%) to abundant (≥1%).

2.6. Statistical analysis

2.6.1. Relative abundance and diversity of each subcommunity and total community

To examine the effects of microbial inoculants on the relative abundance of each subcommunity, we calculated the relative abundance of subcommunities in each treatment ($n = 3$) at each sampling time point, followed by a two-way analysis of variance test (ANOVA). To determine the temporal shift in subcommunity abundance, we calculated the relative abundance of subcommunities in samples at each sampling time point. Our previous study implied that periodic microbial inoculations had few significant effects on microbial alpha diversity (Wang et al., 2021a). Because of this realization and the fact that rare taxa encompass the most diverse microbes in community, here we focus mainly on the temporal variation of the alpha diversity in RT, CRT, OT (taxa other than RT and CRT), and total community.

The Shannon indices were computed and plotted by the plot_richness function in the "phyloseq" package (McMurdie and Holmes, 2013). Beta diversity was visualized by nonmetric multidimensional scaling analysis (NMDS) based on the Bray-Curtis distance calculated by the ordinate function in the "phyloseq" package. Analysis of similarities (ANOSIM) was performed to test the biotic disturbances and temporal effects on community composition with 9999 permutations.

2.6.2. Contribution of each subcommunity to the community dissimilarity between inoculated and non-inoculated soil

To distinguish the effects of different biotic disturbances on soil microbial subcommunities, we compared the dissimilarities (based on Bray-Curtis distances) of communities in soils inoculated with different inoculants, referring to the inoculant-inoculant comparisons (PSB vs NFB, PSB vs PSBNFB, and NFB vs PSBNFB). To assess the impacts of different inoculants on the resident community, we compared communities dissimilarities (based on Bray-Curtis distances) between inoculated and non-inoculated samples, referring to the inoculant-CK comparisons (PSB vs CK, NFB vs CK, and PSB + NFB vs CK). Furthermore, we quantified the contribution of each subcommunity by similarity percentage analysis (SIMPER) in vegan package and tested the significance by ANOSIM analysis.

2.6.3. Shift of subcommunity across time and the underlying abiotic factors

Firstly, to depict the dynamic shift patterns of different subcommunities over time, a Sankey plot was created using the SankeyDiagram function in the "flipPlots" package (https://github.com/Displayr/flipPlots) based on the counts of ASVs in RT, CRT, AT, MT, CAT, and CRAT subcommunities that shifted from one to another during the succession. Only the shifted ASVs were plotted on the Sankey diagram and their taxonomic information was presented in the last column.

Secondly, variation partitioning analysis (VPA) was used to assess the relative contribution of abiotic factors (i.e., soil pH, soil moisture content, and soil nutrient content) in shaping bacterial and fungal subcommunities (Peres-Neto et al., 2006). Bacterial and fungal abundances were CLR (centered log-ratio) transformed (Gloor et al., 2017), and the environmental variables were scaled prior to the VPA analysis. After that, to specifically reveal the impacts of temporal change (time), soil biochemical factors, and inoculant treatments on the shift of rare and abundant subcommunities, we calculated the numbers of each category (RT, MT, AT) for each sample and the abundance of each category for each sampling time point, respectively. Combined with soil data, we were then able to evaluate the coefficients of all factors for the abundance and counts of ASV in each category for both bacteria and fungi using the Gaussian model (Reynolds, 2009).

2.6.4. Random forest-based models and SparCC-based co-occurrence networks for revealing the keystone taxa and interactions between subcommunities

Random forest-based models were built in the R package "randomForest" to predict abundance profiles of RT, CRT, and OT in both bacterial and fungal community (Lima-Mendez et al., 2015). Furthermore, the key microbial predictors for the shift of each category (RT, CRT, and OT) across time were identified by a classification random forest analysis (over 100 iterations) (Zhang et al., 2018). These microbial predictors were ranked in the order of feature importance and visualized by percentage increases in the MSE (mean squared error); higher MSE% values indicate more important features (Jiao et al., 2018). Then, the number of microbial predictors were identified using 10-fold cross-validation implemented with the rfcv() function with five repeats (Fig. S2).

To mitigate the compositional bias of microbial community data, we generated the networks of bacterial and fungal subcommunities (RT, CRT, MT, CAT, AT, CRAT) using SparCC (Friedman and Alm, 2012) analysis, only strong and statistically significant correlations ($|r| > 0.6$, $p < 0.05$) were remained and visualized using Gephi 0.9.2 software (Bastian et al., 2009). The modularity index, degree, betweenness, and closeness were calculated by Gephi to characterize the network topology (Nyirabuhoro et al., 2021). After that, the networks were colored by module, microbial category, and taxonomy information, respectively.

3. Results

3.1. Identification of numbers and abundance of each subcommunity for bacteria, archaea, and fungi

Most ASVs in the bacterial community were identified as RT and CRT for each sampling time point (Table S2), the relative abundance of RT ranged from 19.5% (at 0d) to 26.5% (at 45d), and CRT ranged from 38.6% (at 0d) to 54.0% (at 30d) (Fig. 1b). In contrast, although a large number of ASVs in fungal community were identified as RT (~93%), the relative abundance of RT only accounted for 1.8% (at 10d) – 4.6% (at 180d). A few ASVs were identified as AT in fungal community, but the relative abundance of AT accounted for 35.9% (at 0d) – 69.0% (at 10d).

