



Long-term soil health and microbiome responses to sustainable management under drought stress in tropical coffee agroecosystems

Marina Scalioni Vilela · Lindsey C. Slaughter · Dalyse Toledo Castanheira · Flávio H. V. Medeiros · Márcio R. Nunes · Fernanda C. L. Medeiros · Bruno Montoani Silva · Alisson A. V. Campos · Mauro M. L. Faria · Leandro C. Paiva · Rayan C. Andrade · Milene A. F. Carvalho · Rubens J. Guimarães

Received: 17 June 2025 / Accepted: 3 May 2026
© The Author(s) 2026

Abstract

Background and aims Implementing sustainable crop management to improve soil health can bolster plant and soil resistance to drought stress. This study evaluated the long-term impact of sustainable soil management on soil health in tropical coffee agroecosystems, focusing on how these practices influenced plant yield and quality, as well as soil microbiome composition and function under drought treatment.

Methods Plots were selected from a long-term experiment established in January 2016 in Lavras municipality, Minas Gerais State, Brazil, and treatments had been in place for 7 years by the end of the

current study. Soil management treatments included: (i) annual coffee husk residue amendment within rows + permanent signal grass (*Urochloa decumbens*) cover between rows (CHUD), (ii) annual agricultural gypsum amendment within rows + permanent signal grass cover between rows (GUD), and (iii) a control consisting of coffee monoculture with bare soil.

Results Combining coffee husk + signal grass management improved chemical, physical, and biological soil health indicators compared to bare soil management. These practices were also associated with higher coffee yield and superior beverage quality. Soil fungal and bacterial communities responded to both management and water availability, and soil functional indicators assessed by enzyme activity showed

Responsible Editor: Akanksha Singh.

M. S. Vilela (✉) · D. T. Castanheira · F. C. L. Medeiros · A. A. V. Campos · M. M. L. Faria · R. J. Guimarães
Department of Agriculture, Universidade Federal de Lavras, Lavras, MG, Brazil
e-mail: marinavilela@ufla.br

M. S. Vilela · L. C. Slaughter
Department of Plant and Soil Science, Texas Tech University, Lubbock, TX, USA

F. H. V. Medeiros
Department of Plant Pathology, Universidade Federal de Lavras, Lavras, MG, Brazil

M. R. Nunes
Soil, Water & Ecosystem Sciences Department and Global Food System Institute, University of Florida, Gainesville, FL, USA

B. M. Silva · R. C. Andrade
Department of Soil Science, Universidade Federal de Lavras, Lavras, MG, Brazil

L. C. Paiva
Innovation Hub of Coffee Agroindustry, Instituto Federal de Educação Ciência e Tecnologia do Sul de Minas Gerais, Machado, MG, Brazil

M. A. F. Carvalho
Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA Café), Brasília, DF, Brazil

greater resistance to the drought treatment under coffee husk + signal grass management.

Conclusion Overall, this study indicates that combined residue amendment and soil cover may enhance long-term soil and crop responses in this tropical coffee agroecosystem, with evidence of greater resistance of soil functional indicators to the drought treatment used in the incubation assay.

Keywords *Coffea arabica* L. · Cover crops · Soil amendments · Sustainable management · Drought resistance

Introduction

Drought negatively affects farming worldwide, a challenge increasingly exacerbated by climate change and water shortages (Sá et al. 2011; IPCC 2021). Such adverse conditions can disrupt vital soil functions including nutrient cycling and water retention, ultimately compromising coffee yield and beverage quality (Voltolini et al. 2022). Enhancing soil health is a critical strategy to mitigate these challenges, as it supports ecosystem resilience and sustains productivity even under environmental stress (Naylor and Coleman-Derr 2018; Lal 2020a; Lehmann et al. 2020; Davis et al. 2023). The provision of water is a crucial service provided by healthy soils. Soil water content impacts several physical, chemical, and biological properties and processes, which in turn affect nutrient uptake, crop growth, quality, yield, and health (Silva et al. 2019; Lehmann et al. 2020; Voltolini et al. 2022; Davis et al. 2023; Ghimire et al. 2023; Vilela et al. 2023, 2024). Developing management strategies that improve soil health and water dynamics is essential for creating climate-smart, drought-resilient agricultural systems, particularly in coffee-growing regions increasingly exposed to combined drought and heat stress (Borgo et al. 2025).

Combining management practices such as cover cropping and soil conditioners can enhance soil health and water availability, improving agricultural sustainability and resilience to climate extremes (Silva et al. 2019, 2021; Barbosa et al. 2020; Castanheira et al. 2022; Vilela et al. 2023, 2024). For instance, coffee husk, a by-product of coffee hulling, can improve soil moisture, nutrient availability, and soil organic matter (SOM) when used as a residue amendment

(Castanheira et al. 2022; Voltolini et al. 2022; Vilela et al. 2024). Agricultural gypsum promotes deeper plant rooting by neutralizing aluminum toxicity and aiding plant development under water deficit (Carducci et al. 2015; Silva et al. 2015; Voltolini et al. 2020). *Urochloa* species increase SOM and soil porosity and may retain up to 40 m³ ha⁻¹ of water into the 0–20 cm soil layer when intercropped with coffee plants (Rocha et al. 2014; Galdos et al. 2020). Coffee intercropped with signal grass (*Urochloa decumbens*) has also been shown to increase phosphatase enzyme activity, leading to improved phosphorus (P) cycling (11.5 kg ha⁻¹) (Baptistella et al. 2022).

Agricultural management practices and soil properties, such as pH, nutrient content, texture, water content, and temperature, are primary drivers of soil microbial composition and function (Kavamura et al. 2013; Naylor and Coleman-Derr 2018; Paula et al. 2014; Veloso et al. 2023; Wang et al. 2023; De Silva et al. 2025). Although research indicates that these practices enhance specific soil health metrics such as SOM (Lehmann and Kleber 2015; Lehmann et al. 2020), it is essential to comprehend their long-term impact on the soil microbiome, especially under drought stress. No-till and cover crops can favor bacterial (e.g., Acidobacteria and Firmicutes) and fungal (e.g., mycorrhizal) communities (Wulanningtyas et al. 2020; Singh et al. 2023; Veloso et al. 2023; Vilela 2024). Minimizing soil disturbance leads to an increase in microbially-produced extracellular enzymes such as β -1,4-glucosidase, which breaks down SOM into more stable forms of carbon, and phosphatase, which makes organic phosphorus available for plant uptake (Singh et al. 2023). The living component of the soil actively supports nutrient cycling, SOM decomposition and promotes plant growth, contributing to the development of drought-tolerant and resilient crops (Kavamura et al. 2013; Paula et al. 2014; Lehmann and Kleber 2015; Naylor and Coleman-Derr 2018; Wang et al. 2023). Since specific microorganisms are often recruited from soil by plants to help mitigate drought stress, it is important to understand how microbiomes are altered under drought conditions (Wang et al. 2023; Petermann et al. 2024). Soil microbiomes can exhibit consistent responses to extreme events and management can influence drought resistance and resilience of microbial communities (Knight et al. 2024; Kost et al. 2024). In coffee systems, farm management has

also been shown to shape soil microbiome composition (Kutos et al. 2024; Veloso et al. 2023).

Combining conservation management practices enhances soil health and microbial activity beyond the additive effect of individual practices (Lehman et al. 2019). In addition to yield and quality gains, improved soil health may bolster resistance to drought, a stressor that increasingly threatens coffee production even in high-rainfall systems. Brazil, the world's leading coffee producer and exporter, has faced significant yield losses in recent years due to drought during coffee blossoming (CONAB, 2023). However, coffee-specific evidence integrating long-term management effects on soil health, microbiome composition, agronomic performance, and drought-related soil functional responses remains limited. To address this gap, this study aimed to assess: 1) the long-term impact of conservation soil management on soil health and microbiomes in tropical coffee agroecosystems; 2) the effect of soil health on coffee yield and beverage quality; and 3) the influence of long-term conservation management on the drought resistance of soil microbiome composition and function. We hypothesized that: 1) amendment combinations designed to increase living soil cover and supplement soil carbon would significantly enhance long-term soil health; 2) these improvements in soil health would lead to higher coffee yield and better beverage quality; and 3) increased soil health would contribute to greater drought resistance in soils conditioned by long-term conservation practices. By integrating a long-term field experiment with soil health, microbiome, yield, beverage-quality, and controlled drought-response assessments, this study provides a broader evaluation of how conservation management may shape the resilience of tropical coffee soils and production systems.

Material and methods

Experimental field system design and management

The long-term field experiment was established in January 2016 at the Department of Agriculture of the Universidade Federal de Lavras (UFLA), Lavras, Minas Gerais State, Brazil (−21.226797°S, −44.961208°W, 975 m above sea level), under open-field conditions with natural rainfall and temperature

regimes. By the final sampling in 2023, the experimental plots and cropping system treatments had been maintained for 7 years. The region features a tropical climate with an average annual temperature of 19.4 °C and an average annual precipitation of 1558 mm. Local rainfall distribution and average temperature during the study period (2016 to 2023) is presented in Fig. 1. The soil in the study area has a clayey texture (Table 1) and is classified as *Latosolo Vermelho-Amarelo* (Brazilian Soil Classification System) (Curi et al. 2017; Santos et al. 2018) and Typic Hapludox according to the U.S. System of Soil Taxonomy (Soil Survey Staff 2022). The grove was 0.324 ha and contained about 1,200 coffee plants. The coffee variety used in the experiment was Mundo Novo IAC-379—19 (*Coffea arabica* L.), which is the most widely cultivated cultivar in the South Minas Gerais region and represents the predominant commercial production system in this area. The distance between trees in the row was 0.75 m and 3.6 m between rows. All trees in the grove were planted at the same time and received uniform management for fertilization and pest control (insecticides, herbicides, and fungicides throughout the year), using products registered for coffee crops, in accordance with sustainable agriculture guidelines (Reis and Cunha 2010). All insecticides and fungicides were applied via foliar spray. In the coffee rows of all plots, we used integrated weed management to rotate between pre-emergent (e.g., a.i. oxyfluorfen, flumioxazin, and indaziflam) and post-emergent herbicides (e.g., a.i. clethodim, chlorimuron-ethyl, and glyphosate) based on the weed species present in the area. The herbicides were applied 1.00 m wide on each side of the coffee row without interfering with the treatment application on each plot.

Experimental field treatments

The experimental field study system comprised three treatments comparing conservation management strategies implemented between the coffee rows: CHUD=annual coffee husk amendment+continuous cover of signal grass (*Urochloa decumbens*); GUD=annual agricultural gypsum amendment+continuous cover of signal grass; and Control=bare soil between coffee rows without vegetative cover, coffee husk, or gypsum (Fig. 2). For CHUD and GUD, signal grass seeds were sown

A) Monthly precipitation and mean temperature

Experimental site (South Minas Gerais, Brazil)

