Microbial Ecology (2025) 88:13
https://doi.org/10.1007/s00248-025-02506-3

RESEARCH

Soil Microbial Recovery to the Rubber Tree Replanting Process in Ivory Coast

Aymard Kouakou Kouakou[1,2,3,4] · Paul Collart[5] · Thibaut Perron[6,7] · Yeo Kolo[2] · Frédéric Gay[6,7] · Alain Brauman[3,4] · Caroline Brunel[8]

Received: 2 August 2024 / Accepted: 18 February 2025

Abstract

The resistance and resilience of soil microbial communities to an environmental disturbance are poorly documented, due to the lack on onfield diachronic experiments, limiting our ability to design adapted agroecological practices. This is especially true in rubber plantations, one of the most planted tree in tropical areas. We aimed to understand (1) how soil disturbances occurring during the rubber replanting phase affect the soil microbiome, (2) how agricultural practices combining legumes cover crops and tree logging residues shape community resilience and (3) how microbial responses vary across different edaphic contexts. In two plantations with distinct soil properties in Ivory Coast, soil microbial communities were surveyed every 6 months for 24 months after soil perturbation. Community structure, functioning and networks were described based on a 16S/18S rRNA gene investigation. Prokaryotes were generally more resistant to soil perturbation than microeukaryote communities. Prokaryotic resilience dynamics were faster than those of microeukaryotes, the latter being deeply modulated by cover treatments. These specific dynamics were exacerbated in the sandy site. Co-occurrence network modelling provided useful insights into microbial resilience trajectories. We argue that this tool should be more widely used to describe microbial community dynamics. Practices involving a combination of logging residues and legume cover crops have shown beneficial effects on the community resilience in the sandy site and appears as promising agroecological practices. However, the major influence of soil texture warns of the need to consider pedological context when designing pertinent agroecological practices.

Keywords Logging residues · Microbial communities · Resilience · Rubber plantations · Soil functioning

Introduction

The soil microbiome represents a key component of belowground functioning and plant productivity [1]. Soil microbial communities play major roles, for instance, in organic matter decomposition [2], soil structure formation [3] and carbon and nitrogen cycles [4]. Soil community assembly and microbial interactions are crucial for understanding the mechanisms that regulate ecosystem services [4, 5]. Microbial communities respond quickly to environmental modification (i.e. changes in land use, temperature or water stress, [6–9], and the extent and rate of microbiome responses to perturbations provide important information about soil functional stability and sustainability) [10]. The consequences of shifts in community structures following soil perturbations (i.e. tillage [11, 12], tree logging [13], compaction [14, 15]) on ecosystem functioning are well documented in agroecosystems, but less is known about the drivers of resistance and resilience (i.e. ability to tolerate and recover

Aymard Kouakou Kouakou and Paul Collart contributed equally to this study.

✉ Aymard Kouakou Kouakou
aymard01kouakou@gmail.com

1 Centre de Recherche en Ecologie de L, Université NANGUI ABROGOUA, Abidjan, Côte d'Ivoire

2 Université NANGUI ABROGOUA, Ecology and Sustainable Development Laboratory, Abidjan, Côte d'Ivoire

3 IRD, UMR Eco&Sols, Montpellier, France

4 UMR Eco&Sols, Univ. Montpellier, Cirad, INRAe, IRD, Institut Agro, Montpellier, France

5 Univ. Montpellier, Montpellier, France

6 CIRAD, UMR ABSys, Montpellier, France

7 UMR ABSys, Univ. Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France

8 CIRAD, UPR HortSys, 34398 Montpellier, France

Published online: 13 March 2025

from disturbances, respectively [16]) of microbial communities [17]. Soil microbial functioning is often considered as the sum of individual functions, while soil microorganisms form complex networks and act in concert [18]. Thus, insights into community reassembly after soil perturbation over time are becoming essential for understand agroecosystem sustainability and designing relevant agroecological practices [19].

The respective roles and interdependencies of soil biotic and abiotic components in maintaining soil biological activities are increasingly studied [1, 19]. Soil functioning in agroecosystems depends on microbial processes such as the mineralization of organic nitrogen (N), carbon (C) and phosphorus (P), the transformation of organic matter (OM) in the soil and N_2 fixation by soil microbes [20]. Previous studies have shown significant dependencies of the biogeographical distribution of soil microorganisms and their associated functions on major environmental filters, such as soil pH and redox status, OM quality and quantity, temperature and moisture [21], as well as soil texture and structure. In equivalent agricultural systems subjected to similar climates, soil texture is thus likely to impact soil functioning balance depending on the applied agricultural practices [22]. Soil texture characterizes the distribution mineral particles, which is a key driver for soil OM protection, spatial distribution and associated biological activities [23]. Bacteria and fungi act in concert for soil functioning, and their respective responses (resistance and resilience patterns) to soil perturbation may thus be either exacerbated or alleviated with respect depending on edaphic properties.

Tropical tree plantations are a relevant model for studying the impact of a given perturbation on soil communities because of the disturbances occurring during the replanting process, such as tree clear-cutting, uprooting and soil compaction. In our study, we focus on rubber plantations (*Hevea brasiliensis*). The current and rapid expansion of rubber plantations to meet existing global demand for rubber puts soil biodiversity at risk [24]. Studies have shown that forest replacement by rubber plantation results in an overall loss and extensive replacement of both aboveground (i.e. birds and bats [25]) and belowground (i.e. spiders, arthropods or nematodes [26–28]) biodiversity. However, rubber plantations are no longer a main cause of deforestation. The current trend is to replace annual crops (such as cassava and sugarcane) with rubber plantations [29, 30] and to repeat rubber plantations on the same soils after clear-cutting [31]. After a rotation period ranging from 25 to 40 years [32], rubber plantations require tree replacement, and the replanting process constitutes a significant soil disturbance. This period is characterised by (1) the opening of the canopy following tree clear-cutting, (2) the removal of logging residues with machines and (3) subsoiling (i.e. breaking up of compacted layers) by heavy machinery. Thus, successive rubber plantation cycles impact soil diversity due to long-term modifications of soil physico-chemical properties. For example, Panklang et al. [33] evidenced strong losses of N, K, Ca and Mg in the soil, and a 50% decrease in SOC content between forest and third rotation of rubber trees. Clear-cutting and soil compaction also severely impact nutrient content [34], soil functions (such as structure maintenance, carbon transformation and nutrient cycling [31]) and significantly reduce the biomass while altering the composition of soil microbial communities [17].

Cultural practices such as organic matter inputs and cover crops play a fundamental role in soil functioning. Legumes are commonly grown in industrial rubber plantations after tree replacement to fix nitrogen in the soil, control weeds and limit soil erosion, particularly during the immature phase (0–5 years before latex extraction) [34–36]. The restitution of tree-logging residues (i.e. trunk, branches, leaves and roots of the logged plantation) also represents a relevant and responsible method for releasing organic matter and potentially improving soil biological quality and associated functioning [37]. The restitution of logging residues has multiple benefits [38]: it mitigates long-term changes in soil communities in forest soil [39], significantly increases both soil carbon stock and nutrient availability [39] and stabilizes soil pH, moisture and temperature [40]. The positive impact of retaining logging residues has also been demonstrated on soil fauna resilience [41], soil microbial community abundance and composition [42], topsoil nematode [43] and soil organic carbon and nutrients levels [44]. Recently, Perron et al. [31] showed that the input of logging residues in the inter-rows sustains major soil functions such as soil structure maintenance, carbon transformation and nutrient cycling, after clear-cutting in immature rubber plantations in Ivory Coast.

Here, we aim to address the effect of agroecological practices on both the resistance and resilience of soil microbial communities throughout a replantation cycle. In particular, our objectives are (1) to assess the impact of rubber tree clear-cutting on soil microbial resistance and (2) to determine how agroecological practices (such as logging residues and legume input) modulate microbial resilience over time, and (3) whether and how microbial responses vary across different edaphic contexts. We hypothesize that organic matter inputs improve soil microbial resistance and accelerate resilience, and that the recovery rate may vary according to both organic matter quality and pedological context. Thus, we conducted a diachronic monitoring in two large-scale field experiments in Ivory Coast and described soil microbial communities (including taxonomic and functional diversity, composition and co-occurrence networks) based on 16S and 18S rRNA gene investigations, before rubber tree clear-cutting and then every 6 months over a 24-month period following the perturbation.

Material and Methods

Study Sites

This study was conducted in two industrial rubber plantations in Ivory Coast (Fig. 1A). The Bongo plantation, belonging to the *Société Africaine des Plantations d'Hévéas*, is located in the *Grand Bassam* region and covers an area of 5700 ha in the South-East of the country (latitude 5°30′32.364″ N, longitude 3°32′51.755″ W). The *Société des Caoutchoucs de Grand-Béréby* is located in the South-West (latitude 4°43′9.696″ N, longitude 7°6′41.795″ W) and owns 16,300 ha of rubber plantations. Both sites are subjected to a sub-equatorial hot and humid climate, which is well-adapted to rubber tree plantations. The ranges provided (annual rainfall of 1700–1900 mm and annual average temperatures of 24–27 °C) are general references for the region and apply similarly to both sites. There are no significant differences in climate between the two sites. Soil physico-chemical properties have been described at both sites in a previous study (see Perron et al. [31]): the soil at the Bongo plantation is classified as a yellow ferralic Arenosol (FAO soil classification [45]) with a sandy loam texture (10% clay in the topsoil) and is characterized by an acidic pH (4.3). At the *Grand-Béréby* plantation, the soil is classified as a red Ferralsol with a clayey loam texture (23% clay in the topsoil) and is characterized by a slightly less acidic pH (around 4.7). Hereafter, the Bongo plantation will thus be referred as the sandy site, and the Grand-Béréby plantation as the clayey site. Total carbon and nitrogen content, and CEC are higher in the clayey site, and available phosphorus concentration in the topsoil layer is higher in the sandy site. The sandy site is characterized by slight slopes (< 5%), whereas the clayey site features hilly areas (slopes of 10–25%).

Experimental Design

The experiment began before the logging of the old rubber trees (38–40 years old) by bulldozers, in November 2017. At both sites, the logged stands were the first cycle of rubber plantation replacing natural rainforest. Similar designs were applied at both sites, testing four agroecological practices combining tree logging residues and legume growth (hereafter referred to as treatments): no residues and the legume *Pueraria phaseoloides* (R0L1); fine residues (i.e. leaves, fine branches with a diameter < 20 cm and stumps) with the legume *Pueraria phaseoloides* (R1L1); all residues (i.e. including branches > 20 cm diameter and trunks) with the legume *Pueraria phaseoloides* (R2L1); and a control treatment without legume nor residues (R0L0). Each treatment was replicated into 4 randomized blocks, resulting in a total of 16 plots (40 × 40 m) per site (Fig. 1B). Logging residues were placed between each new rubber row. *P. phaseoloides,* was sown by broadcasting (10 kg ha^{-1} of humidified seeds) in February 2018. Fine logging residues composing the R1L1 treatment amounted to 36 and 51 t ha^{-1} of carbon per hectare in the sandy and the clayey sites, respectively. Input composed of all residues (i.e. both fine and coarse, R2L1 treatment) amounted to 97 and 245 t ha^{-1} of carbon per hectare in the sandy and the clayey sites, respectively. More details about the experimental design is available in Perron et al. [31] and Kouakou et al. [43].