In response to periodic inoculations, the relative abundance of all subcommunities changed over time, but no remarkable effect of inoculations was observed. As shown in Fig. S3, the succession of subcommunities in each treatment showed a similar pattern in which both RT and CRT of bacterial and fungal communities increased their relative abundance. Statistical results showed that the inoculation treatments had no significant effect on the succession of RT, MT, and AT, but significantly affected the relative abundance of CRT (at 10d) and CAT (at 10d and 180d) in treatment NFB, and CRAT (at 135d) in all treatments

(Table S3).

3.2. Temporal variation of bacterial and fungal diversity in subcommunities and total community

To study the temporal variation in microbial diversity, we selected RT and CRT as the subject subcommunities, OT (other taxa including AT, MT, CAT, and CRAT) as the compared subcommunity, and the total community as the reference group.

As shown in Fig. 2a, bacterial and fungal RT and CRT presented higher alpha diversity than OT. Moreover, the variations of RT, CRT and OT were associated with time and inoculation frequency. For instance, in bacterial subcommunities, a significant difference was found between 10d and 30d in CRT and OT, but no significant difference was found in RT during this period, indicating the CRT and OT were more sensitive to the first inoculation. After 30d, no significant temporal variations were found in OT, but significant differences were found in RT, suggesting that the subsequent inoculations caused diversity changes in RT but were not evident in OT. In fungal subcommunities, only RT and OT showed similar temporal variations compared to the reference group and showed significant differences between 45d and 90d, while CRT showed no significant differences.

In terms of beta diversity (Fig. 2b), all bacterial subcommunities as well as the total community changed significantly from 0d to 90d (II_45d) (ANOSIM test $P < 0.05$). Thereafter, only RT and CRT subcommunities differentiated beta diversity between 90d and 180d (IV_45d). In contrast, in fungal community, only OT and total community differentiated the beta diversity between 10d and 0d, and between 90d and 180d (ANOSIM test $P < 0.05$).