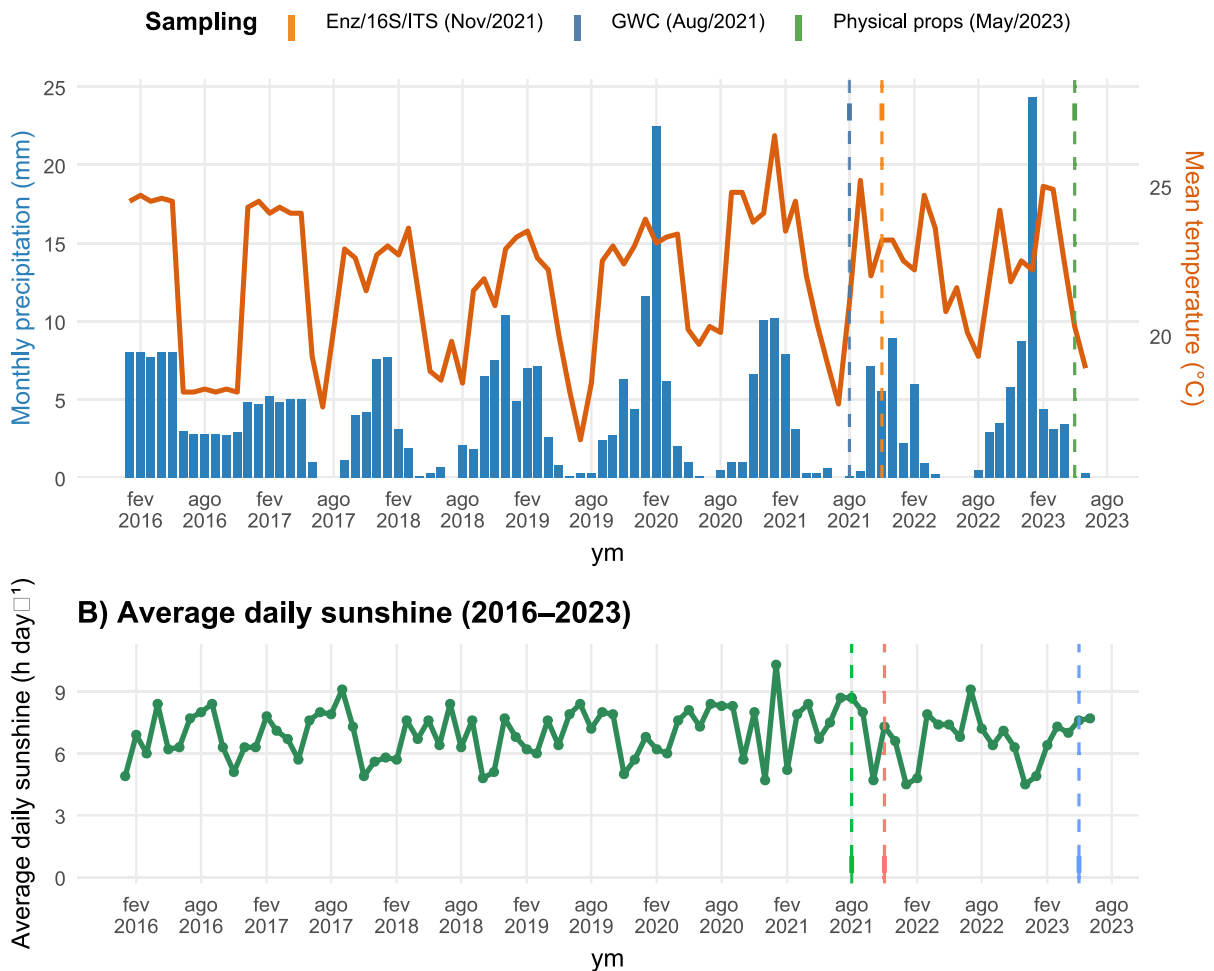


Fig. 1 Climatic characterization of the experimental site in South Minas Gerais, Brazil (2016–2023). **(A)** Monthly precipitation (bars) and mean temperature (line, secondary axis). **(B)** Average daily sunshine duration. Dashed vertical lines indi-

cate key sampling campaigns: August 2021 (GWC), November 2021 (enzymes, 16S, and ITS), and May 2023 (undisturbed soil cores for physical properties). Climatic data were obtained from the local weather station

between the coffee rows in December 2015. This species is a widely used tropical forage grass in Brazil, recognized for its capacity to provide permanent soil cover, which supports its use as a cover crop in coffee agroecosystems. The grass was planted at a distance of 1.00 m from each side of the coffee row, occupying a total between-row width of 1.60 m. Grass cover was mowed before flowering, with biomass deposition under the coffee canopy. Along with the signal grass, coffee husk (CHUD treatment) residue

and agricultural gypsum (GUD treatment) amendments were used as soil conditioners. The CHUD and GUD treatments were selected as practical and low-cost conservation strategies that producers can feasibly adopt, using inputs such as coffee husk (a by-product generated on-farm), gypsum (a widely available and low-cost soil conditioner), and signal grass cover, which improves soil cover and is easy to manage as a cover crop, mainly due to its susceptibility to most herbicides commonly used in coffee

Table 1 Soil's chemical and physical characteristics previous to the experiment installment in 2015

Indicator (unit)	Depth (cm)	
	0–20	20–40
pH (water)	5.0	4.6
P (mg dm ⁻³)	4.5	1.4
K (mg dm ⁻³)	104	48
Ca ⁺² (cmol _c dm ⁻³)	1.5	0.5
Mg ²⁺ (cmol _c dm ⁻³)	0.5	0.2
Al ⁺³ (cmol _c dm ⁻³)	0.2	0.5
H + Al (cmol _c dm ⁻³)	3.5	4.4
SB (cmol _c dm ⁻³)	2.3	0.8
CEC (cmol _c dm ⁻³)	5.7	5.1
BS (%)	39.6	15.9
m (%)	8.1	37.8
SOM (g kg ⁻¹)	21	-
Zn (mg dm ⁻³)	2.9	0.7
Fe (mg dm ⁻³)	102.7	93.5
Mn (mg dm ⁻³)	22.9	10.6
Cu (mg dm ⁻³)	4.1	3.2
B (mg dm ⁻³)	0.3	0.5
S (mg dm ⁻³)	35.9	60.7
Clay (g kg ⁻¹)	440	-
Silt (g kg ⁻¹)	90	-
Sand (g kg ⁻¹)	470	-

pH soil pH in water, *P* soil phosphorus content, *K* soil exch. Potassium, *Ca* soil exch. Calcium, *Mg* soil exch. Magnesium, *Al* soil aluminum content, *CEC* cation exchange capacity at pH 7.0, *BS* base saturation, *m* aluminum saturation, *SOM* soil organic matter, *Zn* soil zinc content, *Fe* soil iron content, *Mn* soil manganese content, *Cu* soil copper content, *B* soil boron content, *S* soil sulfur content

production systems. Both coffee husk and gypsum were applied annually between 2016 and 2021 (a total of six applications) and top-dressed under the coffee canopy within a 1.00 m area on either side of the coffee row. The applications were carried out during the rainy season (October–November), after blossoming and before fruiting. Doses were 0.33 Mg ha⁻¹ of coffee husk and 3 Mg ha⁻¹ of agricultural gypsum, with rates based on the soil nutrient testing within a 20 to 40 cm subsurface depth and soil texture (Table 1) following Guimarães et al. (1999) recommendations. In the Control treatment, bare soil was maintained within a 1.00 m strip on each side of the coffee row through weeding and herbicide applications, while spontaneous vegetation was allowed between rows,

with no amendments added. This management represents the conventional practice most widely adopted by coffee producers in South Minas Gerais, the leading coffee-producing region of Brazil, and therefore provides a realistic baseline for comparison.

Plant analyses

Crop yield

We collected coffee berries from all plants within each plot annually to evaluate the weight and volume of the harvested coffee. Samples containing 3 L of harvested coffee were dried until reaching 11.5% moisture and weighed before and after processing. The data were used to calculate the average yield for the 2020/2021 biennium in kg ha⁻¹. Because coffee production exhibits biennial variability, averaging the yields over two consecutive years provides a more accurate assessment of long-term management effects. We used the 2020/2021 biennium yield to assess the cumulative impact of six years of soil management on coffee production for the current study. The average yield of the 2018/2019 biennium after four years of management was 3450 kg ha⁻¹ in GUD, 2160 kg ha⁻¹ in CHUD and 1320 kg ha⁻¹ in Control as reported in Voltolini et al. (2022).

Coffee sensory analysis

Sensory analysis was performed following the Specialty Coffee Association (SCAA, 2013) protocol, which is the international standard for evaluating coffee beverage quality. This method is widely applied in both research and industry to assess consumer-relevant attributes, providing a robust and integrative measure of beverage quality. Three independent 300 g green coffee samples per plot were used. The beans were roasted and ground according to the SCAA (2013) protocol prior to evaluation. Three quality graders (Q-graders), who were professionally trained coffee tasters at the Coffee Quality Institute, conducted a sensory analysis of the coffee harvested in 2021. Coffees were assessed for fragrance, sweetness, flavor, acidity, uniformity, clean cup, body, aftertaste, balance, overall score evaluation, and global score. The global score was used to represent beverage quality in this study, as it reflects the average of all evaluated attributes and therefore

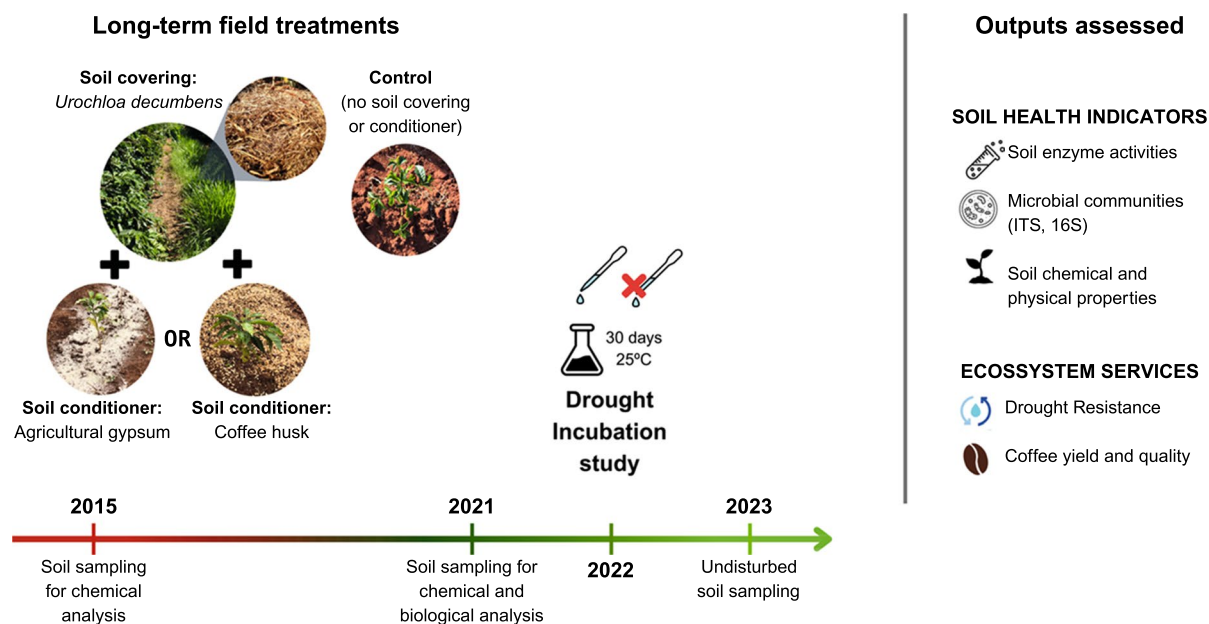


Fig. 2 Schematic representation of the experimental design and methodology. Diagram shows the long-term coffee field experiment with three replicates (blocks) and the soil management treatments evaluated [Coffee husk + signal grass (CHUD), Agricultural gypsum + signal grass (GUD), and

Control]. The scheme also illustrates the sampling timeline: enzyme activities and microbial diversity (2021), gravimetric water content (August 2021), and soil physical properties (May 2023), as well as the drought incubation study

provides a robust measure of beverage quality (SCAA, 2013).

Soil sampling and analyses

Soil samples were collected for chemical, physical, and biological analyses. The selection of indicators followed established soil health assessment frameworks that emphasize the integration of complementary properties reflecting soil functionality and ecosystem services (Karlen et al., 1997; Nunes et al. 2020; Lehmann et al. 2020; Davis et al. 2023). Accordingly, we evaluated chemical indicators (pH, nutrient contents, and soil organic matter), physical indicators (bulk density, porosity, available water capacity, gravimetric and volumetric water contents), and biological indicators (enzyme activities and microbial diversity) to capture the multidimensional nature of soil health under long-term coffee management systems.

Soil chemical properties

Soil samples were collected for chemical characterization to a maximum depth of 20 cm at the beginning of the rainy season in September 2015 (before the experiment was installed) and in September 2021 after 6 years of experimental treatments. We collected two soil samples per plot below the coffee canopy. For chemical analysis, samples were air-dried and sieved (2 mm) prior to laboratory characterization. Soil chemical measurements included soil organic matter (SOM), potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), aluminum (Al), pH, base saturation (BS), and aluminum saturation. The total accumulation of SOM and nutrients was assessed by subtracting 2021 and 2015 values. The annual SOM and nutrient accumulation were calculated by dividing the total accumulation over the six-year experimental period.

