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Seasonal difference in soil health indicators mediating multidiversity-multifunctionality relationship depends on body size of soil organisms: Evidence from rubber plantation agroforestry system

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ABSTRACT

Soil health is the foundation for the maintenance of ecosystem stability and multifunctionality. It is necessary to identify the key indicators of soil health that indicate ecosystem multifunctionality against anthropogenic disturbances such as land use change. Many studies have shown the pivotal role of soil biodiversity in maintaining ecosystem multifunctionality. However, the key role of soil multidiversity (including different body size soil organisms across multitrophic levels) in affecting ecosystem functions is poorly understood. We have implemented a multitrophic perspective to study soil multidiversity by including bacteria, fungi, nematodes (5 feeding types), and arthropods (thripidae, poduridae, and others). Here we show that a multitrophic approach for soil biodiversity assessment is important to highlight trophic interactions and their subsequent effects on the soil multidiversity-ecosystem multifunctionality (MEF) relationship. We postulate that soil multidiversity promotes soil health and thus drives the MEF relationship. We assessed soil multidiversity, 11 variables for ecosystem functions, and ecological network stability (reflected by co-occurrence network patterns) in rubber plantations differing in land-use intensity represented by monoculture (MRP), high (RHD) and low (RLD) diversity of other plant species. We also included tropical rainforest (TRF) as a reference system to compare our results. Results showed that soil multidiversity, multifunctionality, and soil network stability significantly improved in RHD as compared to MRP. Soil multidiversity rather than single diversity component had strong positive effects on multifunctionality. More specifically, we found that the relationship between soil multidiversity and multifunctionality was seasonally dependent on the soil attributes and the body size of soil organisms. We observed a negative correlation between large body size organisms and soil nutrients content in the dry season while a positive correlation between small body size soil organisms and enzymatic activities in the rain season. Particularly, we emphasized the role of soil multidiversity in enhancing ecosystem multifunctionality and stability via its prominent impacts on soil health. Our study elucidates that accurate identification of soil health indicators is an important approach to imply remedial management strategies to maintain soil health and MEF relationship in managed ecosystems such as rubber plantations.

1. Introduction

The land-use intensification driven loss of biodiversity and ecosystem functions will have strong negative influences mainly in tropical ecosystems (Labrière et al., 2015; Dobson et al., 2021). Predominantly, such negative effects are mediated by alterations in soil characteristics that critically affect soil health (Al-Kaisi and Lal, 2017). Consequently, rising concerns over the detrimental effects of land use change on soil health and soil biodiversity have prompted extensive research to investigate soil biodiversity-ecosystem functions (BEF) relationships (van der Plas, 2019). However, the imperative role of soil health indicators in influencing BEF relationships is poorly understood. Soil organisms play key roles in providing biological life to the soil ecosystem and are thus considered as the major indicator of soil health

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and determinants of the BEF relationships (Delgado-Baquerizo et al., 2020; Brooker et al., 2021; Schittko et al., 2022). However, most studies have focused on single or some organism groups to indicate the impact of land use intensification on soil biodiversity loss and BEF relationships (Wagg et al., 2014; Ratcliffe et al., 2017; van der Plas, 2019; Zheng et al., 2019). Therefore, a significant knowledge gap remains regarding the relative importance of diverse soil biodiversity components across different trophic levels for maintaining ecosystem multifunctionality in land use systems. As a result, there is a lack of a broader view of how land use intensification can affect soil multitrophic diversity, alter trophic interactions, and eventually BEF relationships.

Soil biodiversity across different trophic levels such as bacteria, fungi, nematodes, and arthropods (hereafter referred to as soil multidiversity) provides a broader perspective of its role in determining the soil multidiversity-ecosystem multifunctionality (hereafter referred to as MEF) relationships, and hence ought to be the crucial indicator of soil health (Moebius-Clune, 2016; Bünemann et al., 2018; Lehmann et al., 2020). Furthermore, the anticipated magnitude of soil biodiversity loss resulting from habitat destruction or land use change does not affect single taxa but it occurs across many taxa from different trophic levels. As a result, the combined negative effects of biodiversity loss at different trophic levels (several taxa) on ecosystem functions can be more pronounced (Thakur and Geisen, 2019). Thus, including soil multidiversity rather than diversity of single taxa, in the ecological model of MEF provides a rational approach and it becomes even more important in biodiverse ecosystems (for example, tropical forests) where rich diversity affects trophic interactions and successively ecosystem functions.

Soil multidiversity has become a fundamental topic for current research and evidence is mounting that soil multidiversity positively affects ecosystem functions (Soliveres et al., 2016; Delgado-Baquerizo et al., 2020; Jiao et al., 2022). In recent times, research on soil multidiversity has expanded from the consideration of multitrophic soil organisms to the study of different body size soil organisms (Eisenhauer et al., 2019). For example, soil macroorganisms (including invertebrates and earthworms) carry out the decomposition process of plant detritus (Tresch et al., 2019) and dominate the detrital food web (Byrnes et al., 2014). Furthermore, soil microorganisms (such as bacteria, fungi, and bacterivorous nematodes) drive ecosystem functions, such as nutrient cycling and promote the biological transformation of carbon and nitrogen within the micro soil food web (Huo et al., 2017; Kou et al., 2018). Most importantly, body size drives community assembly processes of soil organisms (Zinger et al., 2019; Wang et al., 2022) which are directly related to community functions. Therefore, different body size soil organisms have an intense impact on overall ecosystem functions (Luan et al., 2020). For that reason, the body size of soil organisms can be considered as an additional predictor of soil multidiversity which is essential to envisage its potential influences on ecosystem multifunctionality, also highlighting its capacity to alter MEF relationships to a great extent.