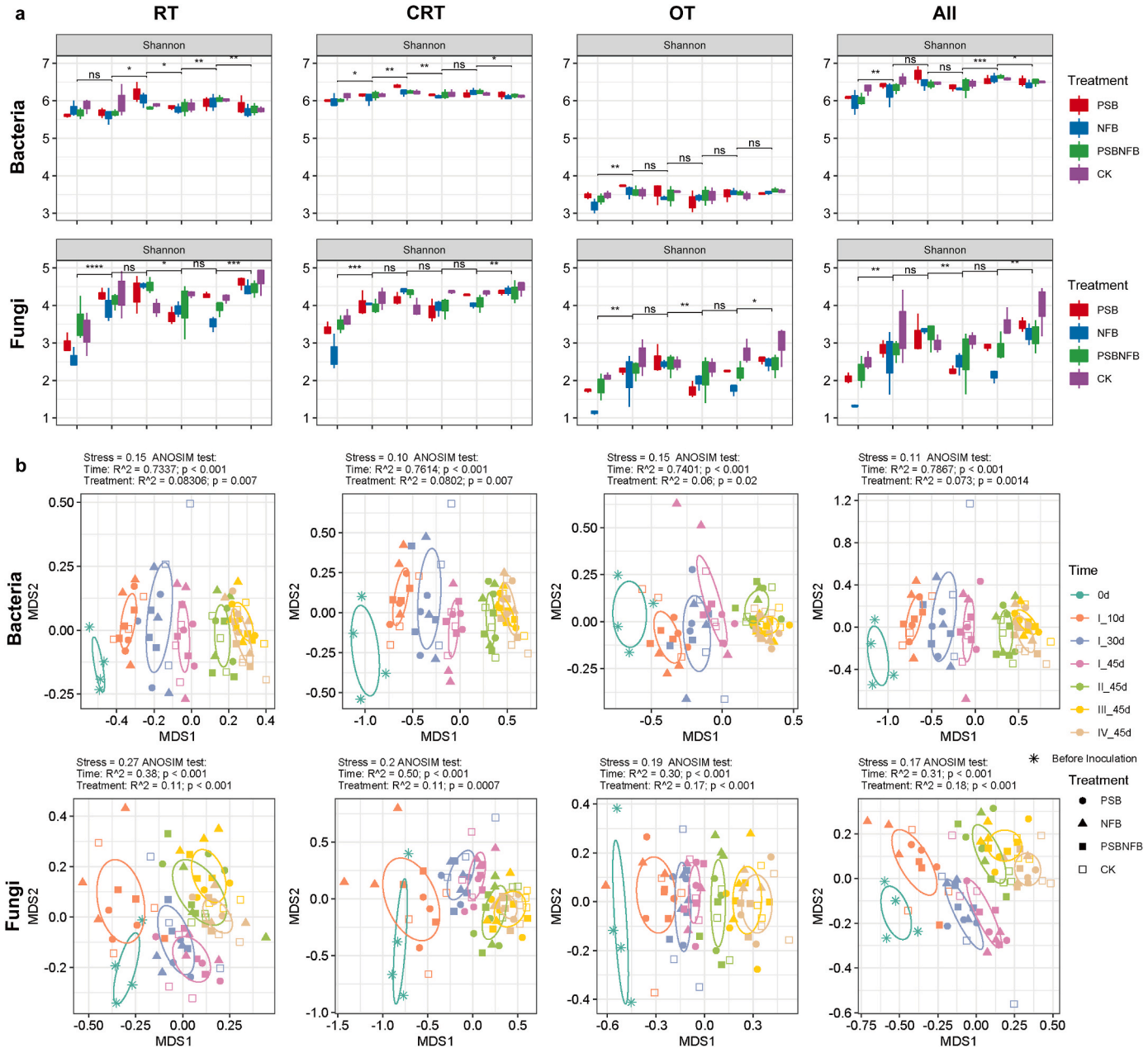

Fig. 2. Variations of microbial diversity across time and treatments in different subcommunities. Alpha diversity (**a**: based on Shannon index) and beta diversity (**b**: based on Bray-Curtis distance) of bacterial and fungal subcommunities. RT: rare taxa. CRT: conditionally rare taxa. OT: other taxa except RT and CRT. All: total community.

3.3. The impacts of inoculants as revealed by community dissimilarity within inoculant-control and inoculant-inoculant comparisons

Within the inoculant-control comparisons (PSB vs CK, NFB vs CK, and PSBNFB vs CK), the bacterial and fungal communities' Bray-Curtis dissimilarities exhibited a temporally nonlinear pattern (Fig. 3a, d): it reached the maximum at 30d and then decreased until 45d (bacteria) to 90d (fungi). Similarly, the Bray-Curtis dissimilarities within the inoculant-inoculant comparisons (PSB vs NFB, PSB vs PSB + NFB, and NFB vs PSB + NFB) also peaked at 30-45d (Fig. 3b, e), indicating the effects of inoculations on soil community were more pronounced in the initial stage of inoculation. However, after the third and fourth inoculations, the inoculated soil community, particularly the fungal community, clearly differentiated from the non-inoculated community at 135d and 180d (ANOSIM test: $P < 0.05$), reflecting the continuous impacts of recurring disturbances.

Besides the influences of temporal changes and inoculations, subcommunities played different roles in explaining the dissimilarities in bacterial and fungal communities (Fig. 3c, f). For example, bacterial RT and CRT explained more than 75% dissimilarities, and their proportions gradually increased after 10d. In contrast, abundant taxa (AT, CAT, and CRAT) in fungal community explained more than 75% dissimilarities at 10d, but their proportions gradually decreased thereafter. The relationship between the abundances of subcommunities and their contributions to the dissimilarities showed that, in each subcommunity, higher abundance resulted in a greater contribution to the dissimilarities between inoculation treatments and control (Figs. S4 and S5).

3.4. Shift between subcommunities and the co-occurrence networks based on SparCC correlations

Sankey plots (Fig. 4) showed how rare and abundant subcommunities shifted over time. Overall, approximately 18.8% (2579/13735) of bacterial ASVs and 20.8% (913/4393) of fungal ASVs shifted their categories over time. Most shifts in both bacterial and fungal subcommunities were observed during the first 45 days (from 0d to 45d), and occurred mainly between RT and CRT. After that, the number of RT and CRT stabilized, although the shifts between them remained a similar proportion as compared to the first 45 days.

Since most dissimilarities in inoculant-inoculant comparisons changed similarly over time, bacterial and fungal community networks were analyzed over time to further discern the dynamic correlations between subcommunities and the topological features of microbial co-occurrence patterns. Based on SparCC correlation analysis, about 1800–2600 nodes and 6000–20000 edges of bacteria, as well as 250–1100 nodes and 360–3700 edges of fungi were shown in the co-occurrence networks (Fig. 5, Table S4). In accordance with the shifts of bacterial and fungal communities (Fig. S6), the modularity analysis and the source of co-occurrence between categories showed that: (i) more modularity classes, nodes and edges, particularly for the fungal communities, were found at 30d and 45d compared to other time points; (ii) interactions occurred mainly between RT and CRT (yellow edges) in bacterial community and pairwise comparison among RT-CRT-CRAT in fungal community; (iii) the fungal community was less sensitive to subsequent inoculations at 90d and 135d compared to 30d and 45d, indicating a reduction in network complexity; (iv) the bacterial