The soil was prepared to assess SOM content by the loss-on-ignition method, in which the soil was heated to 400–550 °C for 4 h to oxidize organic

matter (Silva 2009). Soil pH was determined in water (1:1 soil/water ratio). P and K were extracted with Mehlich⁻¹ solution (consisting of 0.0125 mol L⁻¹ H₂SO₄ and 0.05 mol L⁻¹ HCl) at a 1:10 (v/v) soil/solution ratio and measured by flame emission spectroscopy. Exchangeable Ca and Mg were extracted with a KCl 1 mol L⁻¹ 1:10 v/v soil/solution and determined by atomic absorption spectrophotometry with air-acetylene flame and 5% lanthanum solution to prevent interference. Exchangeable aluminum (Al³⁺) was extracted with 1 mol L⁻¹ KCl (1:10 v/v soil-to-solution ratio) and quantified by titration with standardized NaOH solution (0.025 mol L⁻¹) using phenolphthalein as indicator. Potential acidity (H+Al) was extracted with Ca (OAc)₂ 0.5 mol L⁻¹ buffered at pH 7. The sum of exchangeable basic cations (SB = Ca²⁺ + Mg²⁺ + K⁺), cation exchange capacity at pH 7.0 (CEC = SB + H + Al) and base saturation [BS = ((Ca + Mg + K + H + Al)/CEC) × 100] were then estimated. The assessments followed Silva (2009) methodology.

Soil physical properties

To measure gravimetric water content (GWC), the samples were collected in 2021 with three repetitions per treatment during the dry season (August) from the 0–10 cm depth. The wet soil weight (g) was determined immediately after sampling, and the dry soil mass (g) was obtained after oven-drying at 105 °C until constant mass (Teixeira et al. 2017).

Undisturbed soil cores were also sampled in the 0–10 cm depth with a metallic cylinder and analyzed directly. We assessed available water capacity (AWC), soil bulk density, total porosity, macroporosity (> 0.05 mm) and microporosity (< 0.05 mm), and volumetric water content (VWC) (Teixeira et al. 2017). The soil cores were collected in the dry season, in early May 2023, after the removal of the third experimental block. As a result, two samples were collected per block. Undisturbed soil cores were collected later to complement the long-term dataset with physical indicators of soil quality.

Drought incubation experiment

The drought incubation experiment was conducted in the laboratory, using soil samples collected from the field plots. This experiment was designed to

complement the long-term field study, following established methodology (Delgado-Baquerizo et al. 2017), in order to isolate drought as a stress factor and evaluate the resistance of microbial functions. The samples were used to assay the coffee microbiome's response to drought (Delgado-Baquerizo et al. 2017). The soils from each treatment were incubated under two soil moisture conditions: 1) Control conditions, where samples were maintained at approximately 35% water holding capacity (WHC) to sustain a constant low level of microbial activity before harvest at 30 days, and 2) Drought conditions, where samples were initially wetted to 35% WHC for 15 days and then allowed to dry naturally for 15 days before rewetting and sample harvest. All soil samples were incubated for 30 days at a 25°C temperature (Delgado-Baquerizo et al. 2017). The Control treatment represents a minimally watered condition between the upper and lower levels of moisture experienced in the field based on prior soil moisture monitoring. In contrast, the Drought treatment represents an extended drying period.

Soil microbiome characteristics

Biological analyses were conducted after six years of treatment establishment to assess cumulative management effects on microbial community composition and nutrient-cycling functions. Soil samples for biological assessments were collected from 0–10 cm depth and lyophilized for 48 h in November 2021, then shipped on dry ice to the lab at Texas Tech University in Lubbock, TX, USA. Soil microbiome composition and function were assessed via amplicon sequencing and high-throughput extracellular enzyme assays before and after the drought incubation experiment. Microbial nutrient cycling activities were assessed by assaying extracellular enzymes (β-1, 4, glucosidase, leucine amino peptidase and β-1, 4, N-acetylglucosaminidase, and phosphatase) involved in C, N, and P-cycling, using a fluorescence-based microplate method (Saiya-Cork et al. 2002; Dick et al. 2018). The incubation temperature was 25°C and buffer pH was 5.5, which were set to match the average soil pH and mean annual temperature of the site (DeForest 2009; Petermann et al. 2024).

Total genomic DNA was extracted and purified from the soil of each treatment using commercial extraction kits (DNeasy PowerSoil Kit, Qiagen,

Germantown, MD). DNA purity and concentration were quantified using fluorescence-based assays on a Qubit 2.0 fluorometer (Life Technologies Holdings Pte Ltd, Singapore) and BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., Winooski, VT). DNA from each sample was prepared for next-generation metagenomic sequencing using the Illumina MiSeq platform at the Texas Tech University Center for Biotechnology and Genomics (TTU CBG). Bacterial communities were characterized by amplifying the V3–V4 region of the 16S rRNA gene using primers 16S-V3F (5'-TCGTCGGCAGCGTCA GATGTGTATAAGAGACAGCCTACGGGNGGC WGCAG-3') and 16S-V4R (5'-GTCTCGTGGGCT CGGAGATGTGTATAAGAGACAGGACTACH-VGGGTATCTAATCC-3'). Fungal communities were characterized by amplifying the internal transcribed spacer regions (ITS1 and ITS2) using primer pairs ITS1F (5'-TCGTCGGCAGCGTCAGATGTGTAT AAGAGACAGGATGAAGAACGYAGYRAA-3') and ITS1R (5'-GTCTCGTGGGCTCGGAGATGT GTATAAGAGACAGTCCTCCGCTTATTGATA TGC-3'), and ITS2F (5'-TCGTCGGCAGCGTCA GATGTGTATAAGAGACAGTAGAGGAAGTAA AAGTCGTAA-3') and ITS2R (5'-GTCTCGTGG GCTCGGAGATGTGTATAAGAGACAGTTYRC TRCGTTCTTCATC-3').

Statistical analyses and bioinformatics

All statistical analyses were performed in R version 4.2.1 (R Development Core Team 2020). The field experiment was established in a randomized block design. A randomized block design was used, with management as a fixed effect and block as a random effect for ANOVA (ExpDes package) (Ferreira et al. 2021). The data were tested for the assumptions of analysis of variance, with normality assessed using the Shapiro–Wilk test and homogeneity of variances evaluated using the Bartlett test. Residuals were also inspected to verify model adequacy. For variables obtained from the drought incubation assay, the analysis included soil management treatment, water regime, and their interaction. When significant effects were detected, means were compared using Tukey's test at $P < 0.05$.

For microbiome analyses, soil microbiome composition and functioning were assessed in two datasets: (i) field-collected samples analyzed before the

laboratory incubation experiment, representing the three long-term soil management treatments; and (ii) samples analyzed after the incubation experiment, representing the same soil management treatments under two water regimes (control and drought). Raw reads from microbiome sequencing were processed by removing adapters and primers with Cutadapt (Martin 2011), followed by denoising, chimera removal, and amplicon sequence variant (ASV) inference using DADA2 in QIIME2 (Callahan et al. 2016; Bolyen et al. 2019). Taxonomy was assigned using the SILVA 138 database for bacteria and the UNITE database for fungi (Quast et al. 2013; Nilsson et al. 2018). ASVs classified as mitochondria or chloroplasts were removed before downstream analyses. For field samples, the final number of sequences per sample ranged from 30,670 to 117,369 for 16S rRNA gene libraries and from 26,969 to 78,548 for ITS libraries. For incubation-trial samples, the final number of sequences per sample ranged from 16,746 to 69,198 for 16S rRNA gene libraries and from 10,646 to 184,526 for ITS libraries. Rarefaction was performed to equal sampling depth across samples. Alpha-diversity metrics were calculated using the microeco package (Liu et al. 2021), beta diversity was evaluated by principal coordinates analysis (PCoA) based on weighted Bray–Curtis distance, and beta-diversity differences among treatments were tested by PERMANOVA. Alpha-diversity comparisons were performed using the Kruskal–Wallis rank-sum test. Differential abundance analysis was performed using metagenomeSeq in R (Paulson et al. 2013). Statistical significance for the microbiome analyses was assessed at $P < 0.05$.

In addition, microbial abundance, diversity, and enzyme activity measured under control and drought conditions were used to calculate resistance indices (RS) according to Orwin and Wardle (2004), in order to assess the resistance of each parameter to drought within each soil management treatment (Eq. 1).

$$RS = 1 - \frac{2|D0|}{(C0 + |D0|)} \quad (1)$$

RS Resistance Index,

D_0 Difference between the control (C_0) and the disturbed soil (drought conditions).

Results

Soil health and microbiome responses from long-term field plots

Management impact on chemical soil health indicators and soil organic matter

Both CHUD and GUD significantly enhanced the chemical soil health indicators, improving extractable nutrients over the course of the study period (Table 2). In contrast to bare soil conditions (Control), the use of CHUD resulted in a 30% increase in Cation Exchange Capacity (CEC), a 900% rise in pH, and a 113% decrease in aluminum (Al). Moreover, GUD treatment increased CEC by 91%, elevated pH by 200%, and reduced Al by 75%.

In CHUD management, there was an increase ($p < 0.05$) in soil phosphorus (P) and magnesium (Mg) levels (Table 2). This treatment significantly raised the soil P content by 107% and Mg content by 648% compared to the Control. Additionally, the potassium (K) content in the soil under CHUD increased by approximately 360% compared to the Control. Similarly, GUD led to a 104% increase in K content compared to the Control. Furthermore, CHUD and GUD practices substantially enhanced the calcium (Ca) soil content by 475% in average compared to the Control.

Regarding soil organic matter (SOM) (0–20 cm layer) (Table 2), CHUD management enhanced the SOM accumulation, being 11 times higher than the Control plot, where SOM levels instead declined between 2015 and 2021. Conversely, coffee crops managed with GUD demonstrated a moderate SOM accumulation, increasing by 533% in contrast to the Control.

Management impact on physical soil health indicators

Changing soil management impacted the gravimetric (GWC) (sampled in August 2021) and volumetric water content (VWC) in soils that were sampled following the study period in 2023 to provide a snapshot

Table 2 Total and mean annual accumulation (increase or decrease) of soil chemical indicators in coffee crops under different soil management from 2015 to 2021 at 0–20 cm depth

Soil management	SOM (g kg ⁻¹)	P (mg dm ⁻³)	K (mg dm ⁻³)	CEC (cmol _c dm ⁻³)	Ca	Mg	Al	pH (H ₂ O)
Total Accumulation								
CHUD	14.5 ± 2.5 a	31.5 ± 4.2 a	238.5 ± 2.5 a	3.0 ± 0.1 b	2.9 ± 0.6 a	0.72 ± 0.02 a	-0.1 ± 0.001 c	0.8 ± 0.05 a
GUD	6.5 ± 1.5 b	15.5 ± 1.5 b	105.5 ± 4.7 b	4.4 ± 0.2 a	1.7 ± 0.2 a	-0.21 ± 0.02 b	0.2 ± 0.02 b	0.1 ± 0.05 b
Control	-1.5 ± 0.5 c	15.2 ± 0.4 b	51.8 ± 1.2 c	2.3 ± 0.2 c	0.4 ± 0.1 b	-0.23 ± 0.02 b	0.8 ± 0.03 a	-0.1 ± 0.1 b
Annual Accumulation								
CHUD	2.4 ± 0.4 a	5.3 ± 0.7 a	39.5 ± 7.8 a	0.5 ± 0.01 b	0.5 ± 0.1 a	0.12 ± 0.003 a	-0.02 ± 0.001 c	0.13 ± 0.01 a
GUD	1.1 ± 0.3 b	2.6 ± 0.2 b	16.7 ± 10.5 b	0.7 ± 0.03 a	0.3 ± 0.03 a	-0.04 ± 0.003 b	0.04 ± 0.02 b	0.01 ± 0.01 b
Control	-0.3 ± 0.1 c	2.5 ± 0.1 b	8.5 ± 1.0 b	0.4 ± 0.03 c	0.07 ± 0.01 b	-0.04 ± 0.004 b	0.10 ± 0.03 a	-0.02 ± 0.02 b

Data represent mean ± standard error of $n = 3$ independent blocks. Means followed by the same letter do not differ by Tukey ($p < 0.05$). CHUD Coffee husk + signal grass, GUD Gypsum + signal grass, SOM soil organic matter, P soil phosphorus content, K soil exch. potassium, CEC cation exchange capacity, Ca soil exch. calcium, Mg soil exch. magnesium, Al soil aluminum content, pH soil pH in water

Table 3 Soil gravimetric water content (GWC, g g⁻¹), measured in August 2021, and volumetric water content (VWC, m³ m⁻³), available water capacity (AWC, m³ m⁻³), total porosity(m³ m⁻³), and soil bulk density (g cm⁻³), measured in May 2023, in coffee crops under different soil management in the long-term field experiment

Soil management	GWC	VWC	AWC	Soil total porosity	Soil bulk density
CHUD	13.1 ± 1.9 a	17.5 ± 2.9 a	0.13 ± 0.01 ns	0.58 ± 0.02 b	1.30 ± 0.03 ns
GUD	11.8 ± 0.3 b	14.6 ± 0.8 b	0.14 ± 0.01 ns	0.65 ± 0.02 a	1.30 ± 0.11 ns
Control	10.0 ± 0.1 c	12.4 ± 0.9 c	0.08 ± 0.01 ns	0.53 ± 0.01 c	1.28 ± 0.08 ^{ns}

Data represent mean ± standard deviation. Means followed by the same letter do not differ by Tukey ($p < 0.05$). ^{ns}: non-significant at 95% probability according to Tukey test. *CHUD* Coffee husk + signal grass, *GUD* Gypsum + signal grass

assessment of cumulative treatment effects on moisture dynamics from the continuing experimental management systems (Table 3). CHUD led to a 31% and 41% increase in the GWC and VWC, respectively, compared to the bare soil (Control) at the time of sampling (Table 3). GUD management resulted in the highest soil total porosity (Table 3), 23% greater than the Control, followed by CHUD. Control exhibited the lowest soil porosity (0.53 m³ m⁻³). There were no significant differences in plant-available water content (AWC) across the long-term treatments ($p > 0.05$), around 0.12 m³ m⁻³. Soil bulk density remained consistent across different soil management compared to the Control ($p > 0.05$), with an average of 1.29 g.cm⁻³.