Soil Sampling

Ten soil samples were collected between rows at 0–10 cm depth in each plot and then pooled to form a composite soil sample (Fig. 1C). A first campaign was conducted in October 2017, before the old plantation logging, to assess initial soil properties before clear-cutting: one composite soil sample per block, i.e. 4 samples per site was collected. Sampling was then carried out every 6 months to monitor the temporal

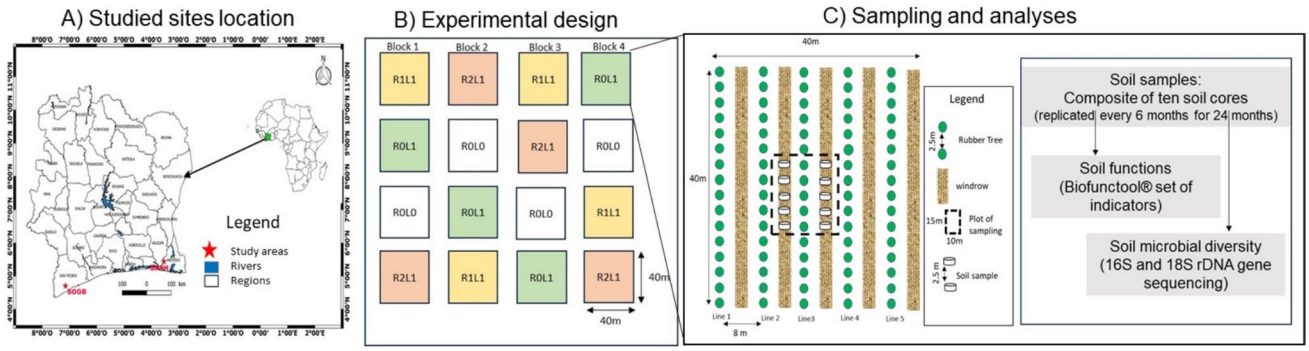

Fig. 1 Overview of the experimental design. **A** Locations of the two studied sites (SAPH and SOGB). **B** The schematic view of the experimental randomized design showing the 16 plots per sites (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues). **C** A summary of the conducted analyses

changes in soil microbial communities according to the application of logging residues and legume. To limit the influence of climate, especially rainfall, sampling was carried out in October and in April. These periods respectively correspond to the start of the dry and beginning of the wet seasons in Ivory Coast. A total of five sampling campaigns were carried out from October 2017 to October 2019.

Soil Functions

We analysed 8 properties related to soil functioning from the Biofunctool® set of indicators [46–48]. Biofunctool® consists of a core set of expert-selected indicators, assessing carbon transformation, nutrient cycling and soil structure maintenance. Briefly, three indicators describe the soil nutrient status: available ammonium (NH_4^+) and nitrate (NO_3^-) from soil extraction with 1 M KCl, as well as NO_3^- dynamics with ion exchange membranes ($AEMNO^+$) [49]. Permanganate oxidizable carbon (POXC) [50] was assessed to estimate soil available carbon content. Four indicators evaluated the soil structure: aggregate stability at 0–2 cm depth (AggSurf) and at 2–10 cm depth (AggSoil) [51], water infiltration speed with the Beerkan method [52] and the VESS method (Visual Evaluation of Soil Structure) [53]. Soil moisture (H) and bulk density (BD) were also assessed to describe soil properties. For these analyses, soil samples were collected on the 0–10 cm soil layer, except for VESS that required a sampling at 0–25 cm depth.

DNA Extraction, Amplification and Sequencing

Soil used for the DNA extraction was sampled simultaneously and nearby soil collected for Biofunctool® analysis. DNA extraction was performed using the "FastDNA™ SPIN kit for soil" extraction kit from MP Biomedicals™ following the manufacturer's instructions. Extracted DNA extracted were then sent to the ADNid company (Qualtech groupe, Montpellier, France) for quantification, library preparation and sequencing. The purity and integrity of the DNA recovered was also verified after migration on a 1% agarose gel. Amplicons were generated by PCR amplification using the primer pair 338F/806R specific to the V3-V4 region of the 16S gene [54] and the primer pair FF390/FR1specific to the V7-V8 region of the 18S RNA gene [55]. PCR was conducted on 10 ng of template DNA into 15 µL total mix, submitted to an initial denaturation of 5 min at 95 °C, followed by 35 cycles of 30 s at 95 °C, 1 min at 55 °C and 30 s at 72 °C. A final extension of 30 min at 60 °C was also included to complete the reaction. Amplicons were verified on 1.5% agarose gel, purified using Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano), and quantified by fluorimetry (Quant-iT™ Pico Green DNA Assay Kit). PCR products concentration was adjusted to 10 ng/µL. A second PCR step was performed using specific Illumina adapter, the index and the Illumina overhang adapter primers into 2 × KAPA Hifi Hotstart Ready Mix (Roche Molecular Systems, Inc). A volume of 5 µL of PCR products previously prepared was used into a 50 µL final volume of PCR mix. A 3 mn at 95 °C denaturation step was performed followed by 12 cycles of 30 s at 95 °C, 30 s at 55 °C, 30 s at 72 °C before a 5 mn at 72 °C final extension step. PCR2 products were purified and pooled together at 15 µg/µL in a final library. The library quality was controlled using a fragment analyzer. Sequencing runs, generating 2 × 250 bp, reads were performed on an Illumina MiSeq using V2 chemistry.

Sequence Data Processing

The raw sequencing data were processed using a custom script from the DADA2 pipeline [56], which is designed to resolve amplicon sequence variants (ASVs) [57]. Raw sequences were first demultiplexed by comparing index reads with a key, and paired sequences were trimmed to uniform lengths. Sequences were dereplicated, and the unique sequence pairs were denoised using the *dada* function. Primers and adapters were screened and removed using the *cutadapt* script [58]. Paired-end sequences were merged, and chimeras removed. Taxonomy assignments were determined with the *IDtaxa* function from the *Decipher* R package [59] against the SILVA taxonomic database for both 16S and 18S sequences (release 132) [60]. Sequence data were then manipulated using the phyloseq R package [61]. ASVs affiliated to chloroplasts, mitochondria (16S rRNA gene dataset) were removed in order to keep only microbial sequences. The *isContaminant* function (default parameters) from the *decontam* package was used to identify contaminant sequences from reagents or introduced during the manipulation of the samples [62]. A total of 9 prokaryote ASVs and 12 microeukaryote ASVs were identified as contaminants and removed from the datasets. Samples were rarefied to 5130 and 13,500 reads for 16S and 18S amplicon datasets, respectively, to account for differences in sequencing depth (rarefaction curves are presented in Fig. A1). Two out of the 290 sample did not quite reach the asymptote but were kept because, as rare taxa were further filtered, the contribution did not introduce biais. ASVs present in only one sample and with less than 3 observations in the entire data set were excluded. The taxonomic affiliation of prevalent ASVs (i.e. observed in more than 5% of samples) was refined using nucleotide basic local alignment search tool (BLASTn) analyses on NCBI nr database [63] based on the best hit or the last common ancestor between best hits. The FAPROTAX database [64] was then used to assign prokaryote function to the filtered 16S data, and 51% of sequence variants (representing 36% of the total prokaryote abundance) were assigned to at least one group. We focused on key functions

involved in nutrient cycling (i.e. nitrate denitrification, nitrogen fixation, nitrification, ureolysis), plant organic matter decomposition (i.e. aromatic compound degradation, chitinolysis, cellulolysis, xylanolysis, fermentation) and other key functions related with plant health (i.e. plant pathogens) and affected by soil compaction (i.e. dark sulphur oxidation).

Co-occurrence Network Computation

To further describe structures of microbial communities, cross-domain co-occurrence networks were computed per site for each treatment first and then for each time point using the SPIEC-EASI (SParse InversE Covariance Estimation for Ecological Association Inference) pipeline [65]. Before computation, 16S and 18S ASV datasets were filtered to keep taxa seen in at least 20% of the samples, as network inference requires sufficient data to estimate correlations. We identified hubs (i.e. the most connected ASVs that are potential keystone taxa) based on their node parameters (method developed by Berry and Widder [66]): a low betweenness centrality (lower quantile, < 0.9), and a high closeness centrality (higher quantile, > 0.8), transitivity (higher quantile, > 0.25) and degree (higher quantile, > 0.8). Microbial networks were then described based on key topological parameters: the node mean degree (i.e. connectivity), betweenness and closeness centralities, transitivity and the respective number of prokaryotic and microeukaryotic hubs and total nodes. We used the *igraph* R package [67] to evaluate the topological properties of the co-occurrence network.

Statistical Analysis

All bioinformatic and statistical analyses were performed using R version 4.2.0 [68]. All graphical presentations have been created with the *ggplot* function of the *ggplot2* package [69].

Changes in β-diversity induced by the sites, time, treatments, and their interactions were assessed using a Permutational Multivariate ANalysis Of Variance (hereafter PERMANOVA), implemented in the *adonis* function from the *vegan* package [70] on a Bray–Curtis dissimilarity matrix. To account for non-independence of samples collected from the same blocks, we included blocks as a random effect in the model using the *strata* option. Pairwise group comparisons were then tested using the *pairwise.adonis2* function from the *pairwiseAdonis* package [71]. Multivariate homogeneity of group dispersion was first tested with the *betadisper* function (*vegan* package). Community structures were then presented with principal coordinates analysis (PCoA), and the *envfit* function from the *vegan* package was used to fit significant correlation with edaphic properties onto the ordination. The same procedure was used to describe prokaryote functional profiles.

Processes at play in community assembly were described by partitioning the turnover and nestedness components of β-diversity from communities before perturbation (T0), measured respectively as Simpson pairwise dissimilarity and nestedness-fraction of Sorensen pairwise dissimilarity [72]. Mixed linear models (using the *lmer* function from *lme4* package [73]) were then used to assess the effect of time, sites and treatment on the Sorensen dissimilarity as well as on the true turnover (i.e. change in community composition) and the nestedness (i.e. differences in species assemblages due to one community being a subset of the more diverse community). When required, data were transformed using the bestNormalize R package [74] to meet model assumption needs (homogeneity of variance and residuals normality). To account for non-independence of samples collected from the same blocks, we included blocks as a random effect in the model. Differences between groups were further determined by Tukey Post hoc tests (using the *glht* function of the *multcomp* package [75].

Changes in α-diversity were addressed by calculating Hill numbers [76], which describe the total number of species ($q = 0$), the Shannon–Wiener ($q = 1$) and the Simpson ($q = 2$) diversity indices [77]. High values of q give much more weight to the most abundant species, whereas low values consider the diversity of all species. Hill numbers were computed using the *entropart* R package [78]. Arithmetic mean was used to create diversity profiles for each combination of site, time, and treatment. Mixed linear models (*lmer* function from *lme4* R package [73]) accounting for block as a random effect were used to assess the effects of time, treatment and their interaction on hill numbers at $q = 0$, $q = 1$and $q = 2$. To describe the nature of diversity changes, differential abundances of microbial phyla were calculated (package *DESeq2* [79]) across time, and across treatment at 24 months. Results with an adjusted p value < 0.05 and an absolute log2fold > 0.5 were considered as significant.

In this study, resistance (disturbance rate) was approximated by comparisons between the pre- (i.e. at T0) and post-disturbance (i.e. after 6 months) soil microbial properties, and resilience (recovery rate) refers to the closeness between the final states (i.e. after 24 months) and the initial state (i.e. at T0).

Results

Taxonomic Profiles of Soil Microbial Communities

A total of 743,850 reads from 145 samples were present in the final 16S dataset, and 1,957,500 reads from 145 samples in the final 18S dataset. Thus, 2878 ASVs of 16S and 2401 ASVs of 18S, belonging to 19 prokaryotic phyla and 15 microeukaryotic order, were detected. Prokaryote

communities were primarily composed of Proteobacteria (36% of 16S sequence reads), Firmicutes (24%) and Actinobacteria (23%). Fungi represented 71% of the 18S reads and were primarily composed of Ascomycota (Aspergillaceae representing 13% of the 18S sequence reads, Hypocreaceae 11%%, and Nectriaceae 3.5%).

Site, Treatment and Time Shaping of Soil Microbial Community Structures

A first global PERMANOVA analysis was performed to test for the effects of sites and agroecological practices on both prokaryotic and microeukaryotic community structures. Significant differences were revealed between sites for both prokaryotes and microeukaryotes ($r^2 = 0.16$; $p < 0.001$ and $r^2 = 0.06$; $p < 0.001$ respectively, data not shown). Therefore, we further subset both datasets to separately assess the relative influence of treatments and time in shaping communities in the sandy and clayey sites, respectively.