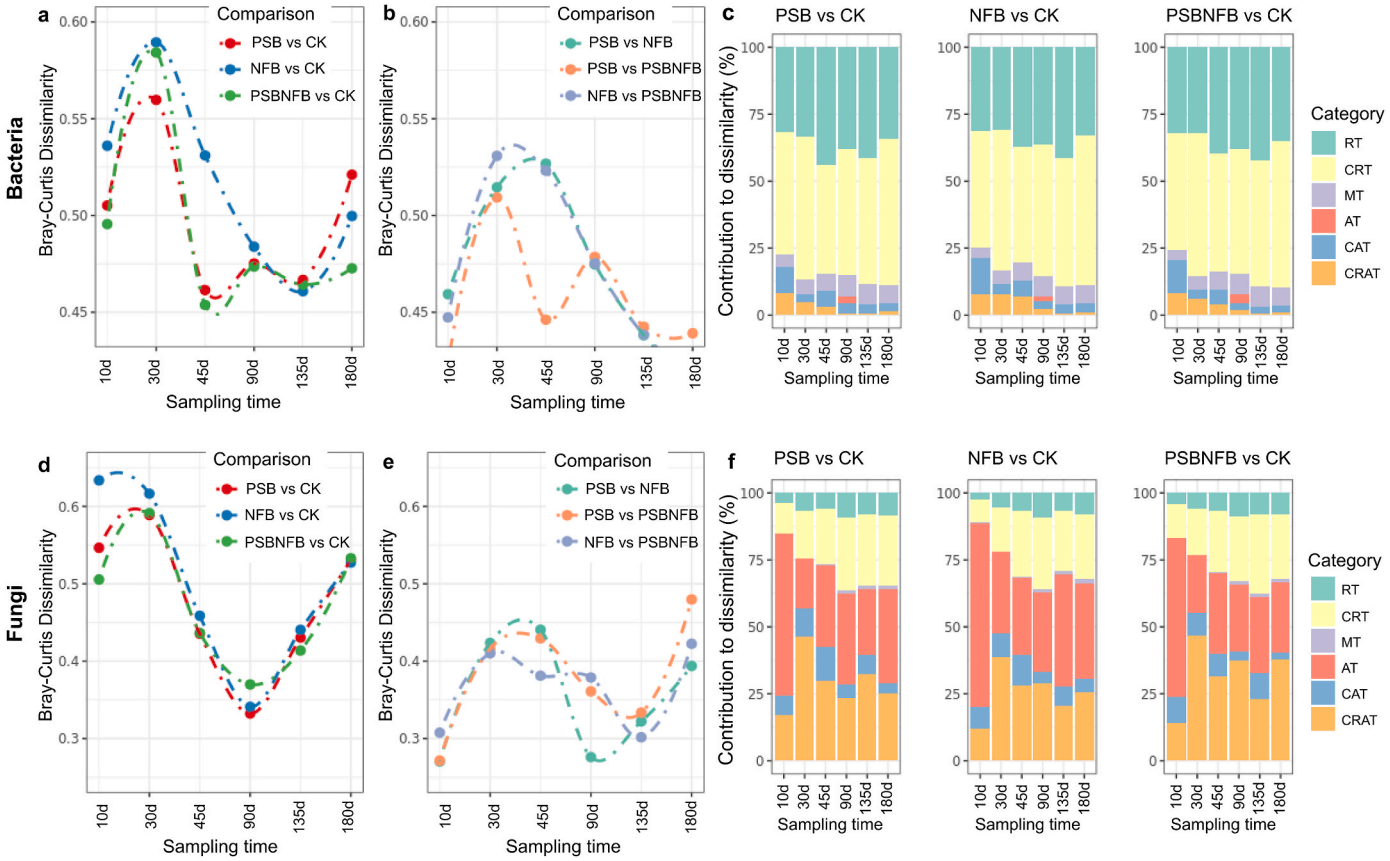

Fig. 3. Effects of different disturbances on the soil-resident community as revealed by community dissimilarity (based on Bray-Curtis distance). Community dissimilarity within the inoculant-control comparisons (**a**, **d**) and inoculant-inoculant comparisons (**b**, **e**) in bacterial and fungal communities. The contribution of each subcommunity to the dissimilarities between inoculated and non-inoculated soil bacterial (**c**) and fungal communities (**f**). PSB: phosphate-solubilizing bacteria. NFB: nitrogen-fixing bacteria. CK: control check. RT: rare taxa. AT: abundant taxa. CRT: conditionally rare taxa. CAT: conditionally abundant taxa. MT: moderate taxa. CRAT: conditionally rare or abundant taxa.