Management impact on biological soil health indicators

The activities of microbially-produced soil extracellular enzymes were affected by management (Fig. 3) based on field-collected freeze-dried samples analyzed prior to conducting the laboratory drought assay. The combined use of signal grass cover with either coffee husk (CHUD) or agricultural gypsum (GUD) led to increased activities of β -1, 4, glucosidase (BG) (Fig. 3a), leucine aminopeptidase (LAP) (Fig. 3b), and β -1, 4, N-acetylglucosaminidase (NAG) (Fig. 3c) enzymes. Under CHUD and GUD management, BG, LAP, and NAG activities were significantly higher, 190%, 435%, and 62%, respectively, than the Control. Regarding phosphatase activity (Fig. 3d), CHUD management showed an increase in this enzyme activity compared to other treatments (167% above Control).

From the same field-collected freeze-dried samples analyzed prior to conducting the laboratory

drought assay, bacterial richness and diversity (PERMANOVA test) were stable across soil management systems (Table 4). Notably, there were differences in fungal richness (Table 4) and diversity (Fisher) (Table 4) based on soil management. Specifically, the fungal richness and diversity were lower in bare soil management (Control) than in CHUD and GUD management practices (Table 4).

Bacterial community composition evaluated by comparing the relative abundance of different phyla represented between treatments remained consistent across various soil management practices (Figure S1A), as observed with alpha metrics assessments. There were also no changes in bacterial relative abundance at the family level (Fig. 4A) with different soil management. The ten most abundant families were found in relatively low proportion, accounting for less than 30% of the total relative abundance (Fig. 4A).

Most fungi observed at the phylum level (Figure S1B) belonged to Ascomycota, although a small presence of Glomeromycota was noted in the GUD management. In the analysis of the fungal community at the family level (Fig. 4B), the Hypocreaceae family (e.g., *Trichoderma* spp.) was present only in the CHUD management. Additionally, we observed the presence of Chaetomiaceae family in the GUD management.

To assess the microbial taxa with significant differences regarding management, we performed a differential abundance test. In the bacteria community (Fig. 5A), most species that significantly differed between treatments were more abundant with CHUD. The CHUD treatment may therefore favor *Paenibacillus* spp and other species from Acidobacteria and Firmicutes phyla. The fungi species with significant differential abundance

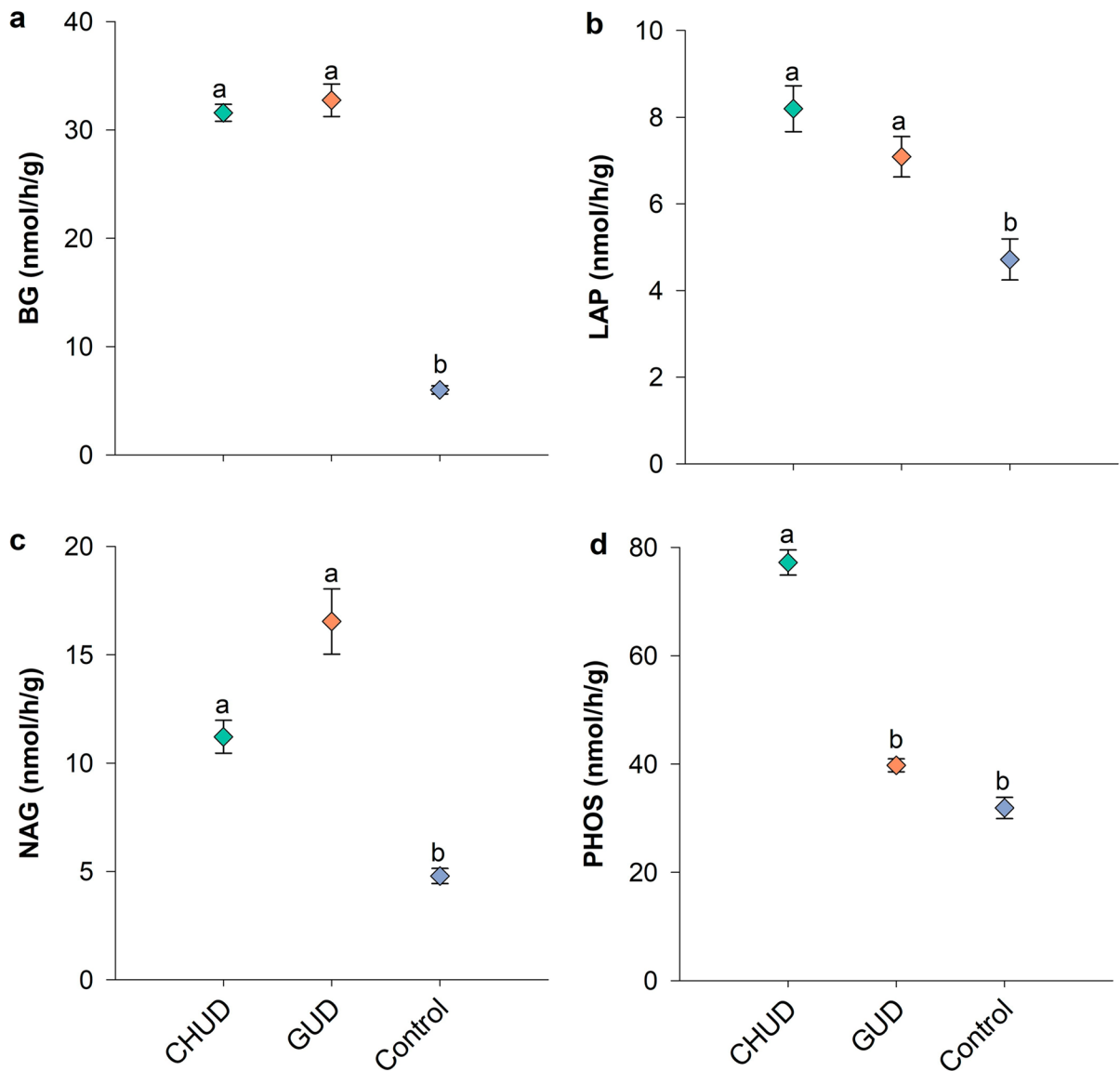


Fig. 3 β -1,4-glucosidase (BG) (a), leucine aminopeptidase (LAP) (b), β -1,4-N-acetylglucosaminidase (NAG) (c), and phosphatase (PHOS) (d) enzyme activities of soils from coffee crop under different soil management. Samples were collected in 2021 from the long-term field experiment. Data represent

mean $\pm$ standard error of $n=3$ independent blocks. Coffee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD). Bars followed by the same letter do not differ by Tukey ($p < 0.05$)

were relatively rare taxa within the community that were affected by soil management practices (Fig. 5B). The CHUD management led to significant increases in *Arthrographis*, *Bifusarium*, *Kernia*, *Fusidium*, and *Arxiella*. In the GUD management, we observed higher

abundance of *Arthrographis*, *Fusidium*, *Atractiella*, and *Rousoella*. Conversely, the Control favored other species such as *Naganishia*, *Myrmecridium*, *Tylopilus*, and *Rousoella*. When comparing CHUD management with others, multiple species had varying abundances (Fig. 5B).

Table 4 Alpha diversity metrics for 16S and ITS ASV richness (observed, Chao1, ACE) and ASV diversity (Shannon, Inverse Simpson, and Fisher)

Soil management	Bacterial Richness			Bacterial Diversity		
	Observed	Chao1	ACE	Shannon	InvSimpson	Fisher
CHUD	565 ± 50 a	575 ± 53 a	577 ± 54 a	5.7 ± 0.06 a	227 ± 11 a	99 ± 10 a
GUD	535 ± 49 a	548 ± 47 a	545 ± 49 a	5.7 ± 0.18 a	229 ± 24 a	92 ± 10 a
Control	668 ± 172 a	681 ± 179 a	678 ± 177 a	6.0 ± 0.5 a	330 ± 86 a	123 ± 38 a
	Fungal Richness			Fungal Diversity		
	Observed	Chao1	ACE	Shannon	InvSimpson	Fisher
CHUD	297 ± 5.8 ab	301 ± 8.9 ab	301 ± 5.1 ab	4.1 ± 0.16 a	27.4 ± 5.2 a	46.8 ± 1.1 ab
GUD	327 ± 25 a	331 ± 26 a	330 ± 26 a	4.3 ± 0.08 a	27.3 ± 4.4 a	52.4 ± 4.8 a
Control	249 ± 26 b	250 ± 16 b	250 ± 15 b	4.1 ± 0.05 a	27.0 ± 1.8 a	38.0 ± 2.7 b

Data represent mean ± standard error of n = 3 independent blocks. Treatments with the same letter do not differ at a 95% significance level (Kruskal–Wallis Rank Sum Test). CHUD: Coffee husk + signal grass; GUD: Gypsum + signal grass

Samples were collected in 2021 from the long-term field experiment

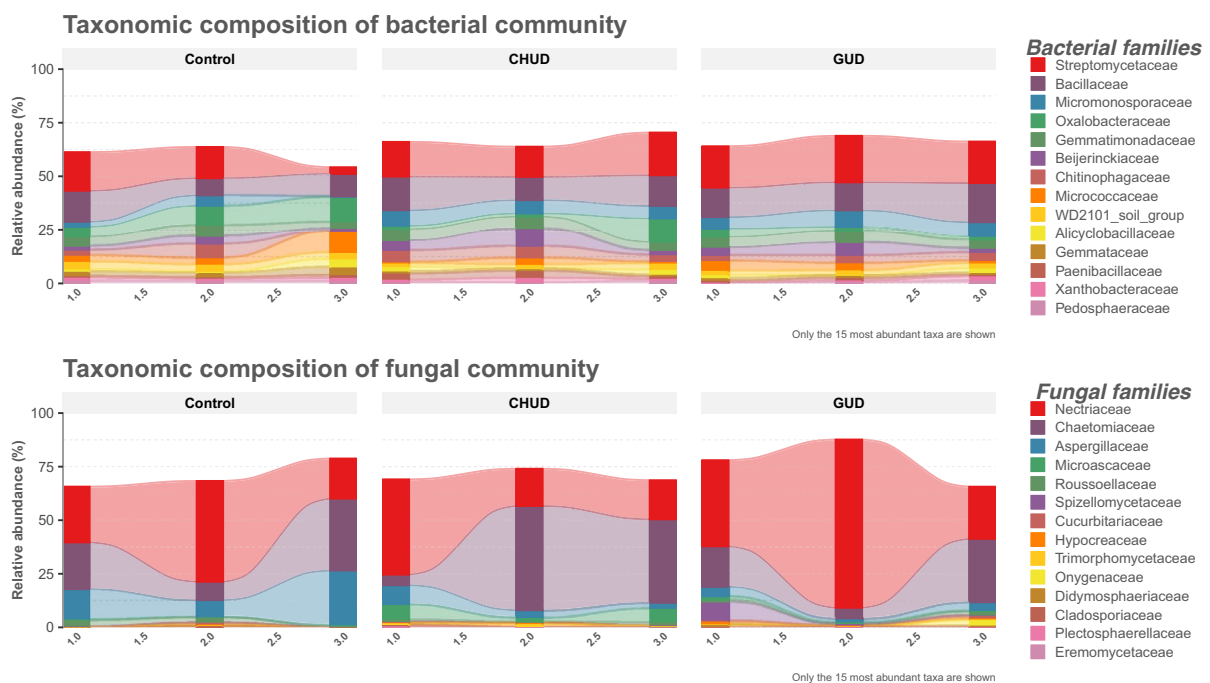


Fig. 4 Relative abundance of the 16S and ITS family level in each treatment, showing the taxonomic composition of the bacterial community and the taxonomic composition of the fungal community. Only the fifteen more abundant taxa are

shown. Samples were collected in 2021 from the long-term field experiment. Coffee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD)