While prior studies have mostly focused on the response of soil biodiversity to land use intensifications (Delgado-Baquerizo et al., 2020; Jiao et al., 2022), the influence of other land use components such as plant diversity, which might play a significant role in determining the magnitude of adversity, has often been neglected. The complexity of land use intensification and its influence on ecosystem functions, cannot be captured by concentrating on belowground attributes only (Maestre et al., 2012; Tresch et al., 2019; Steinauer et al., 2020). This may be particularly the case when considering the tropical rainforest land use system as a study model where plant community composition can have profound impacts on structuring the soil food web via trophic cascades (Rosa et al., 2014). Plant diversity is fundamental to ecosystem functioning because it can directly or indirectly affect soil multidiversity via plant-soil feedback effects (Lavorel et al., 2013; Wan et al., 2020). Despite this, the potential contribution of plant diversity for altering soil multidiversity and MEF relationships has been underestimated in several studies (Fanin et al., 2018; Schuldt et al., 2018; López-Rojo et al., 2019; Steur et al., 2022). Land use driven negative effects on soil biodiversity and ecosystem functions can differ in strength depending on the composition and intensity of the aboveground plant community (Lan et al., 2017a, 2020; Zeng et al., 2021). For instance, high plant diversity increases soil nutrient heterogeneity by elevating plant resource supply in the form of litter and root mass, increases mineralization rates, maintains soil fertility, and supports high soil biodiversity (Eisenhauer et al., 2018; Hemati et al., 2020). Here, we emphasize that understanding the relevance of plant diversity might be significant to predict how soil multidiversity responds to land use intensification and perhaps even more important by serving as a management target to improve soil health and ecosystem multifunctionality.

A shift from natural ecosystems to intensive land use has witnessed a sharp decline in soil biodiversity and ecosystem functions (Geisen et al., 2019; Brooker et al., 2021; Dobson et al., 2021). For instance, in the South of China, such as Xishuangbanna, rubber plantations have faced dramatic land-use changes over the past three decades (Xiao et al., 2019). Xishuangbanna located within the Indo-Burma biodiversity hotspot has been a center of attention for land use based research (Corlett, 2014). Rubber plantation has negatively affected the soil fertility and vital ecosystem functions, such as loss of above and belowground biomass, litter mass, soil organic carbon, soil respiration, plant species richness, animal species richness, soil fauna, and soil microbial richness (Singh et al., 2021; Zeng et al., 2021). Our previous studies conducted in Xishuangbanna have provided evidence that increasing aboveground diversity alleviates the adverse impacts by providing more habitat resources and supporting a high diversity of soil organisms, which altogether increases ecosystem functions and soil health (Xiao et al., 2014; Hemati et al., 2020). However, we still lack empirical evidence for explaining how plant diversity could improve soil health, soil multidiversity, and ecosystem multifunctionality in rubber plantations. For this, we need to expand our vision beyond soil microbes, for accurate identification of soil health indicators by including soil multidiversity of different body sizes, plant attributes, and soil food web stability. Previous studies have identified that soil organisms and some soil properties are required for assessing soil health in rubber plantations (Xiao et al., 2014; Lan et al., 2017b, 2020; Zeng et al., 2021). But their approach to identifying soil health indicators is highly biased and incomplete leaving behind crucial parameters such as soil multidiversity and plant diversity.

We selected different land-use intensities in rubber plantations as follows; (i) monoculture rubber plantation (MRP), (ii) rubber with low understory plant diversity (RLD), (iii) rubber with high understory plant diversity (RHD), and (iv) tropical rainforest (TRF). We selected 10 soil organism groups, including bacteria, fungi, nematodes (5 feeding types), and arthropods (thripidae, poduridae and others) based on body size as an indicator of soil multitrophic multidiversity (Zinger et al., 2019; Wang et al., 2022). To analyze ecosystem multifunctionality, we analyzed 11 measures for ecosystem functions corresponding to litter and root mass, soil nutrient cycling, and soil enzyme activities. Our main aim is to address the following research questions: (a) Whether and up to what extent soil multiversity (based on the body size of soil organisms) can be linked to ecosystem multifunctionality in rubber plantations and be used as an indicator of soil health? (b) Whether plant diversity affects the composition of different body size soil organisms via plant-soil feedback process leading to the seasonal difference in MEF relationships? We first hypothesize that soil multidiversity is an appropriate indicator of soil health because it provides biological life to the soil system and maintains its functional capacity. In addition, we assume that the body size of soil organisms is an integral part of the soil multidiversity concept and should be considered while studying BEF relationships. Secondly, we predict that high plant diversity positively affects soil multidiversity and MEF relationships via positive plant-soil feedback effects.

2. Materials and methods

2.1. Study design

The study was conducted in the Xishuangbanna (Yunnan, China) region located within the Indo-Burma biodiversity hotspot (21°10′-22°40′ N, 99°55′-101°50′ E). It has a monsoon tropical climate (mean annual temperature and precipitation of 21.6 °C and 1478 mm, respectively), with two seasons: a dry season (November–April) and a wet season (May–October) (Corlett, 2014). The reason for including seasonal effects is that there is a demarcation between dry and wet seasons in the Xishuangbanna region due to the monsoon climate which causes a high degree of environmental heterogeneity and high biodiversity as well (Zhu, 1997; Xia et al., 2016; Xu et al., 2016). We established study plots in 3 different land-use types in rubber plantations and tropical rainforest as follows: monoculture rubber plantation (MRP), rubber with low understory plant diversity (RLD), rubber with high understory plant diversity (RHD), and tropical rainforest (TRF) (Fig. 1). The plant richness of RHD (20 species) was significantly higher than RLD (10 species) (Figs. S1a–b, Table S1). Our study used a tropical rainforest as a reference system because rainforests are the most common natural vegetation to be replaced by rubber plantations. The age of the rubber plantations (MRP, RLD, and RHD) selected for our study is about 25 years.

Field sampling was conducted in March (dry season) and September (rain season) 2021. Four replicates were taken in each of the three sites for MRP, RLD, RHD, and TRF. A total of 48 study plots (3 sites (XTBG, NBH, LL) × 4 land use types × 4 replications (5m × 5m)) were set up. In each plot, soil samples were collected from the inter-row zone (space between two rows of rubber trees). We used a five-point sampling method for collecting soil samples at 0–10 cm depth using five soil cores (10 cm in depth, 5 cm in diameter).

2.2. Soil biodiversity analysis

We included 4 main taxa (bacteria, fungi, nematodes, and arthropods) for analyzing soil multidiversity. We used DNA metabarcoding using three corresponding primers for the identification of bacteria, fungi, and nematodes. Further, nematodes were grouped by functional traits into 5 feeding types as follows: bacterivorous, fungivorous, herbivorous, omnivorous, and predator nematodes. In addition, the arthropods community was identified using standard morphological tools and further categorized into 3 groups as follows: thripidae, poduridae, and others.