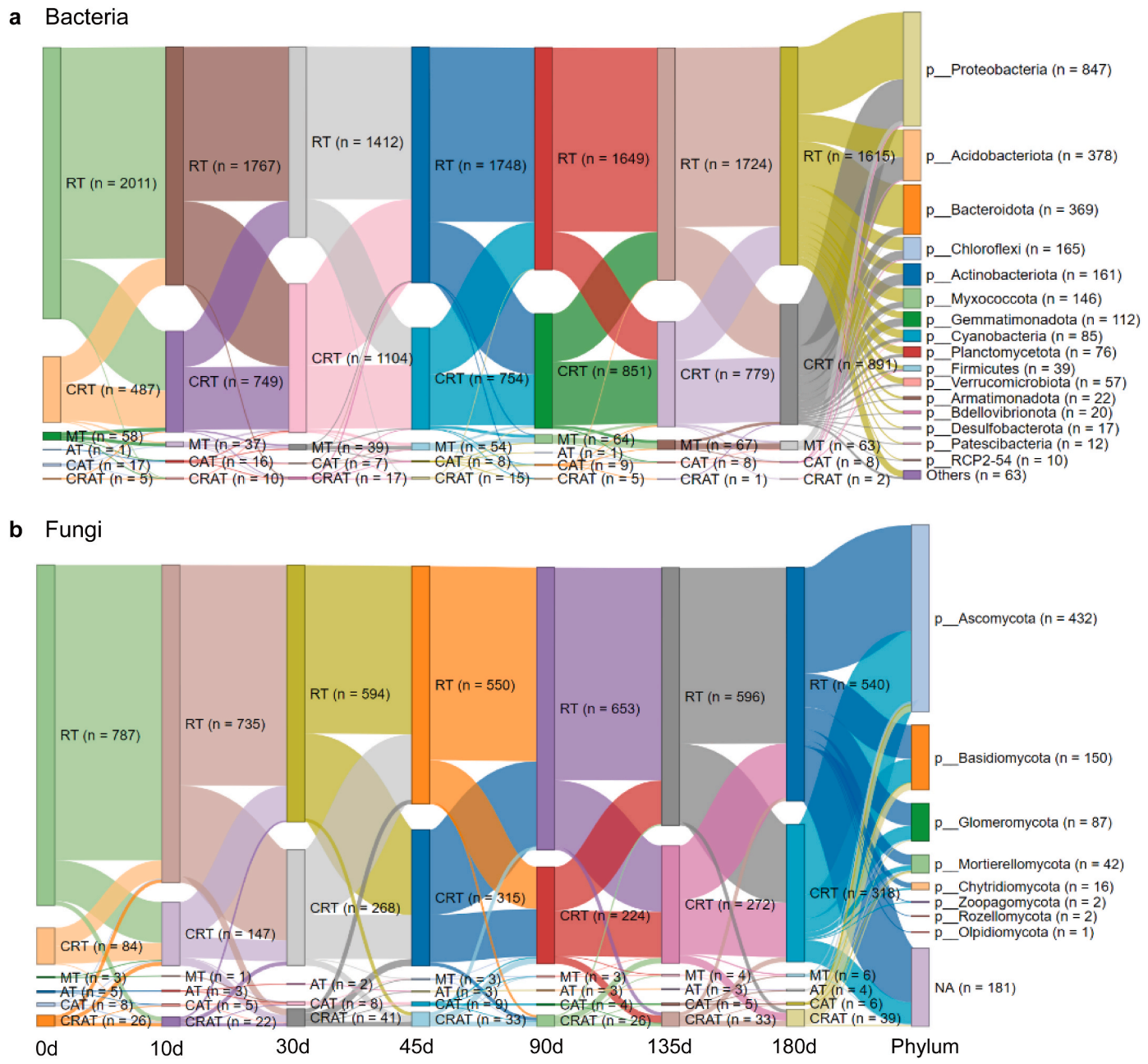

Fig. 4. Shift of soil microbial subcommunities across different sampling time point and taxonomic information at phylum level. RT: rare taxa. AT: abundant taxa. CRT: conditionally rare taxa. CAT: conditionally abundant taxa. MT: moderate taxa. CRAT: conditionally rare or abundant taxa.

community finally (135d and 180d) exhibited similar patterns with the original state at 10d, but fungal community increased the network complexity at 180d. Among these keystone taxa, *Protebacteria*, *Bacteroidota*, *Acidobacteriota*, and *Acitinobacteriota* were the most common phyla in bacterial community, *Ascomycota*, *Basidiomycota,* and *Glomeromycota* were the most common phyla in fungal community.

3.5. Revealing the abiotic and biotic factors for driving the community succession by modeling approaches

Variation portioning analysis revealed that the effects of soil nutrients were more pronounced than the effects of soil moisture content and pH in shaping subcommunity structure (Fig. S7). More specifically, Gaussian model analysis showed the integrated effects of treatments, inoculation time, and soil biochemical factors on the abundances and counts of bacterial and fungal categories (Fig. S8). The effect of inoculation time had similar effects on bacterial and fungal subcommunities: the counts and relative abundance of MT increased along with time, but the counts of RT and relative abundance of CAT decreased. The introduced inoculants had insignificant impacts on the bacterial subcommunities, except that treatment NFB had significantly positive effect on the relative abundance of AT in fungal community. In comparison with fungal community, bacterial subcommunities were more sensitive to changes in the soil environment. For instance, soil nitrate, C/N ratio, nitrogenase had significant effects on the bacterial community but no significant effects on fungal community.