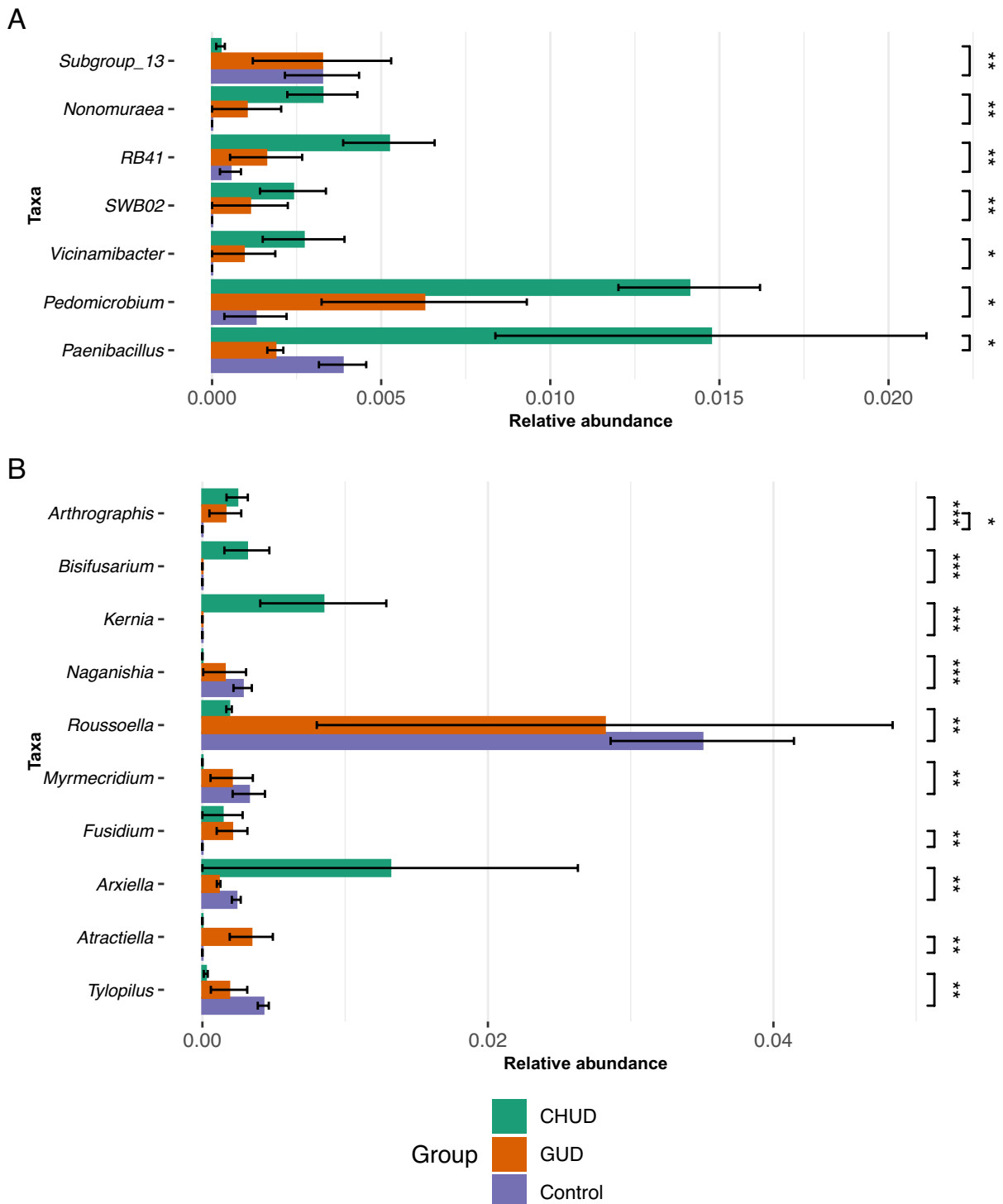


Fig. 5 Differential abundance taxa of the 16S (**A**) and ITS (**B**) genus level. Samples were collected in 2021 from the long-term field experiment. Data represent mean $\pm$ standard error of $n=3$ independent blocks. Coffee husk + signal grass (CHUD),

agricultural gypsum + signal grass (GUD). One (), two (), and three () represent significance at 0.05, 0.01, and 0.001 levels, respectively

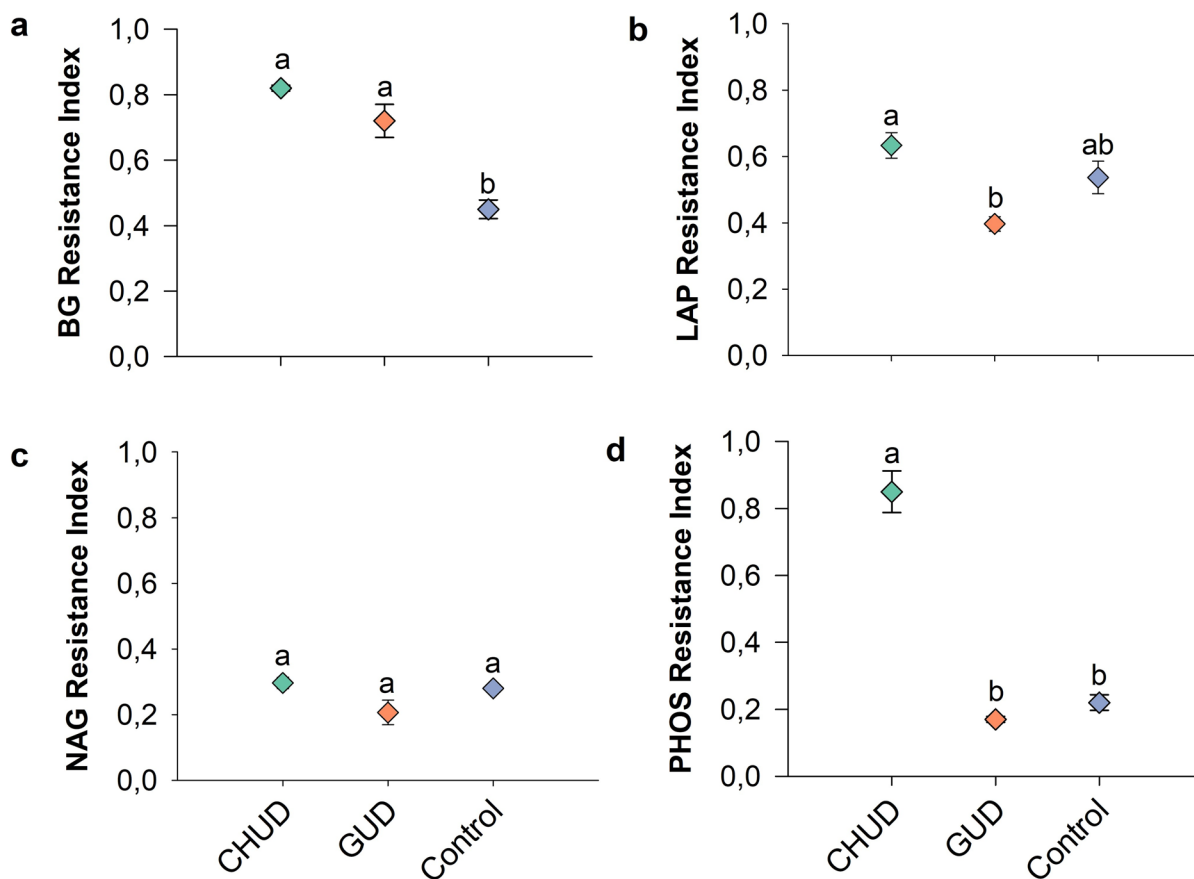


Fig. 6 β -1,4-glucosidase (BG) (a), leucine aminopeptidase (LAP) (b), β -1,4-N-acetylglucosaminidase (NAG) (c), and phosphatase (PHOS) (d) enzyme resistance index of soils under different management. Samples were from the drought incubation study. Data represent mean $\pm$ standard error of

$n=3$ independent blocks. The resistance index is an absolute value calculated from wet vs. drought soils. Coffee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD). Bars followed by the same letter do not differ by Tukey ($p < 0.05$)

Drought response from soils under conservation management

Resistance of microbial soil functions and diversity to drought

There were significant differences in the resistance index (RS) of enzyme activities ($p < 0.05$) (Fig. 6; Table S2) calculated from measured activities in soil samples incubated in Control vs. Drought conditions in the laboratory assay. Regarding BG enzyme activity (Fig. 6a), CHUD and GUD management practices promoted a more drought-resistant environment than Control. CHUD resulted in a higher resistance index for LAP (Fig. 6b) and phosphatase (Fig. 6d) enzymes,

while there were no significant differences in the NAG resistance index (Fig. 6c).

There was no difference in resistance indices calculated using bacterial and fungal alpha diversity ($p > 0.05$; Table S3) measured from soil samples incubated in Control vs. Drought conditions in the laboratory assay. This lack of distinction in calculated resistance indices related to richness (bacterial ~ 0.5 and fungal ~ 0.8) and diversity (bacterial ~ 0.4 and fungal ~ 0.7) would indicate that both bacteria and fungi responded similarly to drought across the different field management treatments. However, consistent changes in the diversity and abundance of bacteria were observed between drought and control conditions across management treatments. In soil samples

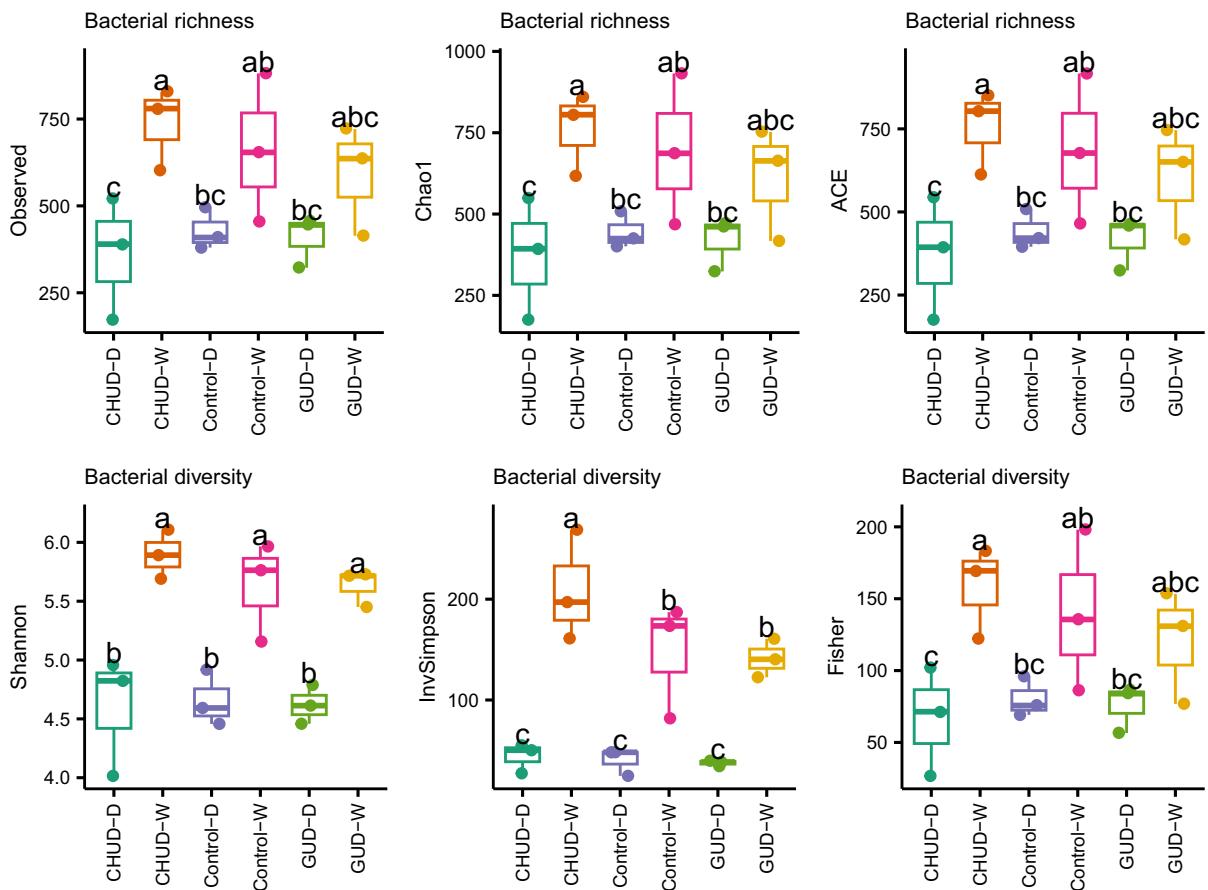


Fig. 7 Alpha diversity metrics for 16S ASV richness (observed, Chao1, ACE) and ASV diversity (Shannon, Inverse Simpson, and Fisher). Samples from the wet (W) vs. drought (D) soils in incubation study. Coffee husk+signal grass

(CHUD), agricultural gypsum+signal grass (GUD). Treatments with the same letter do not have a difference at a 95% statistical significance level of the Kruskal Wallis Rank Sum Test

collected from each management system drought significantly reduced bacterial diversity and richness (Fig. 7). Soil management significantly affected fungal richness and diversity (Fisher) (Fig. 8) regardless of water availability. According to Fisher, the highest increases in fungal richness and diversity were observed with CHUD and GUD management practices (Fig. 8).