Bacteria and fungi. The study used PCR-based protocols described in the Earth Microbiome Project (https://www.earthmicrobiome.org/) to determine the community composition of bacteria and fungi. DNA was extracted using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) from 0.25g soil. For each sample, PCR reactions were performed in triplicate in a 25 µl reaction mixture containing 1 µl of forward and reverse primers at 15 µM concentration, 10 µl Prime Hot MasterMix, 1 µl template DNA, and 12.0 µl H_2O (Leff et al., 2018). The PCR conditions were as follows: initial denaturation at 95 °C for 3 min, 35 cycles of (95 °C for 30s, 55 °C for 1 min, 72 °C for 1 min), and 72 °C for 10 min. The V4-V5 region of the 16S rRNA gene was amplified with primers 515F (5-GTGCCAGCMGCCGCGGTAA-3) and 926R (5-CCGYCAATTYMTTTRAGTTT-3) (Parada et al., 2016). Primers ITSF1 (5-CTTGGTCATTTAGAGGAAGTAA-3) and ITS2 (5-GCTGCGTTCTTCATCGATGC-3) were used for the fungal community (Toju and Thompson, 2014). The raw sequences were demultiplexed and processed using the USEARCH pipeline. Paired-end sequences were then merged and the chimeras were removed. Raw reads were mapped to a de novo database with UNOISE3 (Nearing et al., 2018). For taxonomic annotation of fungal ITS sequences, we used UNITE (version 7) database. Further, fungi functional groups were identified using the FUNGuild database. We used only probable guilds for this analysis (Nguyen et al., 2016).

Nematodes. For nematode extraction from the soil samples, we followed a modified Biermann funnel method as described earlier (Viglierchio and Schmitt, 1983). The extracted nematode samples were stored at −20 °C for DNA extraction using a PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). Extracted nematode DNA was stored at −20 °C for further use. The PCR was performed using the SSU rDNA: NF1 (5-GCCTCCCTCGCGCCATCAGGGTGGTGCATGGCC GTTCTTAGTT-3) and 18Sr2b (5-GCCTTGCCAGCCCGCTCAGTA-CAAAGGGCAGGGACGTAAT-3) (Porazinska et al., 2009). PCR conditions were as follows: initial denaturation at 94 °C for 3min followed by 35 cycles of (94 °C for 30s; 55 °C for 30s; 72 °C for 45s), and final step at 72 °C for 5min. We used SILVA database for the taxonomic assignment of nematodes and information on different nematode feeding types was obtained from the nematode physiological parameter database (http://nemaplex.ucdavis.edu).

Soil arthropods. The soil arthropods were extracted from the litter samples using Tullgreen funnels over a 72h period (Rieske and Buss, 2001). The samples were identified at the family level based on microscopic visualization of external morphological characteristics. Soil

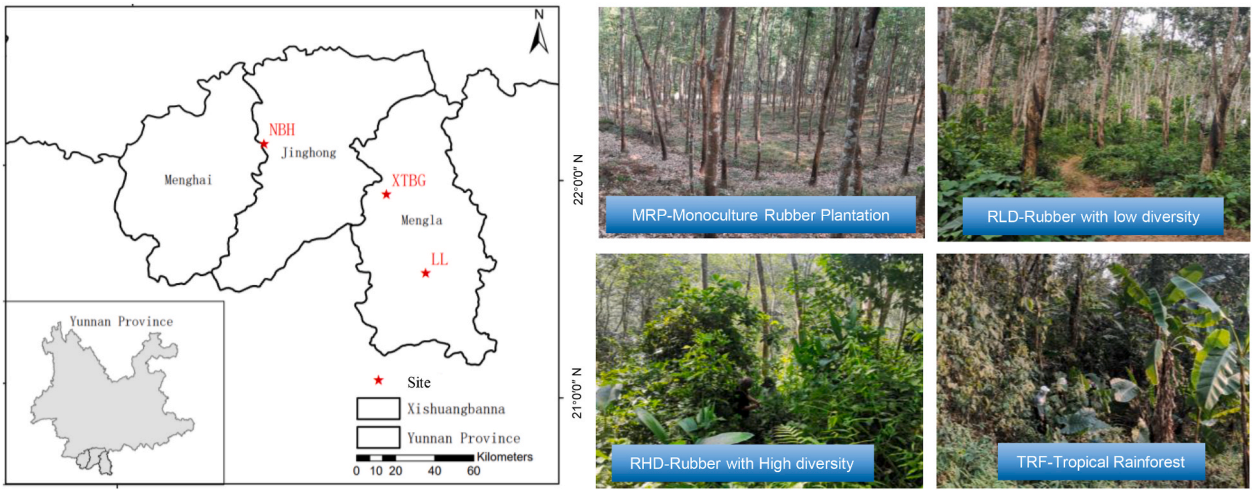

Fig. 1. The experimental outline of this study. Map showing the geographical location of three study sites (shown by 3 red stars) located in Xishuangbanna, Southwest China. Pictures on the right panel show the appearance of different land use types. Abbreviation: monoculture rubber plantation (MRP), rubber with low understory plant diversity (RLD), rubber with high understory plant diversity (RHD), and tropical rainforest (TRF).

arthropods were identified into taxonomic groups according to Yi (2000) and their abundance was measured by counting the number of individuals under a microscope. For visualization, we used a microscope equipped with a digital camera (Nikon Axio Observer, Colibri 7, Axiocam 702 mono, Germany) at the Soil Ecology Group, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

The soil multidiversity index was calculated following the method described by Soliveres et al. (2016). Briefly, we first combined diversity data of bacteria, fungi, nematodes, and arthropods and then calculated standardized scores on a common scale ranging from 0 to 1 by using the following formula: $STD = (X - Xmin)/(Xmax - Xmin)$; where STD is the standardized variable and X, Xmin, and Xmax are the target variables. This approach has been widely used in the current literature (Allan et al., 2014; Jiao et al., 2022).