Random forest model elucidated the keystone microbial predictors relating to the family-level shifts between different subcommunities. As shown in Fig. S9, the top 18 microbial predictors in the total bacterial community were also partially found in RT, CRT, OT, whereas exhibiting different order of importance. For instance, *Xanthomonadaceae* was identified as the most important predictor for both OT and the total

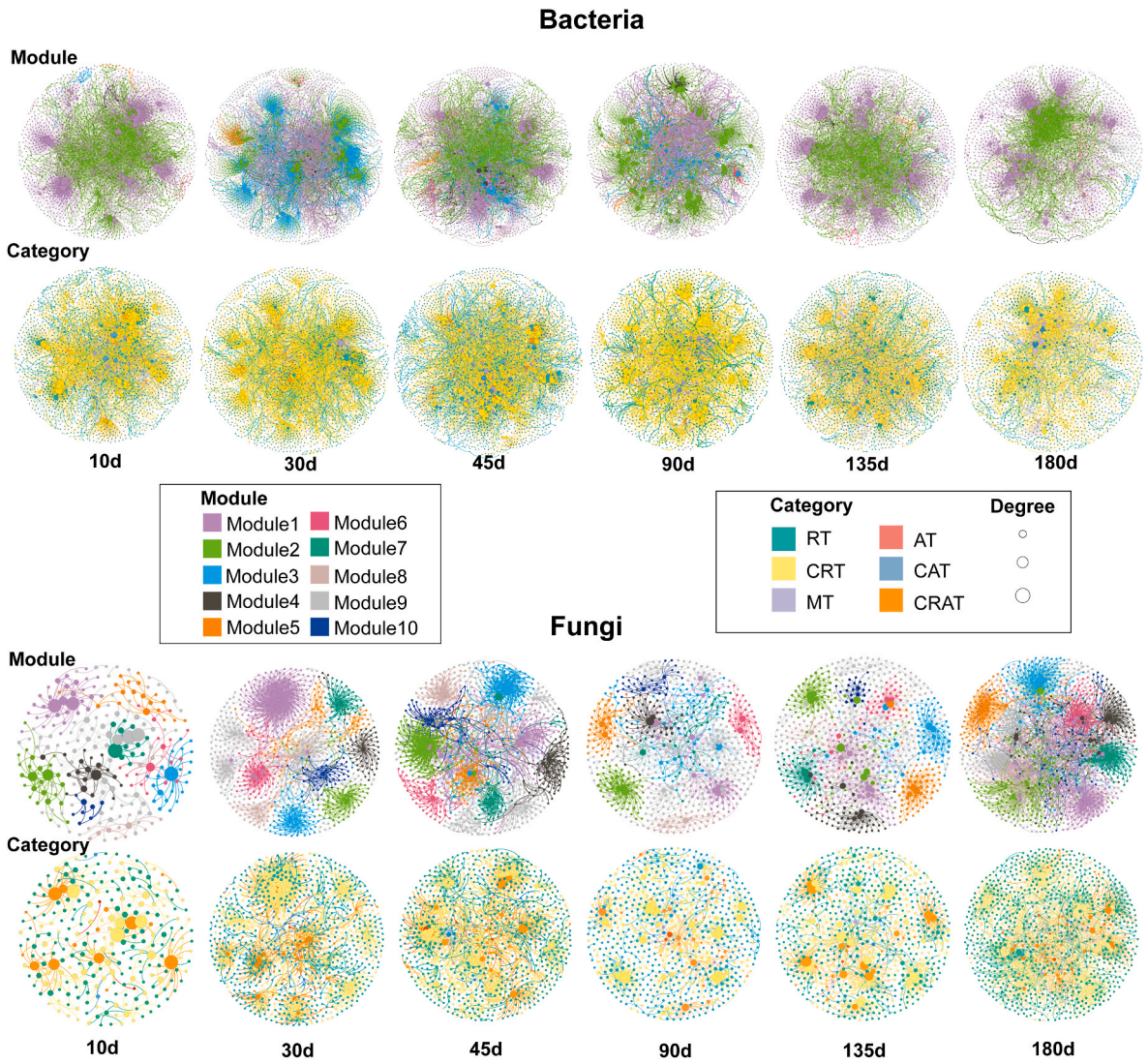

Fig. 5. Co-occurrence networks of bacterial and fungal ASVs (amplicon sequence variants) within all categories based on SparCC correlation analysis. The nodes were colored by the modularity class or taxa category. The edges were colored by the source of correlation between categories, thus representing different correlation patterns (e.g. CRT-RT, RT-CRAT, etc.). The node degree represents the number of direct co-occurrence for a particular node. Only strong and significant correlations ($|r^2| > 0.6$, $p < 0.05$) were presented.

bacterial community. The second predictor in the total bacterial community, *Cellvibrionaceae*, was identified as the first predictor in the RT subcommunity, but was not the predictor in OT and CRT. In contrast, *Methylophilaceae* played important role in both OT and CRT, but were not found in RT.

Relatively fewer predictors of fungal communities were identified in RT, CRT, and OT compared to bacterial subcommunities, although a slightly different pattern was observed. For instance, the first and third predictor in the total community, *Hypocreaceae* and *Didymellaceae*, were also identified as the first and second predictor in OT subcommunity. In addition, the second predictor in the total community, *Mycosphaerellaceae*, was the most important taxa in the CRT subcommunity. However, among the top 6 microbial predictors in RT, only *Glomeraceae* and *Mycosphaerellaceae* were found in the top 10 predictors in the total fungal community.