Changes in microbial composition and abundance by drought

When water availability changed, the bacterial communities were significantly affected (Fig. 9A). In the fungal communities, besides being affected by drought, the relative abundance also changed

among the different soil managements, which was easier to visualize when comparing treatments from the same block (Fig. 9B). There were significant differences in the differential abundance test of fungal and bacterial communities ($p < 0.05$) (Figs. 10 and 11). Different communities emerge in dry environments, with notable changes occurring in the bacterial families Streptomycetaceae and Bacillaceae and the fungal family Nectriaceae. *Streptomyces* spp. was present in all management, with a significantly higher abundance in drought conditions compared to control samples (Fig. 10). More bacterial species were significantly influenced by drought in the CHUD treatment (Fig. 10) than the others, indicating that changes in soil management may increase the variety of bacteria present that

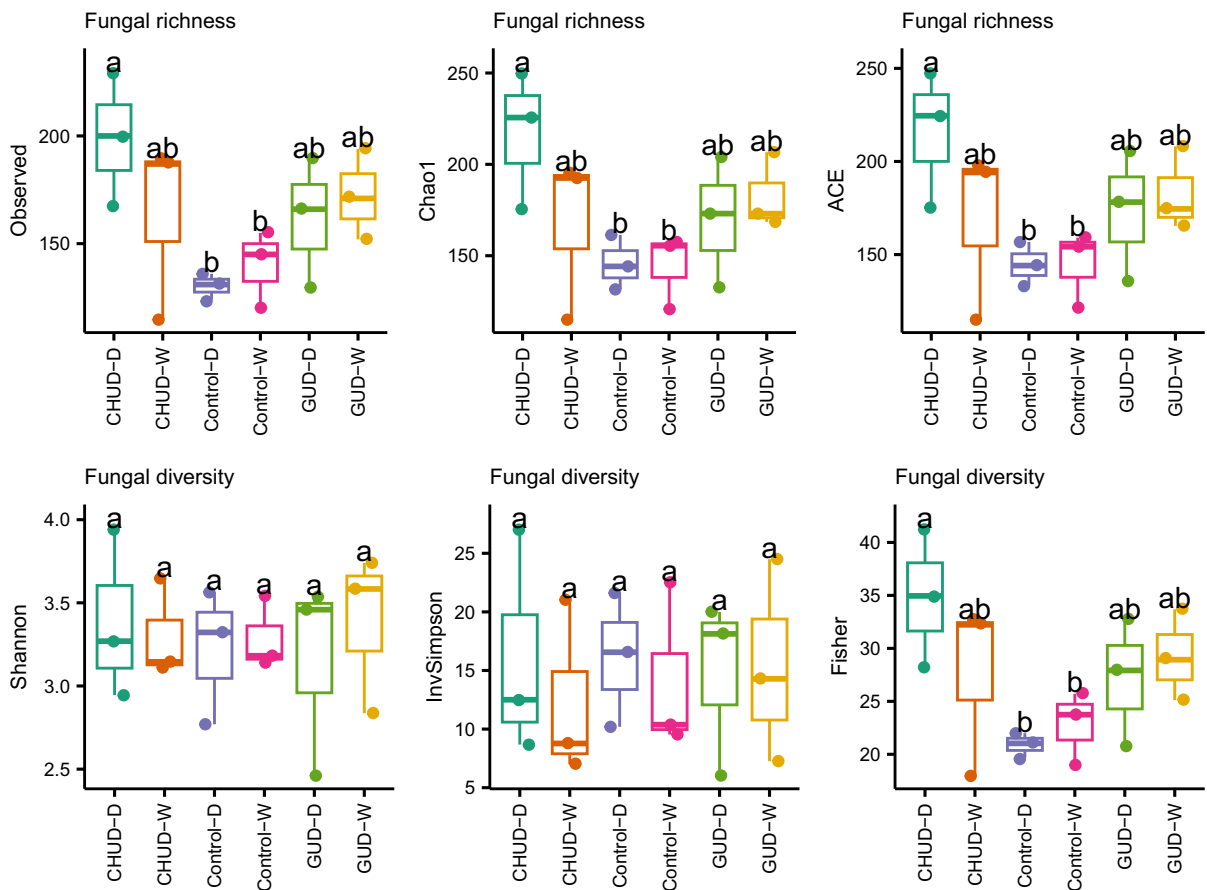


Fig. 8 Alpha diversity metrics for ITS ASV richness (observed, Chao1, ACE) and ASV diversity (Shannon, Inverse Simpson, and Fisher). Samples from wet (W) vs. drought (D) soils in the incubation study. Data represent mean $\pm$ standard

error of $n=3$ independent blocks. Coffee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD). Treatments with the same letter do not differ at a 95% significance level (Kruskal–Wallis Rank Sum Test)

are responsive, both positively and negatively, to drought. *Azospirillum* spp. (Proteobacteria phylum) was observed only in the CHUD treatment and significantly decreased under drought conditions, while *Paenibacillus* spp. was increased by drought conditions in CHUD treatments (Fig. 10).

In contrast, the fungal community was largely unresponsive to drought as assessed by differential abundance analysis, with only one significant difference detected in the CHUD treatment (Fig. 11). In the CHUD management, the only species that changed regarding water availability was *Fusarium* sp., with significantly increased abundance in drought conditions.

Coffee yield and quality beverage

Increasing soil health due to sustainable soil management improves soil functions and ecosystem services, positively affecting plant yield and beverage quality of the crop harvested at the end of the study in 2021 following six years of conservation management (Fig. 12). Soil management with signal grass + coffee husk (2367 kg·ha⁻¹) or gypsum (2684 kg·ha⁻¹) resulted in a yield approximately 70% higher than the Control treatment (1475 kg·ha⁻¹) (Fig. 12A). Regarding beverage quality, the CHUD management (84 points) scored higher than GUD and Control (82 points average) (Fig. 12B).

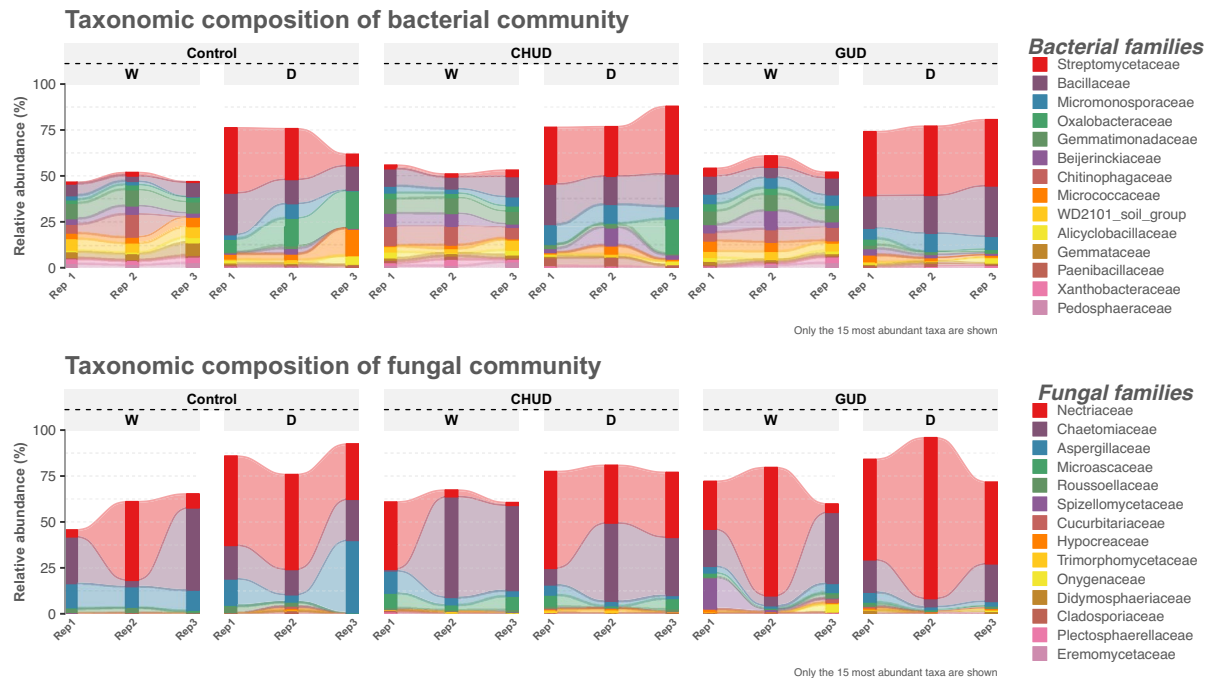


Fig. 9 Relative abundance of the 16S and ITS family level in each treatment, showing the taxonomic composition of the bacterial community and the taxonomic composition of the fungal community. Only the fifteen more abundant taxa are

shown. Samples from the wet (W) vs. drought (D) soils in incubation study. Coffee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD)

Discussion

The findings of this study indicate that combining cover crops and soil amendment conditioners into coffee fields significantly enhances soil chemical, physical, and biological attributes that lead to healthier soils, increased coffee yield and quality, and improved resistance of soil functions to drought stress (Silva et al. 2015, 2019, 2021; Barbosa et al. 2020; Voltolini et al. 2022; Veloso et al. 2023; Vilela et al. 2023, 2024).

Long-term effects of intercropping and soil conditioners on soil health

Chemical indicators

Adding chemical amendments such as gypsum, organic materials like coffee husk, and keeping the soil covered with live plants or crop residues (e.g., signal grass) while minimizing soil disturbance enhances chemical (fertility), physical, and biological

soil properties within the soil profile (Voltolini et al. 2020, 2022; Vilela et al. 2023, 2024). Such management built up a favorable environment for plant root and development, improving overall soil health and potentially reducing the need for chemical inputs (Carducci et al. 2015; Jiang et al. 2015; Withers et al. 2018; Voltolini et al. 2020; Castanheira et al. 2022; Vilela et al. 2024).