Overall, PERMANOVA (Tables 1 and A1) revealed a significant and major effect of time (explaining around 30% of thevariance), and a smaller but still significant effect of treatment (explaining around 10% of the variance) in shaping soil communities at both sites. In the clayey site, distinct community structures were observed between treatments with tree residues (R1L1 and R2L1) and without (R0L0 and R0L1). In the sandy site, responses of soil microbial communities also varied between treatments over time (significant interaction effect, PERMANOVA, around 12% variation). There, after 24 months, each treatment has led to a new and distinct prokaryotic and microeukaryotic community. Differences in community structures to T0 (i.e. Sorensen dissimilarity, Fig. 2 and Tables A2 and A3), which reflect community composition resilience, significantly decreased over time for

Table 1 Effects of time, treatments and their interaction on soil prokaryote (16S) and microeukaryote (18S) communities' composition. Significance of the effects was determined by PERMANOVA analysis on Bray–Curtis distance matrix. Blocks were included as a random effect in the model. Significant effects are indicated by asterisks, significance levels: $*p \leq 0.05$; $**p < 0.01$; $***p < 0.001$

		Sandy site					Clay site				
		Df	**SS**	**r^2**	***F***	***p***	**Df**	**SS**	**r^2**	***F***	***p***
16S	Time	4	5.34	0.30	8.83	0.001***	4	4.98	0.28	7.58	0.001***
	Treatment	3	1.70	0.09	3.75	0.001***	3	1.34	0.07	2.72	0.001***
	Time: Treatment	9	2.05	0.11	1.50	0.002**	9	1.70	0.09	1.15	0.06
	Residual	55	8.32	0.47			56	9.20	0.53		
	Total	71	17.43	1.00			72	17.23	1.00		
18S	Time	4	6.86	0.35	12.57	0.001***	4	5.70	0.26	6.95	0.001***
	Treatment	3	2.35	0.12	5.75	0.001***	3	1.95	0.09	3.17	0.001***
	Time: Treatment	9	2.59	0.13	2.11	0.001***	9	2.48	0.11	1.34	0.004**
	Residual	55	7.50	0.38			56	11.47	0.53		
	Total	71	19.32	1.00			72	21.61	1.00		

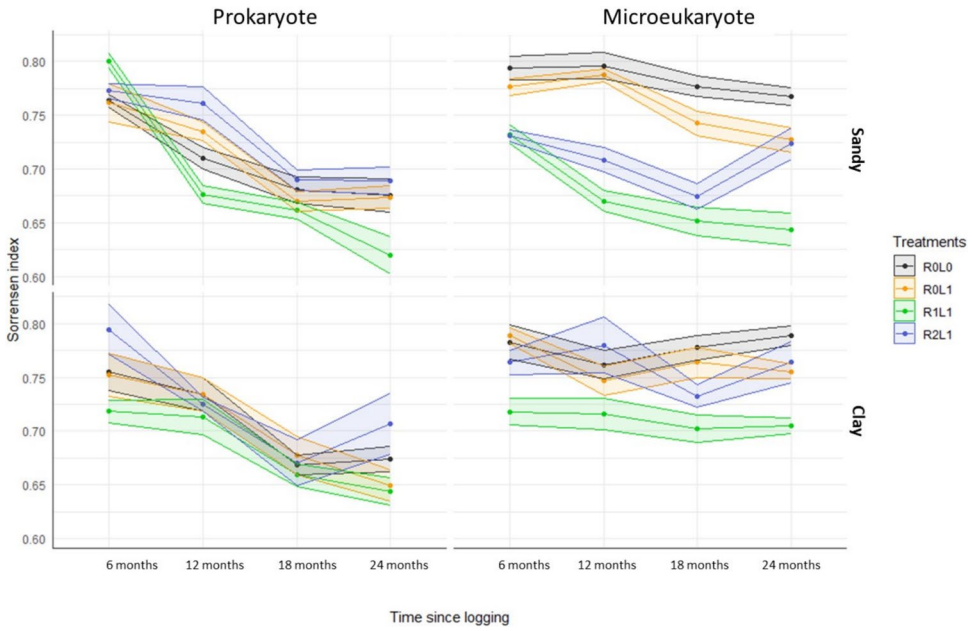

Fig. 2 Sorensen communities' dissimilarity to T0 over time (after 6, 12, 18 and 24 months) as modulated by the different treatments (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues), respectively in the sandy and clay sites. Different letters indicate significant differences over time, all treatment included. Significant differences between treatments are presented in Table A2. Partitioning of communities' dissimilarity into true turnover and nestedness is presented in Fig. A2

Table 2 Networks metrics of cross domain co-occurrence networks computed for each time steps (T0, 6 months, 12 months, 18 months and 24 months) and for each treatment (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues) in the sandy and the clay sites, respectively

Site	Metrics	0 months ($n=4$)	6 months ($n=16$)	12 months ($n=16$)	18 months ($n=16$)	24 months ($n=16$)	R0L0 ($n=16$)	R0L1 ($n=16$)	R1L1 ($n=16$)	R2L1 ($n=16$)
Sandy	16S node	310	277	343	529	435	415	390	480	442
	18S node	309	194	220	480	367	311	319	339	349
	18S/16S node	1.00	0.70	0.64	0.91	0.84	0.75	0.82	0.71	0.79
	Total nodes	619	471	563	1009	802	726	709	819	791
	16S cores	116	84	87	136	106	92	82	77	92
	18S cores	86	58	63	114	94	69	74	66	96
	Total cores	202	142	150	250	200	161	156	143	188
	16S hubs	18	9	11	21	20	16	22	16	10
	18S hubs	8	4	13	20	8	18	18	14	22
	Total hubs	26	13	24	41	28	34	40	30	32
	18S/16S hubs	0.44	0.44	1.18	0.95	0.40	1.13	0.82	0.88	2.20
	Connectivity	14.58	9.12	12.79	21.38	18.61	17.12	16.08	19.36	18.4
	Betweenness	0.002	0.004	0.003	0.001	0.002	0.002	0.002	0.002	0.002
	Closeness	0.36	0.32	0.35	0.37	0.37	0.36	0.36	0.37	0.37
	Transitivity	0.10	0.07	0.09	0.12	0.09	0.10	0.09	0.11	0.09
Clay	16S node	279	363	307	384	320	304	318	322	317
	18S node	325	210	243	237	353	224	276	234	232
	18S/16S node	1.16	0.58	0.79	0.62	1.10	0.74	0.87	0.73	0.73
	Total nodes	604	573	550	621	673	528	594	556	549
	16S cores	130	89	64	116	72	92	75	92	91
	18S cores	106	45	40	68	73	63	50	69	66
	Total cores	236	134	104	184	145	155	125	161	157
	16S hubs	11	12	18	21	15	13	10	10	18
	18S hubs	8	9	6	8	19	15	8	10	15
	Total hubs	19	21	24	29	34	28	18	20	33
	18S/16S hubs	0.73	0.75	0.33	0.38	1.27	1.15	0.80	1.00	0.83
	Connectivity	13.65	11.81	13.10	14.17	15.91	11.59	12.52	12.35	12.55
	Betweenness	0.003	0.003	0.003	0.002	0.002	0.003	0.003	0.003	0.003
	Closeness	0.34	0.34	0.35	0.35	0.36	0.34	0.35	0.35	0.35
	Transitivity	0.13	0.07	0.09	0.08	0.10	0.09	0.08	0.08	0.08

Table 3 Effects of time, treatments and their interaction on prokaryote functions. Significance of the effects was determined by PERMANOVA analysis on Bray–Curtis distance matrix. Blocks were included as a random effect in the model. Significant effects are indicated by asterisks, significance levels: $*p \leq 0.05$; $**p < 0.01$; $***p < 0.001$

	Sandy site					Clay site				
	Df	**SS**	**R2**	**F**	***p***	**Df**	**SS**	**R2**	**F**	***p***
Time	4	1.49	0.58	27.88	0.001***	4	0.95	0.53	22.15	0.001***
Treatment	3	0.18	0.07	4.57	0.001***	3	0.09	0.05	2.96	0.01*
Time: Treatment	9	0.12	0.04	1.01	0.50	9	0.11	0.06	1.19	0.26
Residual	55	0.73	0.29			56	0.60	0.34		
Total	71	2.54	1.00			72	1.76	1.00		

prokaryotes at both sites, a trend much less pronounced for microeukaryotes, particularly in the clayey site where the observed decrease was not significant. The treatment with legume cover combined with fine residues (R1L1) induced a higher resilience for microeukaryotes at both sites, and for prokaryotes only in the sandy site. To further describe assembly processes at play over time after tree logging, Sorensen dissimilarity was partitioned into true turnover and nestedness turnover, i.e. change in community composition (i.e. in the identity of species between the two communities), and nestedness (i.e. differences in species assemblages due to one community being a subset of the more diverse community Fig. A2, Tables A4 and A5). At both sites and for both 16S and 18S datasets, the $\beta_{Nestedness/Sorensen}$ was continuously lower than 0.5 after rubber clear-cutting, indicating a prominent turnover effect in driving communities structuration. As for Sorensen dissimilarity, turnover was mainly modulated over time for prokaryotes, while the different treatments mainly drove microeukaryotes' turnover. Treatments had no effect on nestedness, while time significantly impacted that of prokaryote at both sites, and of microeukaryote community only in the clayey site.

Principal coordinates analysis of communities dissimilarity graphically reflects the shifts in community composition induced after clear-cutting between T0 and 6 months (Fig. 3, Table A6). Communities at T0 were rather similar and then became more heterogeneous (dispersed) after soil perturbation. Resilience of communities was also perceptible as successive communities progressively became closer to T0 after 6, 12, 18 and 24 months, particularly evident for prokaryotes at both sites. To further describe the drivers of microbial community structuration, the influence of ten edaphic properties (i.e. soil ammonium, soil nitrate, nitrate plant availability, labile carbon, aggregate stability at two depths, water infiltration, soil structure, moisture, bulk density) on microbial patterns was studied. Most soil properties were found to be significantly correlated with microbial community structures, highlighting the close link between soil conditions and community assembly. At both sites, contrasting soil structures and humidity (higher soil aggregate stability and moisture at T0) and nutrient content (lower NH_4^+ and NO_3^- at T0) discriminated community composition before and after tree-logging. Additionally, the intensity of soil structuring variables strongly differed between sites for prokaryote communities. In the sandy site, soil aggregate stability was the most structuring property, followed by NH_4^+, water infiltration, bulk density and NO_3^-. In the clayey site, soil moisture was the most structuring factor, followed by NH_4^+ content and water infiltration. For microeukaryotes, similar patterns were observed at both sites, communities were mainly structured by NH_4^+, followed by soil moisture and aggregate stability, although the influence of these environmental filters was even more pronounced in the sandy site.

Co-occurrence Networks for Describing Microbial Resistance and Resilience Dynamics

For each time point and at each site, a cross-domain co-occurrence network was computed (Fig. 4 and Fig. A3 and A4, Table 2). Tree clear-cutting deeply impacted microbial networks. We observed a net reduction in the total number of nodes and of core taxa, along with a decrease in networks connectivity, closeness centrality and transitivity, and an increase in betweenness centrality at both sites. However, the frequency of node degrees, betweenness and closeness centralities clearly indicated less robust network structures at 6 months in the sandy site. The lower 18S/16S node and hub ratios, and a net gain in 16S nodes, highlighted a higher sensitivity of microeukaryotes in the sandy site. The resilience of communities was noticeable by a gradual recovery of initial properties over time. Interestingly, a faster recovery of initial topological properties occurred in the sandy site, where connectivity even exceeded that of T0 at 18 months. This trend was observed together with a net increase in 18S/16S hub ratio after 18 months, suggesting a major role of microeukaryotes in microbiome resilience in the sandy site.