4. Discussion

A growing body of studies have highlighted the importance of rare species and the mismatch between rare and abundant taxa in shaping the total community (Pedrós-Alió, 2012; Dai et al., 2016; Jiao et al., 2017, 2019; Jia et al., 2018; Nyirabuhoro et al., 2021; Zheng et al., 2021). However, defining the rarity of species on the basis of abundance makes it difficult to predict the relationships between rare and non-rare species during community succession. In other words, species originally identified as rare taxa may become abundant species at a later time point and vice versa (Bossolani et al., 2021). So far, it remains unclear how rare and abundant taxa contribute unequally to the changes in microbial diversity and community dissimilarity during community succession in response to recurring biotic disturbances, and how their relationships change over time. In the present study, we attempted to quantify the imbalance between rare and abundant taxa during the succession of soil bacterial and fungal community upon repeated inoculations. Not only did the rare and abundant subcommunities respond differently, but also a contrast pattern was found between bacterial and fungal community. Furthermore, we identified the biotic and abiotic factors responsible for the subcommunities shifts and the dynamic interactions between them. Finally, we proposed a possible ecological theory to explain the rarity and the shifts between subcommunities.

4.1. Imbalanced responses between rare and abundant subcommunities and between bacteria and fungi upon reoccurring biotic disturbances

In the present study, higher alpha diversities were observed in the relatively rare subcommunities (RT and CRT) compared to other subcommunities (OT) in both bacterial and fungal communities. This is consistent with previous studies where rare species contributed the greatest alpha diversity (Lynch and Neufeld, 2015; Jiao et al., 2017). However, the role of OT should not be neglected. For example, our results of alpha diversity indicated that bacterial CRT and OT were more sensitive to the first inoculation than RT. Only OT in fungal community exhibited a similar temporal variation compared to the total community. This indicates that although the RT, CRT, and OT exhibite different subcommunity diversity, all of them are essential for predicting the total community diversity and temporal changes. This has been recognized by previous studies where RT and CRT represented a broad diversity and explained a large proportion of temporal shifts (Shade et al., 2014; Nyirabuhoro et al., 2021), but the other taxa may persist for a longer time (Kim et al., 2013), which could be one of the possible reasons why OT diversity showed similar temporal variations with the total community (Fig. 2a).

In addition to the temporal variations, the responses of RT, CRT, and OT were associated with inoculation frequency. In the early stage (0d–90d), beta diversity of all bacterial subcommunities changed significantly, but only OT in the fungal community differentiated beta diversity between 0d and 10d. After 90d, bacterial RT, CRT and fungal OT differentiated the beta diversity between 90d and 180d (Fig. 2b). This indicates that the changes of diversity in bacterial RT, CRT, and fungal OT are associated with the inoculation time and frequency. In addition, previous studies have indicated that the relatively abundant fungi and rare bacteria are more sensitive to environmental and temporal changes, such as altered precipitation (Zhao et al., 2017), seasons, altitude, and soil depth (Shigyo et al., 2019). The possible reasons could be that (i) fungal diversity is more sensitive to environmental change than bacterial diversity (Xu et al., 2021), or (ii) abundant fungi can adapt to broader environmental change than the rare taxa (Jiao and Lu, 2020), while the rare bacteria act as the main drivers of the basic functioning of the ecosystem after disturbances (Chen et al., 2020).

The impacts of inoculations, as revealed by community dissimilarities between inoculated and non-inoculated samples, changed over time, and subcommunities contributed disproportionally to the dissimilarities. Relatively rare taxa (RT and CRT) explained most of the dissimilarities in bacterial community and exhibited an increasing trend over time. More abundant taxa (AT, CAT, and CRAT) explained most dissimilarities in the fungal community, but their proportions gradually decreased. This is consistent with the above conclusions, that the abundant fungi and rare bacteria show higher susceptibility to inoculations. Understanding why the contribution proportion of subcommunities shift over time is central to understand their distinct roles in community succession (Shade et al., 2014; Shigyo et al., 2019; Liang et al., 2020). We speculated that one reason might be that their counts remain stable, but their abundances changed over time. Another reason could be that a group of microbes might shift from one category to the rare categories, or strengthen their interactions with rare taxa over time, explaining the increasing contribution of bacterial rare taxa and the decreasing contribution of fungal abundant taxa. Our results indicated that the counts of rare bacterial and fungal subcommunities (RT and CRT) remained constant over time (Table S2), but their relative abundance increased (Fig. S3), resulting in a changed contribution to the dissimilarities between inoculated and non-inoculated soil community (Figs. S4 and S5). This indicates that our first speculation is at least one of the possible reasons causing the changes in their contributions. However, to test the second speculation, we should move to the results regarding the shift and interactions between subcommunities during community succession and uncover the underlying factors.

4.2. Underlying ecological theories for succession and interactions of microbial subcommunities

To test the second speculation, it is important to answer the two questions we proposed in the introduction, namely (i) why some microbes changed their abundance due to biotic disturbances and how they interacted with each other during the process; (ii) why the majority of soil microbes contribute to the greatest diversity but remain in low abundance.