Most of the highly-weathered soils found throughout the tropics, which are frequently classified as Oxisols, have naturally poor fertility resulting from low pH, high Al toxicity, low SOM content, and nutrient availability (Sanchez 2019; Moreira et al. 2023). Management strategies that add SOM can increase CEC and P availability due to the carboxylic and phenolic radicals, as observed in the treatments with increased SOM content (CHUD and GUD) in the current study (Withers et al. 2018; Li et al. 2019; Voltolini et al. 2020; Zavaschi et al. 2020). Increased SOM positively impacts soil health and crop yield (Lal 2020b). Conversely, in the Control treatment, SOM

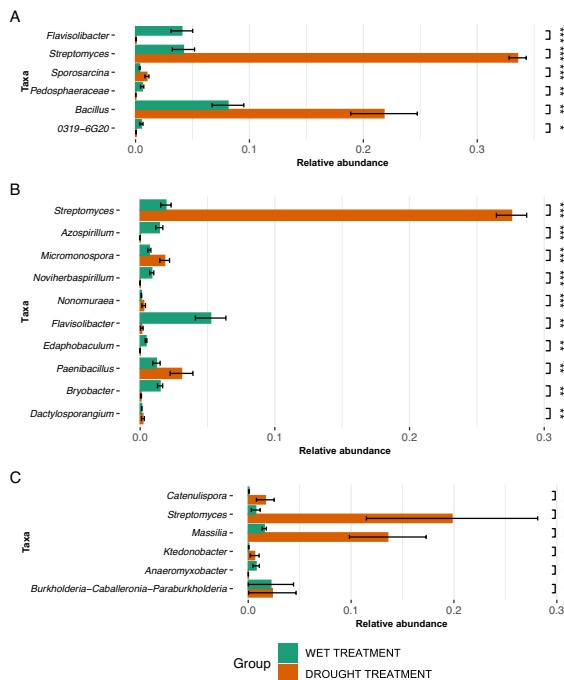


Fig. 10 Differential abundance taxa of the 16S genus level. Agricultural gypsum+signal grass (A), coffee husk+signal grass (B), and Control (C) treatments. Samples from wet vs. drought soils in the incubation study. Data represent mean $\pm$ standard error of $n=3$ independent blocks. One (*), two (**), and three (***) represent significance at 0.05, 0.01, and 0.001 levels, respectively

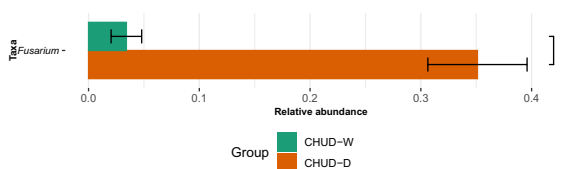


Fig. 11 Differential abundance taxa of the ITS genus level. Coffee husk+signal grass under drought (CHUD-D) and wet (CHUD-W) conditions. Samples from wet vs. drought soils in the incubation study. Data represent mean $\pm$ standard error of $n=3$ independent blocks. One (*), two (**), and three (***) represent significance at 0.05, 0.01, and 0.001 levels, respectively

accumulation was negative, indicating the bare soil contribution to SOM degradation, which impairs soil health due to CO_2 release (Lavalley et al. 2020).

Besides enhancing SOM, the combination of signal grass with coffee husk or gypsum increased extractable soil nutrients. Coffee husk is a rich source

of K, largely supplying the coffee needs of this nutrient (Castanheira et al. 2019; Fernandes et al. 2020; Voltolini et al. 2020; Vilela et al. 2024). Gypsum, a subsurface soil conditioner, reduces Al toxicity and provides Ca in deeper layers of the soil which favors plant rooting capacity, especially when combined with signal grass due to the improvement of nutrient cycling (Ramos et al. 2013; Carducci et al. 2015; Moraes et al. 2016; Baptistella et al. 2020). Additionally, signal grass intercropped with coffee trees may improve P cycling, contributing to the supply of this nutrient (Baptistella et al. 2022).

Physical indicators

The adopted management practices also improved physical soil health indicators. In the current study, we observed that practices that favored SOM accumulation also contributed to an increase in soil water content. Both SOM (Table 2) and soil water content (Table 3) increased following the order Control < GUD < CHUD, highlighting the contribution of coffee husk in enhancing SOM and consequentially increasing soil moisture (Voltolini et al. 2020; Castanheira et al. 2022; Vilela et al. 2023, 2024). Combining signal grass with organic soil amendments further enhanced soil moisture, making it available for uptake by coffee plants (Castanheira et al. 2022; Vilela et al. 2023).

Urochloa species can improve soil porosity and water retention due to their aggressive root system and the formation of root-associated bio-pores, which enhance water infiltration (Franco et al. 2020). Furthermore, the synergistic effect of gypsum and the plant root system increases soil porosity, especially in deeper layers, through Ca input and clay flocculation (Serafim et al. 2013; Ramos et al. 2013; Rocha et al. 2014; Silva et al. 2015; Barbosa et al. 2020).

Climatic conditions at the time of sampling are relevant for interpreting soil water availability. The undisturbed soil cores for physical analyses were collected in early May 2023, at the onset of the dry season. Rainfall in May 2023 was comparable to that observed in August of previous years (e.g., 2020 and 2021). This similarity likely contributed to the absence of significant differences in AWC among treatments, as short-term climatic effects

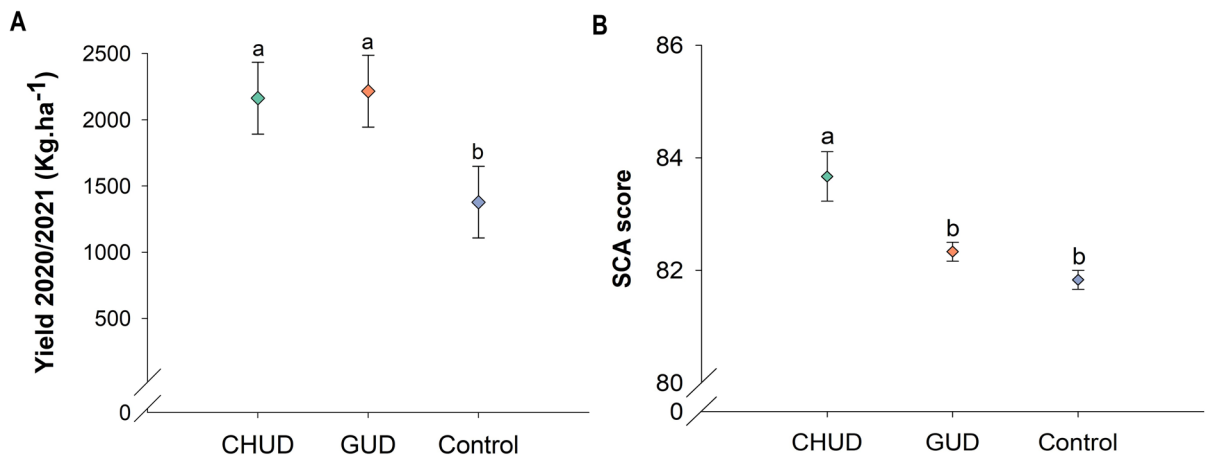


Fig. 12 Yield (2020/2021 biennium) (A) and sensory analysis based on Specialty Coffee Association (SCA) protocol (B) in coffee crops under different soil management. Data represent mean $\pm$ standard error of $n=3$ independent blocks. Cof-

fee husk + signal grass (CHUD), agricultural gypsum + signal grass (GUD). Bars followed by the same letter do not differ by Tukey ($p < 0.05$)

may have masked treatment-related variability and indicate that the measured values largely reflect long-term management.

Soil bulk density did not change between the soil management treatments and the Control, which aligns with expectations due to the intrinsic characteristics of Oxisols, such as their highly weathered clay mineralogy (Azevedo et al. 2022; Pessoa et al. 2024). Long-term changes in soil management leading to increased soil physical quality may not result in differences in soil bulk density and AWC (Silva et al. 2021). The average soil bulk density (1.29 g cm^{-3}) is far from the critical threshold for root and water limitation (1.53 g cm^{-3} for 440 g kg^{-1} clay Oxisol) and close to the beneficial range for crops (1.3 g cm^{-3} for 440 g kg^{-1} clay Oxisol) according to standards obtained for Oxisols under cropping systems in the Brazilian Cerrado (Severiano et al. 2011). These values also align with those previously reported in other Oxisols with coffee intercropped with *Urochloa* spp. (Silva et al. 2015). Because noticeable declines in AWC generally occur only when bulk density approaches such critical thresholds, our results support the interpretation that, under the climatic conditions of May 2023, AWC did not differ significantly among treatments, despite observed differences in soil porosity.

Biological indicators

Integrated conservation management impacts soil functionality, particularly through the SOM input, which contributes to the increase in enzymes related to carbon cycling from organic residues, such as β -glucosidase (Singh et al. 2023). The intercropping of signal grass with coffee plants can increase organic P cycling by boosting phosphatase activity (Baptistella et al. 2022). The enhanced SOM due to coffee husk may also help reduce soil P fixation, which may explain the higher phosphatase activity observed in the combination of signal grass and coffee husk (Voltolini et al. 2020; Castanheira et al. 2022; Singh et al. 2023). Techniques that increase SOM have also been associated with enhanced N cycling, which may explain the higher activity of N-cycling enzymes in the treatments that promoted SOM accumulation due to conservation management (Velooso et al. 2023; Petermann et al. 2024), which is consistent with broader evidence that soil microbial communities and their functions are highly responsive to changes in water availability, organic inputs, and management history (De Silva et al. 2025).

Soil conservation management affected the fungal community without significantly altering bacterial richness and diversity, which supports previous findings that bacterial communities are less sensitive to

management changes than fungal communities (Lau and Lennon 2011). Management without using conservation techniques (e.g., cover crop, no-till), with disturbed soils, may contribute to the reduction of fungal diversity and soil functionality (Veloso et al. 2023; Wang et al. 2023). Although diversity differences were not detected between treatments, the enzyme data indicated reduced functionality in the control (bare soil) compared to signal grass with coffee husk or gypsum treatments. This pattern is also consistent with recent studies showing that soil management can shape coffee-associated soil microbiomes even when responses differ among taxonomic groups and diversity metrics (Kutos et al. 2024).

The fungal community in conservation management was dominated by *Ascomycota*, with some *Glomeromycota* observed in the GUD treatment. *Glomeromycota*, which includes arbuscular mycorrhizal fungi, are generally known to enhance the soil volume explored by roots and increase water and P uptake by the plants (Veloso et al. 2023). Many fungi under conservation management are linked to biological control, suppressing soil-borne pathogens (Köhl et al. 1995). For instance, the CHUD treatment contained *Hypocreaceae* (e.g., *Trichoderma* spp.), known for their role in biological control, while the GUD treatment favored *Chaetomiaceae*, with *Chaetomium* spp. being reported as a biocontrol agent for foliar diseases in coffee (Köhl et al. 1995; Laborde et al. 2019). These observations suggest that conservation management may favor fungal groups associated with biologically active and potentially more functionally balanced soils, although direct biocontrol activity was not evaluated in the present study.

The differential abundance test identified taxa that were significantly affected by the treatments (Paulson et al. 2013). *Coffea arabica* cultivation, influenced by moisture levels, has been shown to drive selection of specific soil microbiome communities and networks (Veloso et al. 2023). CHUD treatment promoted bacteria related to biological control, such as *Paenibacillus* spp., and others from the *Acidobacteria* and *Firmicutes* phyla, which are commonly found in environments with high SOM and moisture (Köhl et al. 1995; Singh et al. 2023). The increase in these bacterial phyla in our study may be associated with enhanced enzyme activities involved in C, N and P-cycling, reflecting improved soil health and

microbial function (Nunes et al. 2020; Davis et al. 2023; Singh et al. 2023; Petermann et al. 2024). More broadly, recent evidence suggests that soil microbiomes can show consistent responses to environmental extremes, although the magnitude and functional implications of these responses remain context dependent across management systems (Knight et al. 2024; Kost et al. 2024).

Consequences of increased soil health for soil functions and ecosystem services

Effects of intercropping and soil conditioners on drought resistance

Conservation management favors soil health and may increase the resistance of some soil functions to disturbances such as drought (Delgado-Baquerizo et al. 2017). Management practices that maintain higher soil moisture and SOM content may improve the resistance of soil functions to drought (Vilela et al. 2023, 2024; Wang et al. 2023). In the present study, the controlled incubation assay was used as a complementary approach to isolate drought as a stress factor and compare soils with contrasting long-term management histories under standardized conditions. Treatments that initially promoted higher enzyme activity (Fig. 3) were those with higher drought resistance indices after the incubation trial (Fig. 6). These results suggest that long-term conservation practices may have contributed to a soil environment better able to sustain some enzyme activities under drought than bare-soil management. This interpretation is consistent with recent evidence that soil microbial communities and functions can respond predictably to extreme events, although the magnitude of resistance and resilience depends on management context (De Silva et al. 2025; Knight et al. 2024; Kost et al. 2024).

The treatments with higher microbial diversity and richness did not necessarily show large declines in calculated resistance indices before and after drought disturbance (Delgado-Baquerizo et al. 2017; Orwin and Wardle 2004). These results may be related to the "resistance trap," in which environments with already low diversity and richness do not decrease (resulting in a high calculated resistance index) but are not necessarily in a positive state after drought disturbance, compared to treatments with higher abundance,

diversity, or activity that experience some loss under drought (Davis et al. 2023). In this study, drought treatments consistently and significantly reduced bacterial richness and diversity, regardless of soil management, whereas fungal communities were largely unaffected, which has been observed in other studies (Wan et al. 2023). Water availability plays a crucial role in regulating bacterial communities in complex microbiomes (Lau and Lennon 2011), while conservation management supports increased richness and diversity of fungi communities (Lau and Lennon 2011; Veloso et al. 2023), and drought responses may differ between bacterial and fungal groups according to their ecological strategies and resistance mechanisms (De Silva et al. 2025).