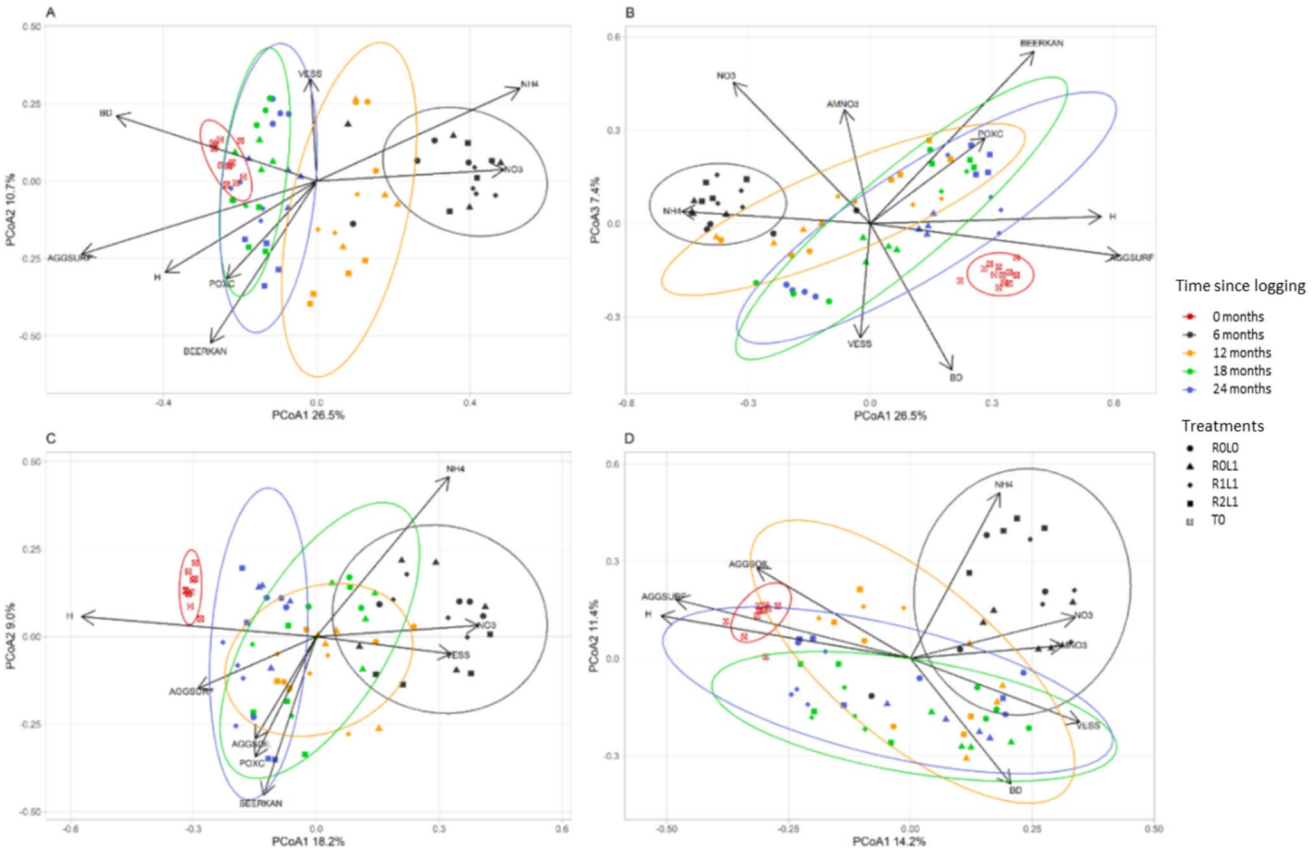

Fig. 3 Principal coordinate analysis based on Bray–Curtis dissimilarity matrices for prokaryote (16S, panel **A** and **C**) and microeukaryote (18S, panel **B** and **D**) communities as shaped by treatments (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues, treatments are illustrated by different symbols) over time (at T0, and then 6, 12, 18 and 24 months after tree-logging, time illustrated by different colours). Panels **A** and **B** show soil communities profiles in the sandy site, panels **C** and **D** stand for the clayey site. Effects of time, treatment and their interaction on communities are presented in Table 1 and A1. Edaphic variables (i.e. NH_4^+, NO_3^-, AEMNO.$^+$, POXC, AggSurf, AggSoil, Beerkan, VESS, moisture, bulk density) shaping soil microbial communities are plotted onto the ordination spaces (Table A6)

Network topological properties were also computed to characterize the effect of the different treatments on soil communities. At both sites, the 18S/16S node ratio favored microeukaryote taxa where only legumes were grown (R0L1), while networks from the control treatments (R0L0) had fewer 18S nodes. The network derived from the treatment involving legume and fine residues (R1L1) was characterized by more 16S nodes. Differences in network topology induced by treatments were more pronounced in the sandy site. There, the two treatments including fine and all logging residues with legume (R1L1 and R2L1) exhibited high connectivity. The highest 18S/16S hub ratio was found in microbial network from soils treated with legume and all residues (R2L1). This trend did not reflect the 18S/16S network nodes ratio, suggesting a key role of microeukaryotes in this agroecological practice in a sandy pedological context. In the clayey site, the effect of treatment on networks properties was less perceptible.

Drivers of Soil microbial α-Diversity and Taxonomic Composition

Microbial α-diversity was studied using Hills number, and the effect of time and treatment was further tested on the diversity profiles, in each site (Fig. 5, Tables A7 and A8). The annotations $q = 0$, $q = 1$ and $q = 2$ respectively denote species richness, Shannon–Wiener diversity, and the distribution (Simpson) of individuals within each species. Diversity loss between T0 and 6 months illustrates the resistance of communities to the tree replacement process. Prokaryote diversity was resistant to soil perturbation, as no changes were observed between T0 and 6 months (except for q0 in specific treatments from the clayey site). Microeukaryote diversity was less resistant

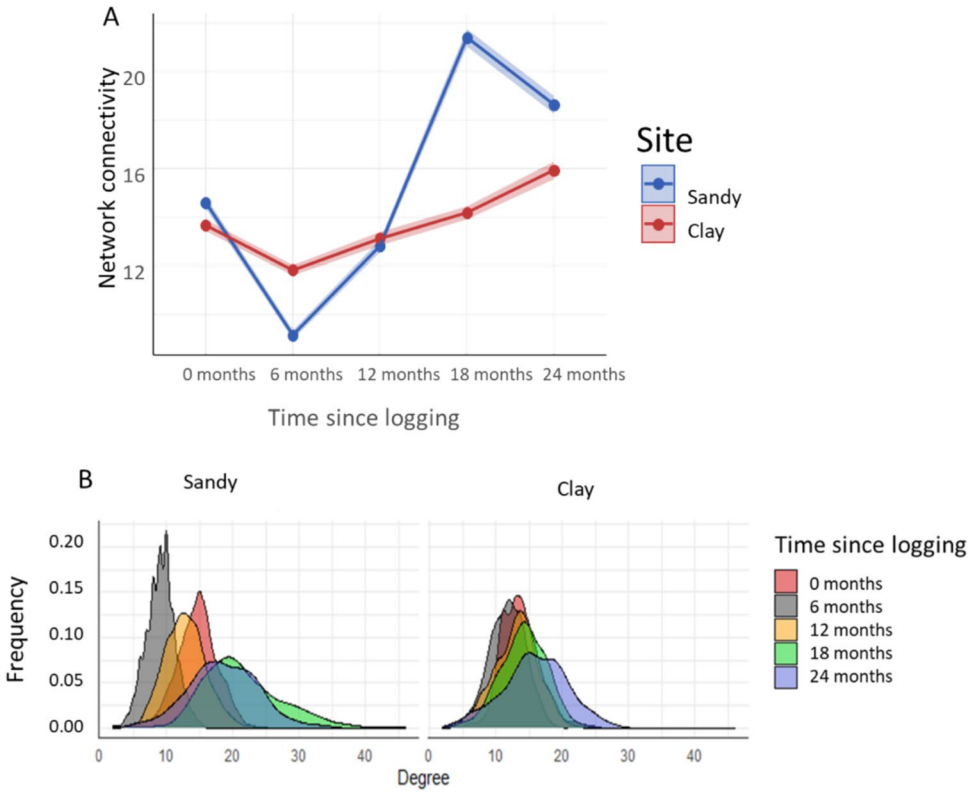

Fig. 4 Connectivity recovery of soil microbial networks after rubber tree clear-cutting. Panel **A** shows cross domain co-occurrence network connectivity (mean nodes degree) over time (at T0, and then 6, 12, 18 and 24 months after tree-logging) respectively in the sandy (blue line) and clay (red line) sites. All treatments are merged. 95% confidence intervals surround curves. Panel **B** shows density plots of node degrees for each network computed over time in the sandy (left panel) and clay (right panel) sites. Networks' properties are further described in Table 2 and Fig. A3

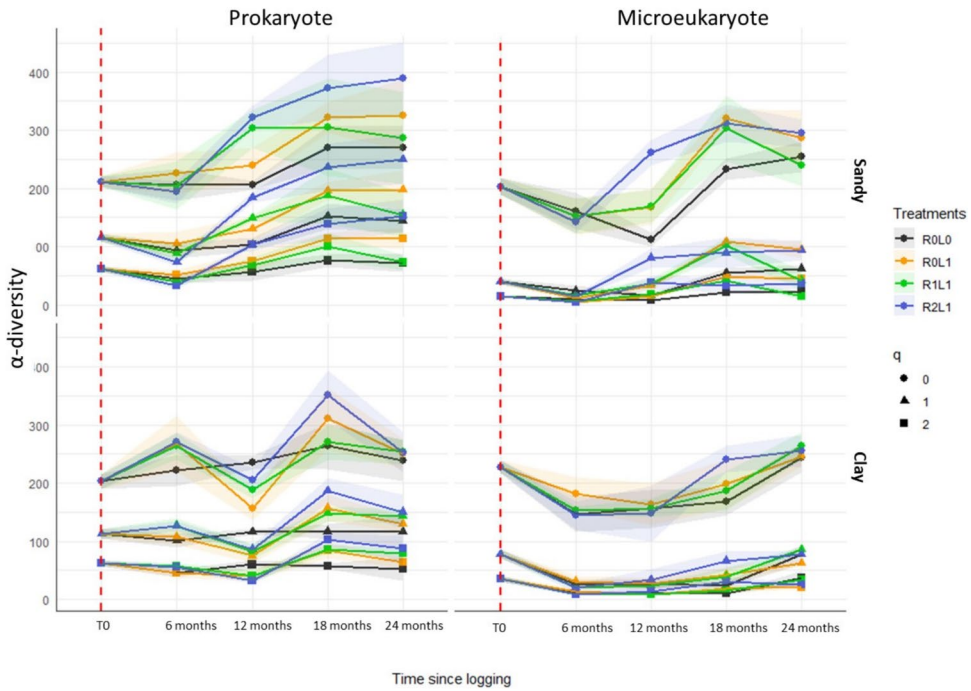

Fig. 5 α-diversity profiles of prokaryote (16S) and microeukaryote (18S) communities as illustrated by Hill numbers for q ranging from 0 and 2 (q = 0 indicates total species richness, q = 1 indicates an index proportional to Shannon diversity and q = 2 indicates the logarithm of Simpson reciprocal diversity). Different colours stands for the different treatments (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues), T0 = Reference levels (Before tree logging). Effects of time, treatment and their interaction on functional communities are presented in Table A7 and A8

than prokaryote communities, as diversity losses were observed at both sites. Time significantly impacted the richness, Shannon diversity, and distribution of prokaryotic and microeukaryotic taxa at both sites, suggesting that tree-logging induced changes in the occurrence of both rare and prevalent microbial taxa.