2.3. Ecosystem multifunctionality analysis

We measured 11 variables of ecosystem functions under the following categories: nutrient transformation and cycling (soil pH, total C, N, P, hydrolyzable nitrogen-HyN, extracellular enzymes: β-1,4-glucosidase (BG), β-N-acetyl-glucosaminidase (NAG), and acid phosphatase (AP)), organic matter decomposition (litter mass: particularly aboveground litter content), belowground primary productivity (root mass) and water availability (soil moisture) (Meyer et al., 2018). To measure the soil moisture, soil samples were dried in an oven at 105 °C for 48h after removing root debris and then reweighed. The soil pH was measured using a pH meter in a 1:5 (w/v) suspension. The total carbon (TC) and total nitrogen (TN) were analyzed using an elemental analyzer (Vario MAX CN, Elementar, Germany). The determination of total phosphorus (TP) was based on the digestion method using iCAP 7400 ICP-OES. The enzymatic activities (μmol g^{-1} dry soil h^{-1}) of β-1, 4-glucosidase (BG), β-N-acetyl-glucosaminidase (NAG), and acid phosphatase (AP) were measured by fluorometric method (Multiskan FC, ThermoFisher Scientific, US) (Paz-Ferreiro et al., 2011). The plant species richness in each study plot was surveyed by a professional botanist. After the separation of arthropods, litter samples were dried at 65 °C for 3 days and further weighed for calculating litter mass. Root mass was obtained after drying fresh root samples at 65 °C for 3 days.

The ecosystem multifunctionality index was calculated following the method described earlier (Soliveres et al., 2016; Jiao et al., 2022). We used 11 key variables (as explained above) for obtaining a quantitative multifunctionality index for each sample. Data were standardized using the z-score transformation. Finally, these standardized variables were then averaged to obtain a multifunctionality index.

2.4. Statistical analyses

To obtain soil biodiversity, we used *diversity()* functions in the vegan package. The normality test of *shapiro.test()* was performed on all variables to meet the premise assumptions of the following analyses. Two-way ANOVA was used to identify the main significant differences and interactions between season and land use types, followed by LSD for multiple comparisons. Hellinger's transformation was performed for sequencing data using the *decostand()* (Legendre and Legendre, 2012). Principal component analysis (PCA) was used to group objects into categories based on their dissimilarities (Delgado-Baquerizo et al., 2020). If variables do not have a uniform scale (11 ecosystem function parameters measured in different units or scales), variables have to be log-transformed before performing further analyses (Ramette, 2007). Correlation analysis was performed to evaluate the relationship between 11 variables of ecosystem functions and the diversity of individual components of soil multidiversity. Molecular ecological co-occurrence network stability is strongly and positively correlated with network complexity (Yuan et al., 2021). Therefore, co-occurrence network analysis was constructed based on Spearman's correlations of OTU abundances, to further assess the importance of key ecological clusters of soil organisms. The Spearman's correlations at $r > 0.65$ and $P < 0.001$ were applied for network construction. Network properties including nodes, edges, modularity, number of communities, and key clusters were calculated using igraph package (Csárdi and Nepusz, 2006). We used Gephi version 0.9.2 software (https://gephi.org) to visualize co-occurrence networks. All statistical analyses were performed in the R environment (version 4.1.1).

3. Results

3.1. The seasonal pattern of soil physico-chemical and biological properties

An in-depth analysis was conducted on soil physico-chemical and biological properties as listed in Table 1. Overall, the soil properties showed the most prominent differences between MRP/RLD and RHD/TRF. Noticeably, TC and TN contents were higher in RHD and TRF in

Table 1

Tukey's HSD Post-hoc test for the main effects of different land use types on the indicators of ecosystem functions (including soil properties, soil enzymes, and plant attributes). Abbreviations: Soil total carbon (TC), soil total nitrogen (TN), soil total phosphor (TP), β-1,4-glucosidase (BG), β-N-acetyl-glucosaminidase (NAG), acid phosphatase (AP), soil moisture (SM), hydrolyzable nitrogen (HyN), litter mass (LM) and root mass (RM). Units of Enzyme activities are expressed as micromole product per gram of dry soil per hour. Different letters indicate a significant difference among levels of different land use types ($P < 0.05$).

Parameters	Season	MRP	RLD	RHD	TRF
TC (g/kg)	Dry	15.75 ± 1.13c	17.90 ± 1.65bc	22.04 ± 1.54ab	22.44 ± 1.78a
	Rain	16.29 ± 0.89c	18.05 ± 1.27bc	20.41 ± 1.42ab	22.25 ± 1.35a
TN (g/kg)	Dry	1.73 ± 0.09b	1.92 ± 0.12b	2.27 ± 0.11a	2.34 ± 0.15a
	Rain	1.78 ± 0.08c	1.92 ± 0.08bc	2.16 ± 0.11ab	2.36 ± 0.14a
TP (g/kg)	Dry	0.35 ± 0.02a	0.34 ± 0.02a	0.40 ± 0.04a	0.36 ± 0.02a
	Rain	0.44 ± 0.05a	0.34 ± 0.02b	0.39 ± 0.03ab	0.39 ± 0.04ab
BG (μmol g^{-1} dry soil h^{-1})	Dry	5.03 ± 1.39a	2.93 ± 0.71a	3.88 ± 0.90a	3.95 ± 0.51a
	Rain	3.90 ± 1.41b	13.28 ± 3.46a	11.02 ± 2.48ab	9.00 ± 2.51ab
NAG (μmol g^{-1} dry soil h^{-1})	Dry	0.71 ± 0.21a	0.43 ± 0.10a	0.66 ± 0.14a	0.74 ± 0.13a
	Rain	0.87 ± 0.27b	2.11 ± 0.56a	1.47 ± 0.27ab	1.06 ± 0.28b
AP (μmol g^{-1} dry soil h^{-1})	Dry	6.97 ± 1.59a	6.62 ± 1.49a	6.50 ± 0.81a	7.21 ± 1.02a
	Rain	4.77 ± 1.06a	7.76 ± 2.63a	6.70 ± 1.40a	6.38 ± 1.51a
pH	Dry	5.30 ± 0.47ab	5.45 ± 0.33ab	5.64 ± 0.57a	5.26 ± 0.42b
	Rain	5.09 ± 0.52a	5.14 ± 0.34a	5.27 ± 0.42a	5.21 ± 0.74a
SM (%)	Dry	29.18 ± 5.54a	26.13 ± 6.47a	26.91 ± 5.34a	19.34 ± 3.74b
	Rain	35.37 ± 7.51a	32.18 ± 10.96a	34.99 ± 6.63a	33.64 ± 6.06a
HyN (g/kg)	Dry	142.86 ± 32.06c	151.98 ± 41.50bc	183.28 ± 29.09a	177.69 ± 30.44ab
	Rain	126.09 ± 26.98c	133.93 ± 23.16bc	147.48 ± 14.45ab	152.37 ± 14.82a
LM (g)	Dry	118.79 ± 14.85a	112.51 ± 8.01a	132.93 ± 12.39a	136.00 ± 12.03a
	Rain	31.58 ± 6.55b	35.06 ± 6.61b	47.22 ± 6.45ab	61.56 ± 4.33a
RM (g)	Dry	0.29 ± 0.05bc	0.19 ± 0.03c	0.34 ± 0.04b	0.53 ± 0.06a
	Rain	1.00 ± 0.19a	1.02 ± 0.19a	1.12 ± 0.22a	0.94 ± 0.14a