First, soil microbiomes are sensitive to environmental changes and anthropogenic activities (Shade et al., 2012; Lourenco et al., 2018). Under a certain disturbance or stress, the microbes are among the first responders and the key taxa tend to interact with each other more often than usual (Hunt and Ward, 2015; Herren and McMahon, 2018). Upon recurring biotic disturbances, here we observed that about 20 percent of the microbes shifted their categories over time, and most of the shifts were observed between RT and CRT during the first 45 days. This lies with our second speculation above that a group of microbes might shift from one category to rare categories, or increase their interactions with rare taxa over time. In response to recurring biotic disturbances, most responsive taxa belong to the rare taxa, partially following the previous studies (Dong et al., 2021; Xiong et al., 2021). Our network analysis further confirmed that microbial interactions were stronger at 30 and 45 days after the first inoculation, and most interactions happened among rare taxa in both bacterial community and fungal community. After that, relatively less interactions were observed. This indicates that the microbial community is less sensitive to subsequent inoculations in comparison with the initial inoculation, and eventually remain stable.

To further identify the keystone taxa, our random forest model found that the families *Cellvibrionaceae* of RT, *Methylophilaceae* of CRT, and *Xanthomonadaceae* of OT, were all important in predicting the change in the overall bacterial community over time. However, the fungal RT subcommunity was poorly able to predict the total community succession and thus showed a different pattern from bacteria. This also explained why fungal RT explained fewer differences between inoculated and non-inoculated soil microbial community. In addition to these biotic interactions and indicators, the 'abiotic selection' is expected to play a crucial role in shaping microbes that exist in a stressed or disturbed environment at low abundance (Rothschild and Mancinelli, 2001; Jia et al., 2018). For instance, in this study, soil inorganic N assisted the increased abundance of AT and CAT, but hindered the abundance of RT, CRT in bacteria. This indicates that abiotic factors together with biotic factors might jointly influence the assembly of subcommunities. The conditionality of rare and abundant taxa is highly context-dependent and correlated with both microbial interactions and soil nutrient factors (Shade et al., 2014; Lynch and Neufeld, 2015; Dong et al., 2021; Xiong et al., 2021).

Second, rare taxa serve as a large reservoir of genetic and functional diversity. Although RT and CRT interacted intimately in the present study, most of the rare microbes were highly diverse and present in low abundance. To explain the low-abundance trait and the changes of rare taxa, we propose to use the trait-similarity hypothesis (MacArthur and Levins, 1967; Wong et al., 2021), which describes a scenario that species share similar traits or niches may compete intense but eventually the co-existing species exhibit different traits or niches. In this study, we speculate that the rare microbes may compete intensely at first, but as competition evolves with time, they can change their traits or niches to survive or be uncompetitive at the cost of decreased abundance (Jousset et al., 2017). However, when they are exposed to the introduction of new microbes and the change of soil nutrient environment, the rare microbes, at least part of them, may benefit from these changes and lead to the changes of their counts or relative abundance. As indicated in this study, we found that 80% of rare species remained low abundance ($<0.1\%$), while the others shifted their abundance to be conditionally rare or abundant. Conversely, a portion of non-rare microbes can also shift to be rare, explaining the bidirectional shifts in this study (Fig. 4).

However, the challenge of quantifying the microbial niches and traits in this study makes it difficult to test this ecological theory. For the future studies, we advocate a combined investigation that includes not only the abundance and taxonomic information but also the microbial traits (e.g. functional genes, body size, metabolites, etc.).

In summary, in terms of microbial diversity change, all subcommunities were essential for predicting the alpha diversity. Inoculation frequency was associated with changes in beta diversity in bacterial RT, CRT, and fungal OT. Regarding the effects of inoculations, rare bacteria and abundant fungi contributed to the most dissimilarities between inoculation and non-inoculation, while their contributions increased and decreased respectively over time. To integrate all the information, it is necessary to illustrate the conditionality of microbial rarity and how the shifts between subcommunities relate to the biological consequences (Graphical Abstract). Our results showed that the shifts between RT and CRT subcommunities accounted for the majority of the shifts in the whole community and presented the shifts as changes in both counts and abundance, with rarity being explained by trait-similarity hypothesis. Both soil environmental factors and biotic factors affected the ASV counts and abundance in RT and CRT, as shown by modeling approaches and network analysis. Furthermore, the microbial networks reflected that, although abundant fungi explained most dissimilarities, most interactions occurred among relatively rare taxa in both bacterial and fungal communities.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The raw sequence data has been deposited to the public database Genome Sequence Archive with accession number CRA007288 (fungi) and CRA008919 (bacteria).

Acknowledgements

We acknowledge Prof. George A. Kowalchuk from Utrecht University for his comments on this experiment. We thank Ziheng Xu and Ziyun Chen from Nanjing Forestry University for lab assistances. This work was supported by the National Natural Science Foundation of China (Grant No. 32071750) and the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD). Zhikang Wang was supported by China Scholarship Council (202008320463) and Natural Science Foundation of Zhejiang Province, China (LQ23C030005). This is the publication number 7499 of the Netherlands Institute of Ecology (NIOO-KNAW).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108913.

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