In the clayey site, prokaryote richness varied over time differently according to the various treatments (interaction

effect). Surprisingly, 16S diversity from every treatment except control was higher at 6 months than at T0. Differences among treatments arose 18 months after perturbation, but then blurred after 24 months. For microeukaryotes, cover treatments did not modulate the impact of soil perturbation on diversity levels. Only time did, diversity indexes being lower at 6 months than at T0, then increasing towards values near the initial state for q1 and q2, and even higher for q0.

In the sandy site, the effect of treatment on microbial α-diversity was more pronounced. Prokaryote communities from all treatments had similar richness at T0 and 6 months, then, 24 months after replanting, richness levels were distinct among treatments, with the highest in soil covered with legume and all residues (R2L1). With this treatment, prokaryote q1 tended to be generally higher than with other treatments. Hill numbers q1 and q2, which consider the most abundant 16S taxa, also increased over time in the sandy site. For microeukaryotes, total richness dropped after 6 months and then exceeded its initial level after 24 months, not being affected by the different treatments. However, q1 and q2 which consider the most prevalent taxa, were significantly influenced by treatments, being higher than at T0 in soil covered with legume only (R0L1), and with legume and all residues (R2L1), 24 months after tree replanting.

Differential abundance testing confirmed that 9 out of the 19 prokaryotic phyla and 53 out of the 115 fungal families were highly sensitive to the tree replanting process (Fig. 6). The soil perturbation reduced the abundance of

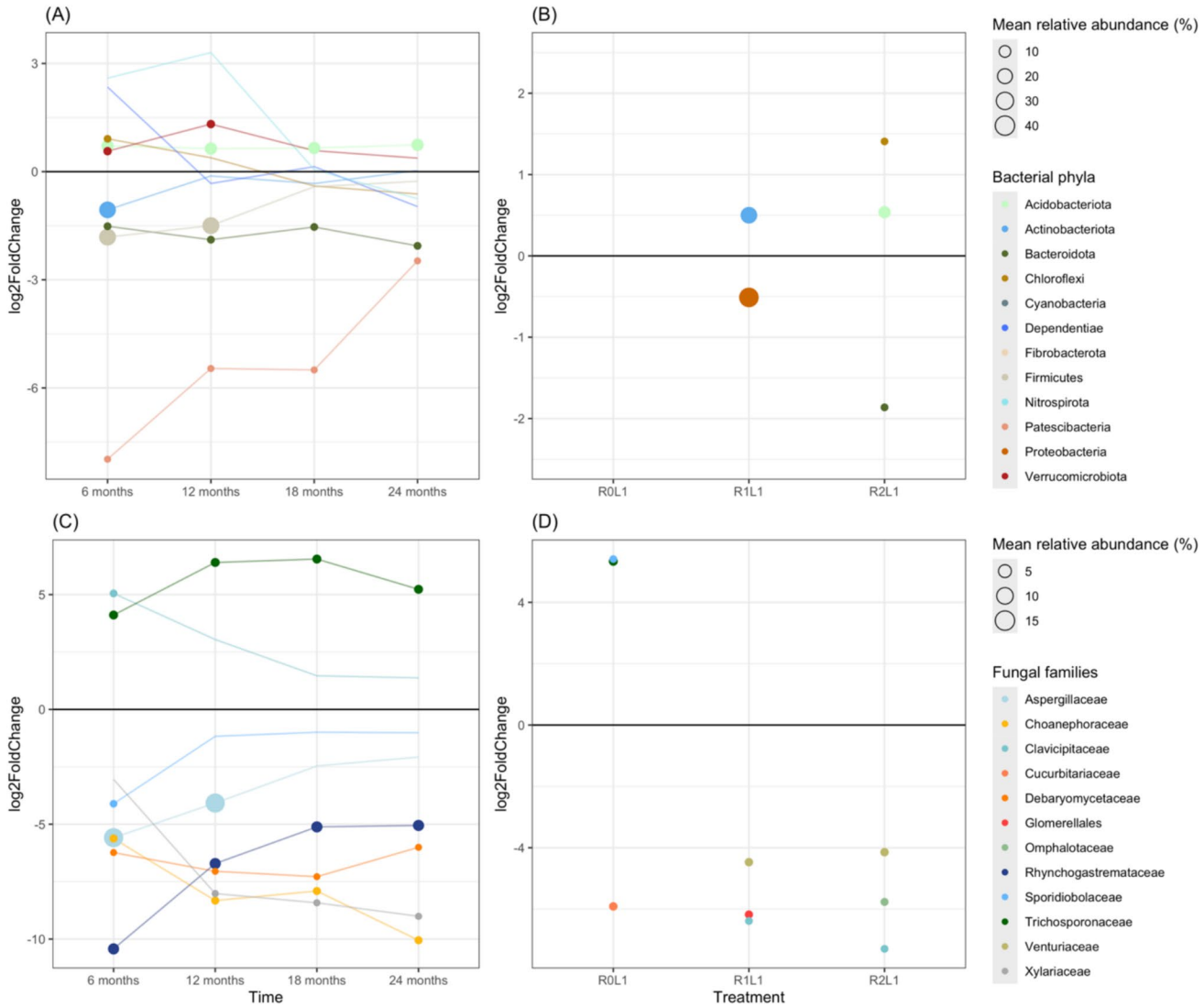

Fig. 6 Differential abundance of bacterial phyla (panels **A** and **B**) and fungal families (panels **C** and **D**) as influenced by time (panel **A** and **C**) and treatments (**B** and **D**). Only results with an adjusted p value < 0.05 and an absolute L2FC > 0.5 are presented for prokaryote, and with an adjusted p value < 0.05 and an absolute L2FC > 4 for microeukaryote. Reference levels are respectively T0 for time and R0L0 for treatment

Actinobacteriota, *Firmicutes*, *Bacteroidota* and *Patescibacteria*, while it stimulated the one of *Acidobacteriota*, *Chloroflexi*, *Verrucomicrobiota*, *Nitrospirot*a and *Dependentiae*. Then, all sensitive bacterial phyla tended towards a resilient trajectory after 24 months. The fungal families most affected by the tree replanting process were Choanephoraceae, Debaryomycetaceae, Rhynchogastremataceae, Sporiodiobolaceae, Trichosporonaceae and Xylariaceae. Aspergillaceae and Clavicipitaceae families abundances increased with soil perturbation. However, not all taxa followed a resilient trajectory, even after 2 years.

Differential abundance revealed the sensitivity of certain microbial phyla to legume growth and residues input, compared to the control R0L0 (Fig. 6). Treatment with legume only favored *Tricosporonaceae* and Sporidiobolaceae and reduced *Cucurbitariaceae*. Legume and fine residues (R1L1) increased the abundances of *Actinobacteriota* and *Cyanobacteria*, and reduced the abundance of *Proteobacteria*, *Clavicipitaceae*, *Glomerellales* and *Venturiaceae*. The input of coarse residues (R2L1) stimulated the abundance of *Chloroflexi* and *Acidobacteriota*, while reducing the abundances of *Bacteroidota*, *Clavicipitaceae*, *Omphalotaceae* and *Venturiaceae*.

Resistance and Resilience of Soil Prokaryote Functioning

Prokaryotes functions were determined by assigning metabolic pathways using the FAPROTAX database on identified taxa, and the effects of time and treatment on functional communities were further analyzed using PERMANOVA analysis (Fig. 7, Tables 3 and A9 and A10). In the two sites, PERMANOVA results indicated a significant treatment effect with a low variation (r^2 ranged from 5 to 7%), while time was the most structuring driver, responsible for more than 50% of the total variation in microbial functions. The effect of treatments on functional profiles was not modulated over time (no interaction effect). PCoA described a functional shift between T0 and 6 months after tree-logging, and then a gradual return towards the initial state at both sites. To further describe how functional communities were impacted, key functions (i.e. nitrate denitrification, nitrogen fixation, nitrification, cellulolysis, dark sulfur oxidation, ureolysis, aromatic compound degradation, plant pathogen, chitinolysis) were projected onto the ordination space. The congruence towards T0 was mainly associated with an increase in denitrification potential ($r^2 > 0.9$ at both sites). Three N-related function (i.e. nitrogen fixation, denitrification and nitrification) pointed away from communities at 6 months, suggesting that these communities were less involved in N cycle. In the sandy site, a higher dark sulfur oxidation potential, which mostly relies on anoxygenic taxa, significantly discriminated functional profile communities at 6 months, while 6 months communities in the clayey site seemed mostly associated with higher ureolysis and aromatic compound degradation potentials. To compare patterns in prokaryote functional resistance and resilience after tree replanting, we computed functional Bray–Curtis distance

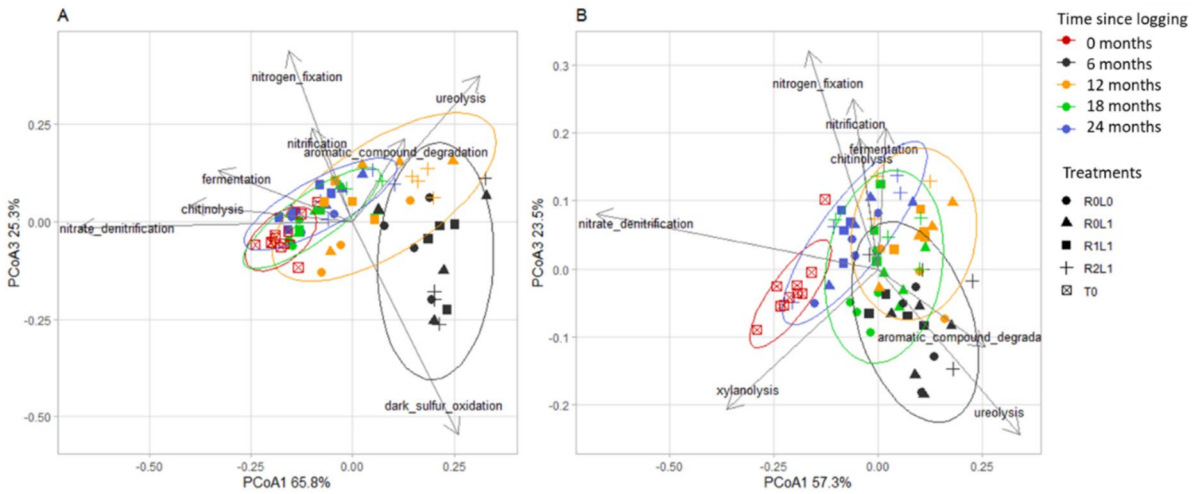

Fig. 7 Principal coordinate analysis of prokaryotic (16S) functional profiles based on a Bray–Curtis dissimilarity matrix derived from functional assignment against the FAPROTAX database, as shaped by treatments (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues, treatments are illustrated by different symbols) over time (at T0, and then 6, 12, 18 and 24 months after tree-logging, time illustrated by different colours). Panels **A** and **B** respectively stand for sandy and clayey sites. Effects of time, treatment and their interaction on functional communities are presented in Table 3 and A9. Functions significantly shaping projected profiles (i.e. aromatic compound degradation, chitinolysis, xylanolysis, fermentation dark sulphur oxidation) are plotted onto the ordination spaces (Table A10)