both seasons. The TP content was higher in RHD and TRF in the dry season but showed a different pattern in the rain season. Soil enzyme (BG) was 2.2–4.5 folds higher in the rain season in all land use types compared to the dry season. In the rain season, soil enzyme activity increased significantly with the increase of understory vegetation diversity. Likewise, litter mass showed a very clear pattern and a 2.2–3.8 folds increase in the dry season. Root mass was 1.8–5.4 folds higher in the rain season. Both litter mass and root mass contents were higher in RHD and TRF in both seasons (Figs. S1c–f). Altogether, most of the soil properties showed a significant trend with maximum content in RHD and TRF as compared to MRP and RLD.

3.2. *Soil multidiversity as a predictor of ecosystem multifunctionality*

We successfully obtained a comprehensive dataset on the soil multidiversity and ecosystem functions for our study sites (Table S2, Table S3, Fig. S2). The soil multidiveristy was observed to be high in the RHD followed by TRF, MRP, and RLD (F (3, 92) = 8.485, $P < 0.001$). Likewise, the ecosystem multifunctionality index was highest in the RHD followed by TRF, RLD, and MRP (F (3, 92) = 7.389, $P < 0.001$, Fig. 2a). There was a positive correlation between the diversity of each soil organism's groups and multifunctionality except for bacterial diversity which showed a negative correlation. The slope of the relationship between soil multidiversity and multifunctionality was steeper than any individual soil organism which explained more variance (Fig. 2b). Interestingly, we observed that soil pH was significantly positively related to bacterial ($R^2 = 0.35$, $P < 0.001$) and fungal diversity ($R^2 = 0.21$, $P < 0.001$). Likewise, root mass was also significantly positively related to bacterial ($R^2 = 0.26$, $P < 0.001$) and fungal diversity ($R^2 = 0.22$, $P < 0.001$). The soil arthropod diversity showed a positive relationship with litter mass ($R^2 = 0.64$, $P < 0.001$) and HyN ($R^2 = 0.42$, $P < 0.001$) (Fig. S3).

3.3. *Seasonal difference in the relationship between soil multidiversity and ecosystem multifunctionality*

The effects of soil multidiversity on multifunctionality depended strongly on the season showing a differential pattern in dry and rain seasons. PCA showed that PC1 (29.74% of the explained variance) was associated with larger organisms including arthropods, thripidae, poduridae, omnivorous, and predator nematodes. This axis mainly represented the dry season. The axis PC2 (23.22%) with a large proportion of smaller organisms, such as bacteria, fungi, bacterivorous, frugivorous, and herbivorous nematodes were mainly clustered together in the rain season (Fig. 3a). Further, the PCA of 11 variables of ecosystem functions (soil properties and plant attributes) also showed a seasonal pattern. For instance, PC1 explained 30.58% of the total variation which was largely associated with the soil nutrients (TC, TN), pH, and litter mass in the dry season. Differently, PC2 explained 22.68% of the variance in soil enzymes, soil moisture, and root mass which mainly clustered together in the rain season (Fig. 3b).

Based on the results of the correlation analysis, a negative correlation ($R^2 = 0.28$, $P = 0.045$) between soil multidiversity (large soil organisms) and multifunctionality (soil nutrients and litter mass) was observed (Fig. 4a), while, a positive relationship ($R^2 = 0.29$, $P = 0.041$) between soil multidiversity (small soil organisms) and multifunctionality (soil enzymes and root mass) was found (Fig. 4b) (Graphical Abstract).

3.4. *Linking the stability of soil network to multifunctionality*

The ecological co-occurrence network analysis suggested that fungi occupied more than half proportion of ecological network nodes (47.01–50.90%), followed by bacteria (18.80–20.91%), arthropods (13.22–21.15%), and nematodes (12.90–20.91%) (Fig. 5a–b). The number of nodes, edges, modules, and the modularity coefficient was highest in the RHD, followed by the TRF and RLD, and lowest in MRP (Fig. 5c–d). Because of the importance of fungi in the network, we performed predictive functional profiling of fungal communities using the FunGuild database. Our results showed that the relative abundance of symbiotrophic and pathogen fungi was highest in TRF, followed by RHD, RLD, and MRP (Fig. S4, Fig. S5). A complete list of taxa composition within each ecological cluster is provided in Table S4.

4. Discussion

Considering biodiversity loss as a global concern, it is important to investigate to what level soil biodiversity is responding to land use intensifications and altering ecosystem functions. By performing an extensive study in rubber plantations with different understory plant diversity levels, we demonstrated interactive effects of soil multidiversity and plant diversity on the MEF relationships that were also observed to show different patterns in dry and rain seasons. In particular, soil multidiversity differed distinctly in response to different rubber plantations which was more likely to be stimulated by plant communities indicating plant-soil feedback effects. It underlines the fact that enhancing soil multidiversity via nutrient resources (litter and root mass) input is a key to promoting soil biological health and sustaining ecosystem functions. Our data support the relevance of soil multidiversity in determining the soil health capacity which is essential to the functioning of the ecosystem. Knowing whether all soil organisms or any specific organism groups are important for maintaining ecological processes, can be enormously helpful for achieving future sustainability.