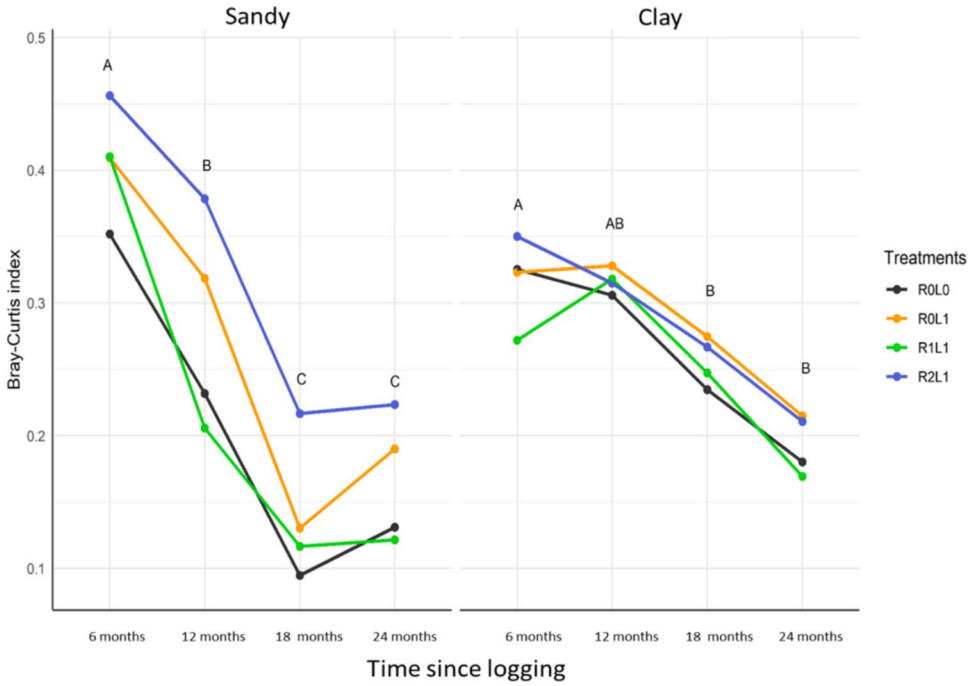

Fig. 8 Functional dissimilarity of prokaryote to communities at T0, over time (after 6, 12, 18 and 24 months) and for the different treatments (R0L0 = control, R0L1 = only legumes, R1L1 = legumes and fine residues, R2L1 = legumes and all residues). Effects of time, treatment, and their interaction are presented in Table A11 and A12. Different letters indicate significant differences over time, all treatment included

to T0 and thus studied the effect of time and treatment on functional resilience (Fig. 8, Tables A11 and A12). At both sites, time had a significant effect on prokaryote functional distance to T0. We found a greater difference in functional communities between T0 and 6 months in the sandy than the clayey site, which again attests of a higher sensitivity of functional communities in the sandy site. After 24 months, the community from the sandy site also got closer to the initial state than communities from the clayey site, suggesting better functional resilience. Interestingly, treatment had an effect on functional distance to T0 only in the sandy site, where the treatment with legume and all residues (R2L1) led functional communities towards an equilibrium farther from the initial state.

Discussion

Our study, based on a 24-month investigation of soil microbiota in two different experimental fields with distinct edaphic contexts, quantified and analyzed the resistance and resilience of prokaryotic and microeukaryotic communities following a disturbance induced by the tree replanting process with regards to different cover treatments (i.e. the use of logging residues and legume cover). Prokaryotes were generally more resistant to soil perturbation, while microeukaryotic communities were more affected. Prokaryotic recovery was also faster than that of microeukaryotes, the latter being deeply influenced by the cover treatments. These specific reassembly dynamics were particularly pronounced in the sandy site.

Resistance of the Soil Microbiota to the Rubber Tree Replanting Process

The rubber tree replanting process induced a sudden and deep reassembly of the soil microbiota at both sites. Indeed, 6 months after soil perturbations, net changes in microbial community structure, taxonomy and functioning, together with losses in network connectivity, were observed. The rubber tree replanting resulted in a shift in the taxonomic composition of both prokaryotic and microeukaryotic communities in both clayey and sandy pedological contexts after 6 months. We showed that communities at 6 months were concomitant with low soil moisture, weak aggregate stabilities, and high soil NH_4^+ and NO_3^- contents. Wheeling with a heavy agricultural vehicle has been shown to increase bulk density in the topsoil and to substantially reduce air permeability and gas diffusion [80], which can thus lead to anoxic conditions [14]. In addition, the removal of tree vegetation and subsequent opening of the canopy might also have led to shifts in soil microbial populations by altering the feedback system between plants and soil and changing soil microclimate [81, 82]. Soil perturbations promoted microbial taxa with lifestyle adapted to the observed harsh conditions (i.e. reduced moisture and soil compaction) such as facultative aerobic (i.e. *Nitrospirota* [83], parasites (i.e. *Dependentiae* [84] and *Clavicipitaceae* [85]) or competitive bacteria (i.e. *Acidobacteria* [86]). Soil compaction can impact microbial metabolic activities by limiting or interrupting aerobic processes, such as nitrification and mineralisation [87]. For instance, we observed that bacterial communities at 6 months were less susceptible to performing

N-related functions (i.e. nitrogen fixation, nitrification, and denitrification). The observed functional changes could be explained by soil compaction, which shifts bacterial communities towards anaerobic bacteria [17, 88], that might have inhibited N fixation and nitrification, and thus denitrification by substrate provision interruption.

For prokaryote specifically, diversity levels of abundant taxa have not fallen after the tree replanting process and were sometimes even higher 6 months after soil perturbation. Similar findings have been reported by Hartmann and colleagues [17] in response to forest soils' compaction. Authors found an increase in bacterial diversity that they attributed to taxa with low oxygen availability and capable of anaerobic respiration in compacted soils. Conversely, microeukaryotic diversity was less resistant to the tree replanting-induced disturbances at both sites. Indeed, fungi are known to be particularly sensitive to soil compaction induced by deforestation [89]. This can partly be explained by the generally higher sensitivity of microeukaryotes to low oxygen availability induced by soil compaction [14] and other studies pointed such differential response to compaction [17]. In our study, observations derived from co-occurrence network modelling also support the hypothesis of less resistant microeukaryote communities to the tree replanting process. At both sites, a net loss in network connectivity was observed, and this complexity reduction was mainly imputable to a loss of 18S nodes. While fungal network sensitivity to soil labor has been previously demonstrated [90], this is, to our knowledge, the first study to report lower resistance of the microeukaryote network over prokaryotes to soil compaction.

Microbial Resilience Was Modulated by Soil Cover Treatments

We observed that cover practices had only a weak impact on the resistance (observed 6 months after perturbation) of microbial communities to the tree replanting process. This was anticipated as neither legume growth nor tree residue decomposition had really started yet. The treatment effects were noticeable later in the resilience trajectory and varied between prokaryotes and microeukaryotes, with microeukaryotes being more responsive to logging residue inputs. This particular sensitivity may be related to the high potential of mycelia to actively colonize plant residues [91] or to the niche modification induced by organisms from the tree phyllosphere that are inoculated with tree residues. These organisms are the early colonizers and decomposers of dead plant biomass and might play a key role in microbial succession during organic matter decomposition [92]. This latter hypothesis is supported in our study by a higher complexity in networks from treatments that include tree residues.

Soil properties improvement (higher C and N contents) in rubber-based diversified systems compared to monoculture was also evidenced in the study by [93]. Microbial communities and the ratio between fungal and bacterial biomass are strongly influenced by the C/N ratio [94]. Organic matter inputs used in our study had distinct C/N ratios (i.e. legumes only < legume with fine residues < legume with all residues) that we expected to affect soil microbial successions and community resilience. *Pueraria phaseoloides* is able to recruit a specific cohort of arbuscular mycorrhizal fungi (AMF) communities [95], and bacterial communities are dependent on mycorrhizae for their carbon resources [96]. One could expect that legume cover should thus be an efficient strategy for soil properties recovery. However, in this study, the treatment involving only legume cover has led to intermediate resilience trajectories. An explanation could be that hampered N metabolism due to the anoxic soil conditions brought on by soil compaction [80] has partially interrupted microbial successions.

The treatment combining fine tree residues and legume cover has led to a better (though still incomplete) recovery of the Sorensen index at both sites for microeukaryotes and in the sandy site for prokaryotes after 24 months. The high C/N ratio of woody debris is well known to benefit to the fungal biomass. Indeed, fungi are the main decomposers of tree residues because of their ability to catabolize woody complex carbon molecules (i.e. cellulose and lignin) with the nutrient-mineralizing extracellular enzymes they produce and their hyphal extension capabilities [97]. Carbon organic matter combined with sufficient N input might have favored the hyphal production. The latter is responsible for the formation of macro-aggregates that host most microbiological activities [98]. It is thus likely that tree residues, by indirectly improving soil structure, favored microbial activities and speed up their succession.

In the sandy site specifically, the treatment combining all tree residues with legume cover harbored the highest prokaryotic and microeukaryotic α-diversity levels 24 months after perturbation. This result is surprising as C:N stoichiometry has been globally shown to have some negative effects on microbial alpha diversity [99]. It is possible that the high microbial richness observed after 24 months hides a diversity decline in the following months. Indeed, Dossa et al. [100] observed fungal succession in decomposing woody debris across a tropical forest. They showed a decline in fungal diversity after 18 months that they explained by increasing competition through time for remaining resources. In this context, care needs to be taken in drawing any conclusions about a beneficial effect of this specific treatment; a longer diachronic study should provide more insights.

A Leading Influence of Pedological Context in Driving Community Dynamics?

The field site was the predominant driver of microbial recovery dynamics. The two studied field sites are subjected to a similar climate but harbor soil key textural and chemical differences. Briefly, both soils have acidic pH. The clayey site is more finely textured (clayey loam with 23% clay) than the sandy site (sandy loam with 10% clay) and is characterized by a higher N and C contents and lower available phosphorus, as fully described in Perron et al. [31, 37]. Soil texture, a well-known driver of microbial diversity [101], may explain the differences in microbial community structure across the two sites that already existed before the establishment of the experiment.

Sandy soils exhibited less resistance but a better resilience than clayey soils to the soil tillage and compaction induced by the tree replantation process. This is not fully in line with Hartmann and colleagues [17], who observed less resistance and resilience in clayey than in sandy compacted soils. In their study, they exclusively focused on the effect of soil compaction, which contrasts with the subsoiling and windrowing that our studied soils underwent. We observed that the lowest resistance of sandy soils could be largely attributed to microeukaryotes. Fungi may better colonize sand-associated large pores, and recent studies have pointed out that fungal diversity was consistently promoted in coarse-textured soils [102]. Altogether, this suggests that the particular sensitivity of sandy soils may thus be the consequence of soil tillage and successive compaction, known to disrupt the mycorrhizal network [103], and to particularly reduce fungal biomass [104].

Due to its small particle size (< 2 µm), clay provides the largest surface area to bind organic material [105]. Thus, soil organic matter associated with clay is more stabilized by chemical or physico-chemical binding to soil minerals [106, 107], which could also partly explain the better resistance of the communities in the clayey site. A minor effect of treatment was observed on shaping microbial community structures and diversities in the clayey site. However, the effect of treatment varied over time for both prokaryotic and microeukaryotic communities in the sandy site, where, after 24 months, each treatment has led to new and distinct communities. It describes a study conducted by Neumann et al. [108], emphasizing the microbial responsiveness to organic matter inputs across different particle sizes, with a specific focus on the protective capacity of clay fractions against changes. The buffering effect of clay particles size could explain why we did not observe a clear effect of the various treatments in the clayey site.

Our results suggest that differential impact of soil perturbation on the two textures might be responsible for the different resistance and resilience trajectories [109]. However, as the amount of applied organic matter differed between the two sites and because only two sites were compared here, a proper dedicated empirical study should be conducted in order to validate such hypothesis.

Conclusion

Our diachronic monitoring emphasized a predominant role of the pedologic context in shaping the soil microbiome responses to rubber trees clear-cutting. The impact of tree-logging on soil communities was much more pronounced in the sandy site, particularly for microeukaryotes. The significant importance of soil texture in microbial response dynamics draws attention to the need to consider soil pedological context when designing agroecological practices that sustain soil functioning.

The practice involving a combination of logging residues and legume cover in rubber plantation has shown certain beneficial effects on the resilience of microbial communities after tree-logging and associated soil perturbation in the sandy site. It thus appears as a promising agroecological practice that should be further studied.

Despite the statistical power of our sampling design not allowing a deep description of the effect of treatments across time on microbial networks, cross-domain co-occurrence network modelling provided useful insights into the soil microbiome resistance and resilience. It not only supported the trend observed with alpha and beta diversities, but also highlighted the key role of microeukaryotes in the resilience dynamic. We argue that this tool should be more widely used to describe microbial community dynamics, and that microbial ecologists should thus anticipate the number of replicates required for its efficient use.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00248-025-02506-3.

Acknowledgements We particularly thank the managers of the SAPH and SOGB plantations for providing all facilities and labour during the sampling period. We thank Daouda Kouassi and Antoine Manizan at SOGB and Soumahoro Mouman, Angelica N'chot, Richmond Konan and Jean-Marc Toto at SAPH for their great help in the supervision of the fieldwork.

Author Contributions K. A. Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Visualization, Writing original draft, Writing, review & editing. P. C. Formal analysis, Writing, Methodology, Visualization, Writing, review & editing. T. P. Data curation, Investigation, Writing – review & editing. Y.K. Validation, Writing, review & editing, Supervision. F. G. Methodology, Conceptualization, Project administration, Funding acquisition. A B. Conceptualization, Methodology, Validation, Writing, review & editing, Supervision, Project administration. C. B. Formal analysis, Writing, Methodology, Visualization, Writing, review & editing, Supervision.

Funding This research was financially supported by the "Institut Français du Caoutchouc" (IFC), MICHELIN, SIPH and SOCFIN Companies (PFI: 7250A1, Centre de coût: 210F2CVNB). Additional funding was provided by the IRD PhD Grant Program (ARTS, 2019).

Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of Interest The authors declare no competing interests.

References

1. Bhatia CR (2008) Role of microbial diversity for soil, health and plant nutrition. In: Nautiyal CS, Dion P (eds) Molecular mechanisms of plant and microbe coexistence. Springer, Berlin, Heidelberg, pp 53–74
2. Zhang Q-C, Shamsi IH, Xu D-T et al (2012) Chemical fertilizer and organic manure inputs in soil exhibit a vice versa pattern of microbial community structure. Appl Soil Ecol 57:1–8. https://doi.org/10.1016/j.apsoil.2012.02.012
3. Daynes CN, Field DJ, Saleeba JA et al (2013) Development and stabilisation of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi and plant roots. Soil Biol Biochem 57:683–694. https://doi.org/10.1016/j.soilbio.2012.09.020
4. Mooshammer M, Wanek W, Hämmerle I et al (2014) Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling. Nat Commun 5:3694. https://doi.org/10.1038/ncomms4694
5. Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856. https://doi.org/10.1126/science.1188321
6. Manzoni S, Schimel JP, Porporato A (2012) Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93:930–938. https://doi.org/10.1890/11-0026.1
7. Moghimian N, Hosseini SM, Kooch Y, Darki BZ (2017) Impacts of changes in land use/cover on soil microbial and enzyme activities. CATENA 157:407–414. https://doi.org/10.1016/j.catena.2017.06.003
8. Tian Q, Taniguchi T, Shi W-Y et al (2017) Land-use types and soil chemical properties influence soil microbial communities in the semiarid Loess Plateau region in China. Sci Rep 7:45289. https://doi.org/10.1038/srep45289
9. Nottingham AT, Bååth E, Reischke S et al (2019) Adaptation of soil microbial growth to temperature: using a tropical elevation gradient to predict future changes. Glob Change Biol 25:827–838. https://doi.org/10.1111/gcb.14502
10. Kennedy AC, Stubbs TL, Hall J (2006) Soil microbial communities as indicators of soil health. Ann Arid Zone 45:287–308
11. Kraut-Cohen J, Zolti A, Shaltiel-Harpaz L et al (2020) Effects of tillage practices on soil microbiome and agricultural parameters. Sci Total Environ 705:135791. https://doi.org/10.1016/j.scitotenv.2019.135791
12. Srour AY, Ammar HA, Subedi A et al (2020) Microbial communities associated with long-term tillage and fertility treatments in a corn-soybean cropping system. Front Microbiol 11
13. Li S, Huang X, Lang X et al (2020) Effect of selective logging on soil microbial communities in a Pinus yunnanensis forest. Land Degrad Dev 31:2268–2280. https://doi.org/10.1002/ldr.3600
14. Schnurr-Pütz S, Bååth E, Guggenberger G et al (2006) Compaction of forest soil by logging machinery favours occurrence of prokaryotes. FEMS Microbiol Ecol 58:503–516. https://doi.org/10.1111/j.1574-6941.2006.00175.x
15. Frey B, Kremer J, Rüdt A et al (2009) Compaction of forest soils with heavy logging machinery affects soil bacterial community structure. European Journal of Soil Biology 45:312–320. https://doi.org/10.1016/j.ejsobi.2009.05.006
16. Griffiths BS, Philippot L (2013) Insights into the resistance and resilience of the soil microbial community. FEMS Microbiol Rev 37:112–129. https://doi.org/10.1111/j.1574-6976.2012.00343.x
17. Hartmann M, Niklaus PA, Zimmermann S et al (2014) Resistance and resilience of the forest soil microbiome to logging-associated compaction. ISME J 8:226–244. https://doi.org/10.1038/ismej.2013.141
18. de Menezes AB, Richardson AE, Thrall PH (2017) Linking fungal–bacterial co-occurrences to soil ecosystem function. Curr Opin Microbiol 37:135–141. https://doi.org/10.1016/j.mib.2017.06.006
19. Manlay RJ, Feller C, Swift MJ (2007) Historical evolution of soil organic matter concepts and their relationships with the fertility and sustainability of cropping systems. Agric Ecosyst Environ 119:217–233. https://doi.org/10.1016/j.agee.2006.07.011
20. Joniec J (2018) Enzymatic activity as an indicator of regeneration processes in degraded soil reclaimed with various types of waste. Int J Environ Sci Technol 15:2241–2252. https://doi.org/10.1007/s13762-017-1602-x
21. Fierer N (2017) Embracing the unknown: disentangling the complexities of the soil microbiome. Nat Rev Microbiol 15:579–590. https://doi.org/10.1038/nrmicro.2017.87
22. Sheng Y, Wang H, Wang M et al (2020) Effects of soil texture on the growth of young apple trees and soil microbial community structure under replanted conditions. Hortic Plant J 6:123–131. https://doi.org/10.1016/j.hpj.2020.04.003
23. Scott Bechtold J, Naiman RJ (2006) Soil texture and nitrogen mineralization potential across a riparian toposequence in a semi-arid savanna. Soil Biol Biochem 38:1325–1333. https://doi.org/10.1016/j.soilbio.2005.09.028
24. Ahrends A, Hollingsworth PM, Ziegler AD et al (2015) Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. Glob Environ Change 34:48–58. https://doi.org/10.1016/j.gloenvcha.2015.06.002
25. Aratrakorn S, Thunhikorn S, Donald PF (2006) Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. Bird Con Int 16:71. https://doi.org/10.1017/S0959270906000062
26. Xiao HF, Tian YH, Zhou HP et al (2014) Intensive rubber cultivation degrades soil nematode communities in Xishuangbanna, southwest China. Soil Biol Biochem 76:161–169. https://doi.org/10.1016/j.soilbio.2014.05.012
27. Zheng G, Li S, Yang X (2015) Spider diversity in canopies of Xishuangbanna rainforest (China) indicates an

alarming juggernaut effect of rubber plantations. For Ecol Manag 338:200–207. https://doi.org/10.1016/j.foreco.2014.11.031
28. Singh D, Slik JWF, Jeon Y-S et al (2019) Tropical forest conversion to rubber plantation affects soil micro- & mesofaunal community & diversity. Sci Rep 9:5893. https://doi.org/10.1038/s41598-019-42333-4
29. Chambon B, Ruf F, Kongmanee C, Angthong S (2016) Can the cocoa cycle model explain the continuous growth of the rubber (Hevea brasiliensis) sector for more than a century in Thailand? J Rural Stud 44:187–197. https://doi.org/10.1016/j.jrurstud.2016.02.003
30. Peerawat M, Blaud A, Trap J et al (2018) Rubber plantation ageing controls soil biodiversity after land conversion from cassava. Agric Ecosyst Environ 257:92–102. https://doi.org/10.1016/j.agee.2018.01.034
31. Perron T, Kouakou A, Simon C et al (2022) Logging residues promote rapid restoration of soil health after clear-cutting of rubber plantations at two sites with contrasting soils in Africa. Sci Total Environ 816:151526. https://doi.org/10.1016/j.scitotenv.2021.151526
32. Oku E, Iwara A, Ekukinam E (2012) Effects of Age of Rubber (Hevea brasiliensis Muell Arg.) plantations on pH, organic carbon, organic matter, nitrogen and micronutrient status of ultisols in the humid forest zone of Nigeria. Kasetsart J 46:684–693
33. Panklang P, Thaler P, Thoumazeau A et al (2022) How 75 years of rubber monocropping affects soil fauna and nematodes as the bioindicators for soil biodiversity quality index. Acta Agric Scandin B — Soil Plant Sci 72:612–622. https://doi.org/10.1080/09064710.2022.2034930
34. Leff JW, Jones SE, Prober SM et al (2015) Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. Proc Natl Acad Sci USA 112:10967–10972. https://doi.org/10.1073/pnas.1508382112
35. Broughton WJ (1976) Effect of various covers on soil fertility under Hevea brasiliensis muell. arg. and on growth of the tree. Agro-Ecosystems 3:147–170. https://doi.org/10.1016/0304-3746(76)90113-X
36. Liu C-A, Nie Y, Zhang Y-M et al (2018) Introduction of a leguminous shrub to a rubber plantation changed the soil carbon and nitrogen fractions and ameliorated soil environments. Sci Rep 8:17324. https://doi.org/10.1038/s41598-018-35762-0
37. Perron T, Mareschal L, Laclau J-P et al (2021) Dynamics of biomass and nutrient accumulation in rubber (Hevea brasiliensis) plantations established on two soil types: Implications for nutrient management over the immature phase. Ind Crops Prod 159:113084. https://doi.org/10.1016/j.indcrop.2020.113084
38. Gustafsson L, Baker SC, Bauhus J et al (2012) Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62:633–645. https://doi.org/10.1525/bio.2012.62.7.6
39. Mayer M, Prescott CE, Abaker WEA et al (2020) Tamm review: influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. For Ecol Manag 466:118127. https://doi.org/10.1016/j.foreco.2020.118127
40. Kranabetter JM, Chapman BK (1999) Effects of forest soil compaction and organic matter removal on leaf litter decomposition in central British Columbia. Can J Soil Sci 79:543–550. https://doi.org/10.4141/S98-081
41. Carron MP, Pierrat M, Snoeck D et al (2015) Temporal variability in soil quality after organic residue application in mature oil palm plantations. Soil Res 53:205. https://doi.org/10.1071/SR14249
42. Lu L, Hu M, Wang J et al (2023) Impact of downed logs of masson pine (Pinus massoniana Lamb.) on soil microbial community in a climate transitional forest of central China. Forests 14:955. https://doi.org/10.3390/f14050955
43. Kouakou AK, Trap J, Diakhaté S et al (2023) Temporal changes of topsoil nematode communities in rubber plantations in Ivory Coast in response to logging residue management and legumes introduction. Plant Soil. https://doi.org/10.1007/s11104-023-06369-w
44. Huang Z, He Z, Wan X et al (2013) Harvest residue management effects on tree growth and ecosystem carbon in a Chinese fir plantation in subtropical China. Plant Soil 364:303–314. https://doi.org/10.1007/s11104-012-1341-1
45. FAO (2001) Lecture notes on the major soils of the world. https://www.fao.org/3/Y1899E/Y1899E00.htm. Accessed 28 May 2022
46. Thoumazeau A, Bessou C, Renevier M-S et al (2019) Biofunctool®: a new framework to assess the impact of land management on soil quality. Part A: concept and validation of the set of indicators. Ecol Indic 97:100–110. https://doi.org/10.1016/j.ecolind.2018.09.023
47. Thoumazeau A, Bessou C, Renevier M-S et al (2019) Biofunctool®: a new framework to assess the impact of land management on soil quality. Part B: investigating the impact of land management of rubber plantations on soil quality with the Biofunctool® index. Ecol Indic 97:429–437. https://doi.org/10.1016/j.ecolind.2018.10.028
48. Brauman A, Thoumazeau A (2020) Biofunctool® : un outil de terrain pour évaluer la santé des sols, basé sur la mesure de fonctions issues de l'activité des organismes du sol. Etude et Gestion des Sols 16
49. Qian P, Schoenau JJ (2002) Practical applications of ion exchange resins in agricultural and environmental soil research. Can J Soil Sci 82:9–21. https://doi.org/10.4141/S00-091
50. Culman SW, Snapp SS, Freeman MA et al (2012) Permanganate oxidizable carbon reflects a processed soil fraction that is sensitive to management. Soil Sci Soc Am J 76:494–504. https://doi.org/10.2136/sssaj2011.0286
51. Herrick JE, Whitford WG, de Soyza AG et al (2001) Field soil aggregate stability kit for soil quality and rangeland health evaluations. CATENA 44:27–35. https://doi.org/10.1016/S0341-8162(00)00173-9
52. Lassabatère L, Angulo-Jaramillo R, Soria Ugalde JM et al (2006) Beerkan estimation of soil transfer parameters through infiltration experiments-BEST. Soil Sci Soc Am J 70:521–532. https://doi.org/10.2136/sssaj2005.0026
53. Guimarães RML, Ball BC, Tormena CA (2011) Improvements in the visual evaluation of soil structure. Soil Use Manag 27:395–403. https://doi.org/10.1111/j.1475-2743.2011.00354.x
54. Li Y, Zhang Q, Zhang F et al (2015) Analysis of the microbiota of black stain in the primary dentition. PLoS ONE 10:e0137030. https://doi.org/10.1371/journal.pone.0137030
55. Prévost-Bouré NC, Christen R, Dequiedt S et al (2011) Validation and application of a PCR primer set to quantify fungal communities in the soil environment by real-time quantitative PCR. PLOS ONE 6:e24166. https://doi.org/10.1371/journal.pone.0024166
56. Callahan BJ, Sankaran K, Fukuyama JA et al (2016) Bioconductor workflow for microbiome data analysis: from raw reads to community analyses. F1000Res 5:1492. https://doi.org/10.12688/f1000research.8986.2
57. Callahan BJ, McMurdie PJ, Holmes SP (2017) Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. ISME J 11:2639–2643. https://doi.org/10.1038/ismej.2017.119
58. Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.journal 17:10–12. https://doi.org/10.14806/ej.17.1.200
59. Murali A, Bhargava A, Wright ES (2018) IDTAXA: a novel approach for accurate taxonomic classification of microbiome