4.1. *Soil multidiversity as an indicator of soil health relies on body size*

The relationship between soil multidiversity and multifunctionality has received markedly increased attention in recent years (Allan et al., 2015; Meyer et al., 2018; Jiao et al., 2022). In a variety of biomes, there

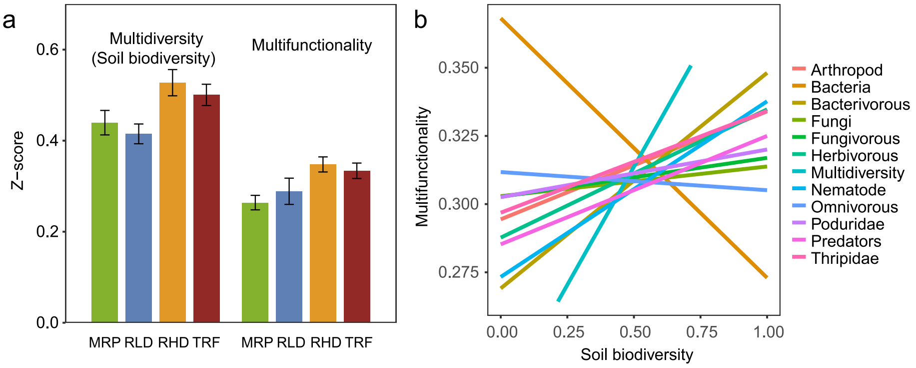

Fig. 2. **(a)** The pattern of soil multidiversity and ecosystem multifunctionality in different land use types. **(b)** The fitted linear relationships between multifunctionality and individual components of soil multidiversity.

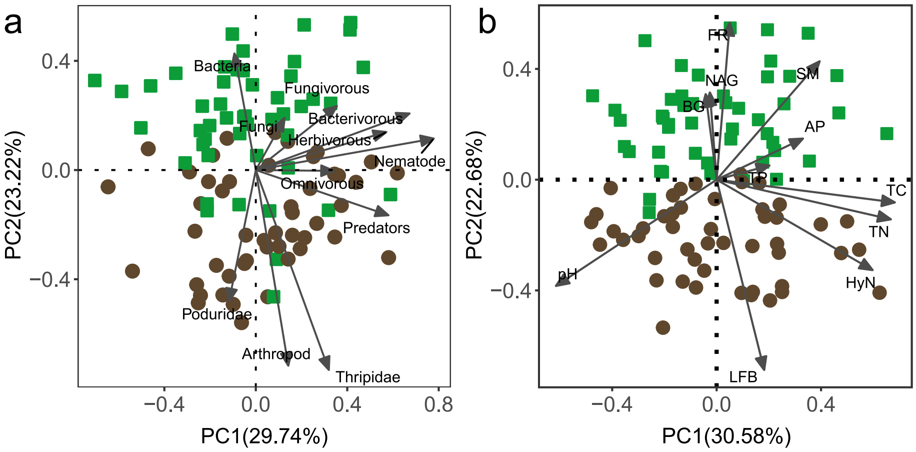

Fig. 3. Principal component analyses (PCA) of soil organisms **(a)** and ecosystem function parameters **(b)** showing seasonal differences in the dry (brown circles) and rain (green squares) seasons.

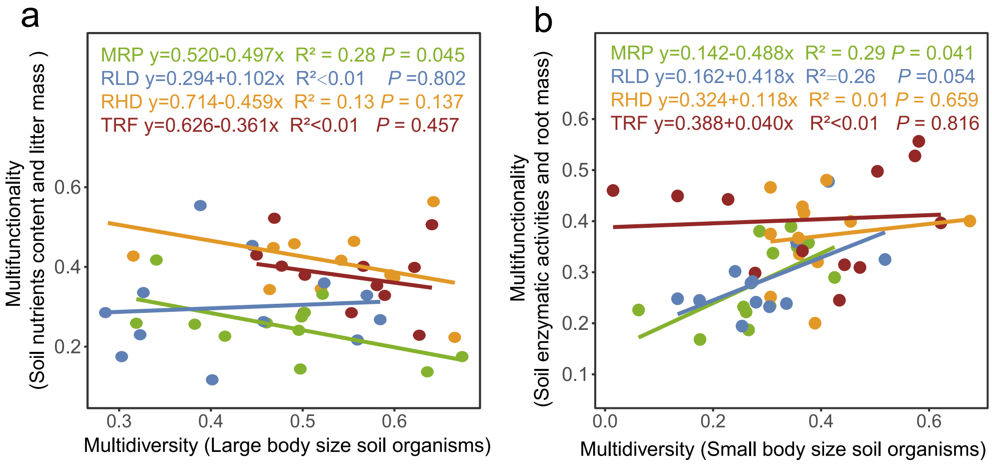

Fig. 4. **(a)** The fitted linear relationships between multifunctionality (soil nutrients content and litter mass) and soil multidiversity (large body size soil organisms). **(b)** The fitted linear relationships between multifunctionality (soil enzymatic activities and root mass) and soil multidiversity (small body size soil organisms).

is a broad consensus that the relationship between multidiversity and multifunctionality is positive. Nevertheless, the explained variance and significance of a single trophic group to multifunctionality are smaller compared to multidiversity (Delgado-Baquerizo et al., 2020). Likewise, we also observed that the soil multidiversity was superior to any individual trophic group, with the largest slope and explained variance, which showed a significant linear relationship with multifunctionality which supports the part of our first hypothesis. Here, we want to extend this concept by discussing that the body size of soil organisms matters while considering their contribution to ecosystem functions which is supported by our data. Body size is an important life-history trait that influences the community assembly processes of soil organisms and maintains species diversity at local to global scales (Luan et al., 2020). In turn, soil multidiversity effects on ecosystem functions cannot be rationally considered without acknowledging the fundamental role of body size. On one hand, the individual component of soil multidiversity (which we categorized based on body size) showed a linear positive relationship with ecosystem multifunctionality except for bacterial diversity. Further, soil multidiversity as a whole showed a significant positive relationship with ecosystem multifunctionality. This exceedingly indicates the need to include body size as a good predictor of soil multidiversity and sheds light on the soil health concept that should be included in the BEF model. It is worth mentioning here that the negative relationship shown by bacterial diversity is attributed to its negative correlation with multifunctionality. It was mainly due to the high bacterial diversity in rubber plantations and the low bacterial diversity in tropical rainforest. However, the ecosystem multifunctionality showed the opposite pattern. This is consistent with a previous study conducted in Xishuangbanna showing that the bacterial diversity index in the rubber plantation was significantly higher than that of the tropical secondary forest and the tropical rainforest in both dry and rain seasons indicating increase in the bacterial diversity after conversion (Lan et al., 2017b). Another study also showed that due to the management processes of rubber plantations, such as fertilization, the bacterial richness of rubber mono-plantations was higher than that of tropical rainforests (Cai et al., 2018).

In our study, we noticed that there were prominent interaction effects of body size and season on the MEF relationships. Large body size soil organisms (arthropods including poduridae & thripidae, and omnivorous & predator nematodes) showed a negative relationship with multifunctionality elements (soil nutrients and litter mass) in the dry season, while small size soil organisms (bacteria, fungi, and bacterivorous/fungivorous/herbivorous nematodes) showed a positive correlation with multifunctionality components (soil enzymes and root mass) in the rain season. Our results are in partial accordance with previous studies conducted in maize and rice agricultural ecosystems which showed that large body size soil organisms at different trophic levels (invertebrates or protist predators) appeared to exhibit weaker or no relationship with multifunctionality when compared to those with smaller size (archaea, bacteria, fungi, and protist) (Allan et al., 2015; Liu

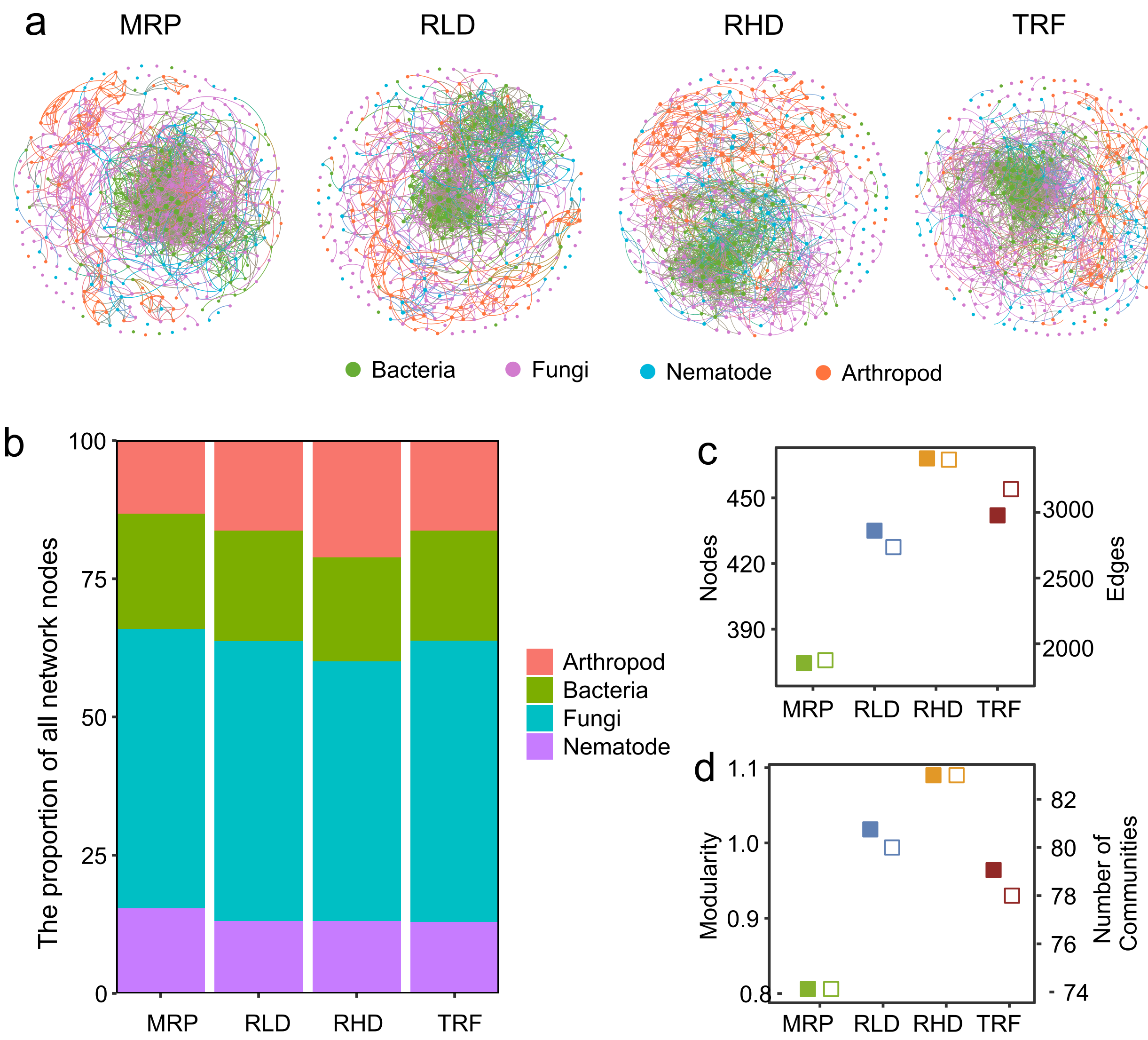

Fig. 5. The architecture of soil co-occurrence networks. **(a)** The pattern of co-occurrence network interactions in the monoculture rubber plantation (MRP), rubber with low understory plant diversity (RLD), rubber with high understory plant diversity (RHD), and tropical rainforest (TRF). Effects of different land use types on **(b)** The proportion of soil biological groups in the network nodes and network topography features including **(c)** nodes and edges, **(d)** modularity and the number of communities.

et al., 2021). These season-wise contrasting effects obtained in our study are more likely due to changes in environmental variables between the two seasons. Our study sites are located in tropical monsoon climate zone having contrasting dry-wet seasons which significantly contribute to environmental heterogeneity (Corlett, 2014; Xia et al., 2016). Some fast-changing soil parameters such as soil moisture, nutrient content, and ecological processes (decomposition rate) can vary over a short time period and show a significant difference between dry and rain seasons (Wu et al., 2017; Krashevska et al., 2022). Alternatively, it is also possible that seasonal differences in plant resource input can structure the community composition of soil organisms (Leff et al., 2018), for instance, in our case, high litter mass during the dry season might provide a resource pool to large body size soil organisms, while high root mass in the rain season facilitated microbial activities of small size soil organisms. The negative correlation between large soil organisms and total soil C, N, P, and litter mass is due to the fact they provide a habitat for large soil arthropods. Soil arthropods use these resources as food and play an important role in the process of fragmentation and decomposition of litter (Tresch et al., 2019).