sequences. Microbiome 6:140. https://doi.org/10.1186/s40168-018-0521-5
60. Quast C, Pruesse E, Yilmaz P et al (2013) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res 41:D590–D596. https://doi.org/10.1093/nar/gks1219
61. McMurdie PJ, Holmes S (2013) phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. PLOS One 8:e61217. https://doi.org/10.1371/journal.pone.0061217
62. Davis NM, Proctor DM, Holmes SP et al (2018) Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. Microbiome 6:226. https://doi.org/10.1186/s40168-018-0605-2
63. Zhang Z, Schwartz S, Wagner L, Miller W (2000) A greedy algorithm for aligning DNA sequences. J Comput Biol 7:203–214. https://doi.org/10.1089/10665270050081478
64. Sansupa C, Wahdan SFM, Hossen S et al (2021) Can we use functional annotation of prokaryotic taxa (FAPROTAX) to assign the ecological functions of soil bacteria? Appl Sci 11:688. https://doi.org/10.3390/app11020688
65. Kurtz ZD, Müller CL, Miraldi ER et al (2015) Sparse and compositionally robust inference of microbial ecological networks. PLOS Comput Biol 11:e1004226. https://doi.org/10.1371/journal.pcbi.1004226
66. Berry D, Widder S (2014) Deciphering microbial interactions and detecting keystone species with co-occurrence networks. Front Microbiol 5
67. Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal, Complex Syst 1695:1–9
68. R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
69. Wickham H (2016) ggplot2 : elegant Graphics for Data Analysis. Springer International Publishing, Cham
70. Oksanen J, Blanchet FG, Kindt R et al (2019) Vegan: community ecology package. R package version 2:5–4
71. Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 04:1
72. Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. Glob Ecol Biogeogr 19:134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x
73. Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv:14065823 [stat]
74. Peterson RA (2021) Finding optimal normalizing transformations via bestNormalize. The R Journal 13:310. https://doi.org/10.32614/RJ-2021-041
75. Hothorn T, Bretz F, Westfall P, et al (2022) multcomp: simultaneous inference in general parametric models
76. Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432. https://doi.org/10.2307/1934352
77. Alberdi A, Gilbert MTP (2019) A guide to the application of hill numbers to DNA-based diversity analyses. Mol Ecol Resour 19:804–817. https://doi.org/10.1111/1755-0998.13014
78. Marcon E, Hérault B (2015) entropart : an R Package to measure and partition diversity. J Stat Soft 67(8):1–26. https://doi.org/10.18637/jss.v067.i08
79. Love MI, Huber W, Anders S (2014) Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biol 15:550. https://doi.org/10.1186/s13059-014-0550-8
80. Longepierre M, Widmer F, Keller T et al (2021) Limited resilience of the soil microbiome to mechanical compaction within four growing seasons of agricultural management. ISME Commun 1:1–13. https://doi.org/10.1038/s43705-021-00046-8
81. Bennett JA, Klironomos J (2019) Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. New Phytologist 222:91–96. https://doi.org/10.1111/nph.15603
82. Wang X, Liu J, He Z et al (2021) Forest gaps mediate the structure and function of the soil microbial community in a Castanopsis kawakamii forest. Ecol Indic 122:107288. https://doi.org/10.1016/j.ecolind.2020.107288
83. D'Angelo T, Goordial J, Lindsay MR et al (2023) Replicated life-history patterns and subsurface origins of the bacterial sister phyla Nitrospirota and Nitrospinota. ISME J 17:891–902. https://doi.org/10.1038/s41396-023-01397-x
84. Weisse L, Héchard Y, Moumen B, Delafont V (2023) Here, there and everywhere: ecology and biology of the Dependentiae phylum. Environ Microbiol 25:597–605. https://doi.org/10.1111/1462-2920.16307
85. Zhang Z-Y, Feng Y, Tong S-Q et al (2023) Morphological and phylogenetic characterisation of two new soil-borne fungal taxa belonging to Clavicipitaceae (Hypocreales, Ascomycota). MycoKeys 98:113–132. https://doi.org/10.3897/mycokeys.98.106240
86. Kielak AM, Barreto CC, Kowalchuk GA et al (2016) The ecology of acidobacteria: moving beyond genes and genomes. Front Microbiol 7. https://doi.org/10.3389/fmicb.2016.00744
87. Li Q, Lee Allen H, Wollum AG (2004) Microbial biomass and bacterial functional diversity in forest soils: effects of organic matter removal, compaction, and vegetation control. Soil Biol Biochem 36:571–579. https://doi.org/10.1016/j.soilbio.2003.12.001
88. Longepierre M, Feola Conz R, Barthel M et al (2022) Mixed effects of soil compaction on the nitrogen cycle under pea and wheat. Front Microbiol 12
89. Shi L, Dossa GGO, Paudel E et al (2019) Changes in fungal communities across a forest disturbance gradient. Appl Environ Microbiol 85:e00080–e00019. https://doi.org/10.1128/AEM.00080-19
90. Banerjee S, Walder F, Büchi L et al (2019) Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. ISME J 13:1722–1736. https://doi.org/10.1038/s41396-019-0383-2
91. Boddy L, Hynes J, Bebber DP, Fricker MD (2009) Saprotrophic cord systems: dispersal mechanisms in space and time. Mycoscience 50:9–19. https://doi.org/10.1007/S10267-008-0450-4
92. Fanin N, Lin D, Freschet GT et al (2021) Home-field advantage of litter decomposition: from the phyllosphere to the soil. New Phytologist 231:1353–1358. https://doi.org/10.1111/nph.17475
93. Chen C, Liu W, Jiang X, Wu J (2017) Effects of rubber-based agroforestry systems on soil aggregation and associated soil organic carbon: Implications for land use. Geoderma 299:13–24. https://doi.org/10.1016/j.geoderma.2017.03.021
94. Wan X, Huang Z, He Z et al (2015) Soil C:N ratio is the major determinant of soil microbial community structure in subtropical coniferous and broadleaf forest plantations. Plant Soil 387:103–116. https://doi.org/10.1007/s11104-014-2277-4
95. Guo Y, Bei Q, Dzomeku BM et al (2022) Genetic diversity and community composition of arbuscular mycorrhizal fungi associated with root and rhizosphere soil of the pioneer plant Pueraria phaseoloides. iMeta 1:e51. https://doi.org/10.1002/imt2.51
96. Rillig MC, Mummey DL, Ramsey PW et al (2006) Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated bacteria. FEMS Microbiol Ecol 57:389–395. https://doi.org/10.1111/j.1574-6941.2006.00129.x
97. Lustenhouwer N, Maynard DS, Bradford MA et al (2020) A trait-based understanding of wood decomposition by fungi. Proc Natl Acad Sci 117:11551–11558. https://doi.org/10.1073/pnas.1909166117

98. Hoorman JJ, de Moraes JC, Reeder R (2011) The biology of soil compaction
99. Zhou Z, Wang C, Luo Y (2020) Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. Nat Commun 11:3072. https://doi.org/10.1038/s41467-020-16881-7
100. Dossa GGO, Yang Y-Q, Hu W et al (2021) Fungal succession in decomposing woody debris across a tropical forest disturbance gradient. Soil Biol Biochem 155:108142. https://doi.org/10.1016/j.soilbio.2021.108142
101. Bach EM, Baer SG, Meyer CK, Six J (2010) Soil texture affects soil microbial and structural recovery during grassland restoration. Soil Biol Biochem 42:2182–2191. https://doi.org/10.1016/j.soilbio.2010.08.014
102. Xia Q, Rufty T, Shi W (2020) Soil microbial diversity and composition: Links to soil texture and associated properties. Soil Biol Biochem 149:107953. https://doi.org/10.1016/j.soilbio.2020.107953
103. Hartmann M, Howes CG, VanInsberghe D et al (2012) Erratum: significant and persistent impact of timber harvesting on soil microbial communities in Northern coniferous forests. ISME J 6:2320–2320. https://doi.org/10.1038/ismej.2012.100
104. Chen H, Dai Z, Veach AM et al (2020) Global meta-analyses show that conservation tillage practices promote soil fungal and bacterial biomass. Agric Ecosyst Environ 293:106841. https://doi.org/10.1016/j.agee.2020.106841
105. Witzgall K, Vidal A, Schubert DI et al (2021) Particulate organic matter as a functional soil component for persistent soil organic carbon. Nat Commun 12:4115. https://doi.org/10.1038/s41467-021-24192-8
106. Hassink J (1997) The capacity of soils to preserve organic C and N by their association with clay and silt particles. Plant Soil 191:77–87
107. Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241:155–176. https://doi.org/10.1023/A:1016125726789
108. Neumann D, Heuer A, Hemkemeyer M et al (2013) Response of microbial communities to long-term fertilization depends on their microhabitat. FEMS Microbiol Ecol 86:71–84. https://doi.org/10.1111/1574-6941.12092
109. Hartmann M, Six J (2023) Soil structure and microbiome functions in agroecosystems. Nat Rev Earth Environ 4:4–18. https://doi.org/10.1038/s43017-022-00366-w