4.2. *Plant diversity positively affects soil multidiversity and MEF relationships*

In support of our second hypothesis, our data provide experimental evidence that high plant diversity has the potential to promote not only soil multidiversity but also affect MEF relationships positively, which coincides with earlier findings indicating that plant diversity is the foremost factor in maintaining the belowground communities (Xiao et al., 2014; Hemati et al., 2020). This could be due to the reason that diverse plant communities critically influence the availability of plant resources for soil organisms in their microhabitat and induce more nutrient input to the soil (Wang et al., 2022). In the case of forests, it has been reported that a 10% decline in aboveground plant richness can cause a 5% decline in microbial biomass and an approximately 2–3% decrease in plant productivity (Chen et al., 2019). These effects are anticipated because high plant diversity increases soil moisture, carbon, and nitrogen content which supports the dominant fraction of soil organisms e.g., bacteria and fungi (Lange et al., 2015; Yang et al., 2021). Our results demonstrated that the RHD significantly improved soil multidiversity and multifunctionality as compared to MRP. Importantly, the performance of RHD was similar to TRF in terms of soil multidiversity effects on multifunctionality. Previously, Scherber et al. (2010) conducted a long-term controlled biodiversity experiment and demonstrated that plant diversity produced a strong influence on bacterial and fungal diversity. This indicates that lower plant diversity can dampen soil health to a greater extent by negatively affecting bacterial and fungal communities because these two groups of soil organisms have a strong control on driving nutrient cycling.

It is known that plant diversity can enhance ecosystem functions, such as soil carbon storage (Chen et al., 2018), and facilitates beneficial interactions at different trophic levels which eventually improve ecological processes (Wan et al., 2020). In our study, the most obvious difference in different intensive land use is the understory diversity of aboveground plant communities. In comparison to MRP, there are herbs, shrubs, and small trees under the rubber trees in RLD and RHD which can continuously regulate the input of plant resources. For instance, our study sites have 185.17% more litter in the dry season than in the rain season, providing a suitable niche for soil arthropods, such as thripidae, and poduridae. There is an upsurge of 66.84% of the root mass in the rain season providing suitable habitat for small body size soil organisms. In other words, these small body size soil organisms occupy a key position in the detrital food web and are involved in the recycling of available resources in the soil to ensure the functioning of terrestrial ecosystems (Paz-Ferreiro et al., 2011). Concisely, our findings underline the seasonal differences in the significant relationships between soil multidiversity and ecosystem multifunctionality. It also explains that plant resource input has a strong effect on structuring the composition of multitrophic soil communities and their contribution to multifunctionality. More specifically, we also figured out that soil health indicators are season-specific where large body size organisms are active in the dry season, while small body size organisms are in the rain season.

4.3. The robustness of MEF relationships and ecosystem stability in different land use types

The plant diversity in rubber plantations contributed significantly to explaining changes in MEF relationships. Overall, soil multidiversity and MEF relationships were positively affected by high plant diversity in RHD and TRF. It indicates that maintaining high plant diversity in land use can revitalize soil health by supporting multitrophic soil organisms and improve the overall performance of the ecosystem. This is in accordance with the previous study demonstrating that plant diversity has a strong influence on multitrophic interactions, particularly bottom-up effects on lower trophic levels such as bacteria and fungi (Scherber et al., 2010). In addition, it is also important to investigate the stability of MEF relationships which in long term could amplify. Ecosystem stability depends on the interactions among co-existing members of soil multidiversity that build an ecological network (Jiao et al., 2022). The degree of interactions and network stability can be assessed by co-occurrence network analysis which can eventually help us to infer the stability of the ecosystem (Yuan et al., 2021).

In general, monoculture plantations show weak resilience to disturbances as compared to rich and diverse ecosystems such as rainforests (Hutchison et al., 2018; Krashevska et al., 2022). However, we do not know the processes providing resilience capacity to species-rich ecosystems. In our study, the high stability in the MEF relationships maintained by RHD in both seasons provides empirical evidence for the notion that high biodiversity is important for sustaining ecosystem multifunctionality and stability (Allan et al., 2015). This was further validated by co-occurrence network topology traits such as the number of nodes (network size), edges (interactions), and the number of modules (functional guilds) which were found to be maximum in RHD indicating that the increased intensity of the understory plants can strengthen soil communities co-existence (Yuan et al., 2021). Our data showed that fungi accounted for 47.01–50.90% of the ecological network nodes in MRP, RLD, RHD, and TRF. This might be due to the increased diversity of understory plants which modulates the underground ecosystem by providing suitable niches for the colonization of symbiotic fungi (Lovelock and Ewel, 2005).

4.4. Conclusion

With this study, we have demonstrated that multitrophic soil organisms of different body sizes are a good predictor of soil biodiversity and are essential to maintain ecosystem multifunctionality in tropical land use systems. In particular, we emphasized the role of different body size soil organisms in enhancing ecosystem functions and stability via their prominent impacts on soil health. Moreover, our study provides experimental evidence that maintaining high plant diversity in land use types can promote soil biodiversity and influence the MEF relationships positively through plant-soil feedback effects. Based on our data, we found that multitrophic soil organisms respond differently to land use change and their contribution to the MEF relationships was seasonally dependent on the soil attributes and their body size. Therefore, we propose that there is potential utility in considering the soil multidiversity as a bioindicator of soil health to monitor land use driven impacts on the ecosystem functions. Moreover, this approach could provide a more complete understanding of the role of soil biota in maintaining soil health which ultimately affects the overall ecosystem health and stability. Finally, our study confirms the significance of protecting soil multidiversity to improve multiple soil functions and soil health for sustainable land use.

Authorship contribution statement

Wenting Wang: Conceptualization, Investigation, Data curation, Writing - review & editing. Sandhya Mishra: Investigation, Writing - review & editing. Xiaodong Yang: Supervision, Conceptualization, Resources, Funding acquisition, Writing - review & editing, Project administration.

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 sequences data have been deposited in the NCBI (PRJNA870041). The soil ecosystem functions data and metadata have been deposited to the Figshare (https://doi.org/10.6084/m9.figshare.20495193).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.108968.

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