There were more changes in the taxonomic composition of bacterial communities than in fungal communities in response to drought. In *Coffea arabica* production, dry conditions may select for microbial communities with lower diversity than those in humid environments (Veloso et al. 2023). The most significant changes in bacterial families (Streptomycetaceae and Bacillaceae) and fungal families (Nectriaceae) may be related to their development of resistance structures (e.g., exospores, endospores, and chlamydospores) which enable them to survive in drought conditions (Köhl et al. 1995). Wet conditions may increase competition due to the germination of these resistance structures, which alters microbial networks and impacts soil functions (Köhl et al. 1995; Veloso et al. 2023; Wang et al. 2023).

The Chaetomiaceae family was stable across water-availability conditions and was not significantly affected by drought in this study. Members of this family have been reported as biological control agents, including against foliar disease pathogens such as *Cercospora coffeicola* (Köhl et al. 1995; Laborde et al. 2019). This interpretation is also consistent with previous results from the same experimental platform, in which coffee plants intercropped with signal grass and treated with coffee husk showed reduced incidence and severity of brown eye spot caused by *Cercospora coffeicola*, although the present study does not allow direct attribution of this response to specific microbial taxa (Resende et al. 2022b, a).

In the differential abundance test, each treatment selected specific microbial communities, with rare bacterial taxa influenced by soil management and drought. Bacterial species such as *Streptomyces* spp.

increased under drought due to their ability to form resistant structures (e.g., exospores), enhancing their stability in dry conditions (Köhl et al. 1995). The presence of *Azospirillum* spp. in the CHUD treatment highlights an environment conducive to growth-promoting bacteria that may help plants resist drought stress (Fukami et al. 2018). This species is also a nitrogen-fixing bacteria (NFB) commonly associated with grasses (Fukami et al. 2018), which may be related to the improvement of enzymes related to N-cycling in the soil (Fig. 3B,C) (Petermann et al. 2024). In addition, *Paenibacillus*, a biocontrol agent, was favored in drought conditions due to its endospores (Köhl et al. 1995). Overall, these findings suggest that drought did not eliminate the occurrence of taxa with reported growth-promoting or biocontrol potential in the signal grass with coffee husk or gypsum treatments; however, the functional activity of these taxa under drought was not directly tested in the present study.

Only one significant shift in fungal taxa was observed, with an increase in *Fusarium* under the CHUD treatment under drought conditions. While *Fusarium* forms resistant structures (chlamydospores) that give it an advantage in dry conditions, this species is less competitive in moist soils, allowing other fungi to thrive (Pfenning and Martins 2000). Although this result prompts further questions regarding the influence of drought on plant-soil pathogen interactions, we note that not all *Fusarium* species are pathogenic to coffee plants, so their presence may not necessarily indicate a threat (Pfenning and Martins 2000). Future studies should directly evaluate whether these compositional shifts are translated into measurable effects on soil functioning or plant health under drought.

Coffee yield and quality

The results of this study further indicate that long-term sustainable soil management may enhance coffee yield and support beverage quality through improvements in soil health, including chemical, biological, and physical attributes. Combined techniques that favor the soil covering (mainly signal grass) together with improvements in soil health indicators (e.g., SOM) contributed to increasing coffee yield and reducing biennial variability (Lal 2020b; Voltolini et al. 2022).

Many aspects affect coffee quality, which may be related to the environment, *terroir*, management in the field, and post-harvest techniques. In this study, the changes at the field level with sustainable management (CHUD) may have resulted in an environment that favored the improvement of coffee quality due to better plant nutrition and soil microbiome networks (Martinez et al. 2014; Veloso et al. 2023). These soil microbial communities may also influence the microbiome of coffee fruits, with potential implications for beverage quality (Veloso et al. 2023).

Conclusion

This six-year field study showed that soil management combining coffee husk application with signal grass cover in coffee interrow was associated with improved soil chemical, physical, and biological indicators relative to bare-soil management in a representative coffee-growing region of South Minas Gerais, Brazil. These responses were accompanied by higher coffee yield and beverage quality, and by greater resistance of some soil functional indicators to the drought treatment evaluated in the laboratory incubation assay. Among the management systems evaluated, the coffee husk+signal grass treatment showed the most consistent positive responses across soil health indicators and agronomic performance.

These findings should be interpreted in light of the study scope. A major strength of this work is the long-term field evaluation integrating soil health, microbiome, yield, and beverage-quality assessments under representative tropical coffee-growing conditions. At the same time, the drought-related responses were assessed using a controlled laboratory incubation, which provides a useful comparative approach but does not capture the full complexity of field drought dynamics. In addition, the different datasets were collected as complementary components of the long-term assessment rather than as simultaneous measurements within a single sampling campaign. Therefore, the results support the potential of combining residue amendment and permanent cover to improve soil functioning and coffee performance under the conditions evaluated, while broader validation across sites, years, and drought scenarios would further strengthen inference on transferability. Future

studies should also directly test the functional relevance of the microbial taxa associated with drought response and plant health.

Acknowledgements The authors would like to thank the Consórcio Pesquisa Café, INCTCafê, the Texas Tech University (TTU) Soil Ecology Lab, the Department of Plant and Soil Science at TTU, the Texas Tech Center for Biotechnology and Genomics, CAPES, FAPEMIG, CNPq, the Coffee Sector/UFLA, and the Department of Soil Science/UFLA for their support.

Authors contributions All authors contributed to the study conception and design, data acquisition, analysis, interpretation, and drafting of the manuscript. All authors read and approved the final version.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This project was supported by Consórcio Pesquisa Café, INCTCafê, CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais), CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), and Texas Tech University. Funding also included institutional support from the Coffee Sector/UFLA and the Department of Soil Science/UFLA.

Data availability The raw 16S rRNA and ITS sequencing data generated in this study have been deposited in the **National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA)** under the following accession:

BioProject: PRJNA1348911 — *Soil Health and Microbiome Interactions: Enhancing Drought Resistance in Tropical Coffee Agroecosystems*.

Bacterial and fungal sequences have been uploaded to the NCBI Sequence Read Archive under accession PRJNA1348911. All other data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Azevedo RP, Corinto LM, Peixoto DS et al (2022) Deep tillage strategies in perennial crop installation: Structural changes in contrasting soil classes. *Plants* 11:1–21. <https://doi.org/10.3390/plants11172255>
- Baptistella JLC, De ASAL, Favarin JL, Mazzafera P (2020) Urochloa in tropical agroecosystems. *Front Sustain Food Syst* 4:1–17. <https://doi.org/10.3389/fsufs.2020.00119>
- Baptistella JLC, Teles APB, Favarin JL et al (2022) Phosphorus cycling by *Urochloa decumbens* intercropped with coffee. *Exp Agric* 58:1–16. <https://doi.org/10.1017/s0014479722000321>
- Barbosa SM, Silva BM, de Oliveira GC et al (2020) Deep furrow and additional liming for coffee cultivation under first year in a naturally dense inceptisol. *Geoderma* 357:113934. <https://doi.org/10.1016/j.geoderma.2019.113934>
- Bolyen E, Rideout JR, Dillon MR et al (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat Biotechnol* 37:852–857. <https://doi.org/10.1038/s41587-019-0209-9>
- Borgo L, Rabêlo FHS, Marchiori PER, Guilherme LRG, Guerra-Guimarães L, Resende MLV (2025) Impact of drought, heat, excess light, and salinity on coffee production: Strategies for mitigating stress through plant breeding and nutrition. *Agriculture* 15:9. <https://doi.org/10.3390/agriculture15010009>
- Callahan BJ, McMurdie PJ, Rosen MJ et al (2016) DADA2: High-resolution sample inference from Illumina amplicon data. *Nat Methods* 13:581–83. <https://doi.org/10.1038/nmeth.3869>
- Carducci C, Oliveira G, Curi N, Heck R (2015) Gypsum effects on the spatial distribution of coffee roots and the pores system in oxidic Brazilian Latosol. *Soil Tillage Res* 145:171–180
- Castanheira DT, Barcelos TR, Guimarães RJ et al (2019) Agronomic techniques for mitigating the effects of water restriction on coffee crops. *Coffee Sci* 14:104–115. <https://doi.org/10.25186/cs.v14i1.1542>
- Castanheira DT, Guimarães RJ, Rezende TT et al (2022) Optimization of water use in “*Coffea arabica*” L. grown under different agronomic practices. *Aust J Crop Sci* 16:870
- Curi NC, Ker JC, Novais RF et al (2017) Pedologia: solos dos biomas brasileiros. Sociedade Brasileira de Ciência do Solo, Viçosa
- da Silva FC (2009) Manual de Análises Químicas de Solos, Plantas e Fertilizantes, 2nd edn. Embrapa Solos, Brasília, DF
- da Silva RF, da Severiano EC, de Oliveira GC et al (2021) Changes in soil profile hydraulic properties and porosity as affected by deep tillage soil preparation and Brachiaria grass intercropping in a recent coffee plantation on a naturally dense Inceptisol. *Soil Tillage Res* 213:105127. <https://doi.org/10.1016/j.still.2021.105127>
- da Severiano EC, de Oliveira GC, de Júnior MSD, et al (2011) Structural changes in latosols of the cerrado region: I - relationships between soil physical properties and least limiting water range. *Rev Bras Cienc do Solo* 35:773–782. <https://doi.org/10.1590/S0100-06832011000300013>
- Davis AG, Huggins DR, Reganold JP (2023) Linking soil health and ecological resilience to achieve agricultural sustainability. *Front Ecol Environ* 131–139. <https://doi.org/10.1002/fee.2594>
- de Moraes NC, Jakelaitis A, Cardoso IS et al (2016) Effects of herbicides and foliar fertilizer in tank mix in soybean. *Magistra* 28:233–243
- De Silva S, KariyawasamHettiGamage L, Thapa VR (2025) Impact of drought on soil microbial communities. *Microorganisms* 13:1625. <https://doi.org/10.3390/microorganisms13071625>
- DeForest JL (2009) The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using MUB-linked substrates and l-DOPA. *Soil Biol Biochem* 41:1180–1186. <https://doi.org/10.1016/j.soilbio.2009.02.029>
- Delgado-Baquerizo M, Eldridge DJ, Ochoa V, Gozalo B (2017) Soil microbial communities drive the resistance of ecosystem multifunctionality to global change in drylands across the globe. 1295–1305. <https://doi.org/10.1111/ele.12826>
- Dick RP, Dick LK, Deng S et al (2018) Cross-laboratory comparison of fluorimetric microplate and colorimetric bench-scale soil enzyme assays. *Soil Biol Biochem* 121:240–248. <https://doi.org/10.1016/j.soilbio.2017.12.020>
- Fernandes A, Júnior E, de Santana M et al (2020) Use of organic fertilization with irrigation in coffee production in Brazilian cerrado. *Rev Ambient e Água* 15:1–13
- Ferreira EB, Cavalcanti PP, Nogueira DA (2021) ExpDes: Experimental designs package. R package version 1.2.2. Available at: <https://cran.r-project.org/web/packages/ExpDes/index.html>. Accessed 12 Nov 2024
- Franco ALC, Cherubin MR, Cerri CEP, et al (2020) Linking soil engineers, structural stability, and organic matter allocation to unravel soil carbon responses to land-use change. *Soil Biol Biochem* 150. <https://doi.org/10.1016/j.soilbio.2020.107998>
- Fukami J, Cerezini P, Hungria M (2018) *Azospirillum*: benefits that go far beyond biological nitrogen fixation. *AMB Express* 8:1–12. <https://doi.org/10.1186/s13568-018-0608-1>
- Galdos M V, Brown E, Rosolem CA, et al (2020) Brachiaria species influence nitrate transport in soil by modifying soil structure with their root system. *Sci Rep* 10. <https://doi.org/10.1038/s41598-020-61986-0>
- Ghimire R, Thapa VR, Acosta-Martinez V et al (2023) Soil health assessment and management framework for water-limited environments: examples from the great plains of the USA. *Soil Syst* 7:22. <https://doi.org/10.3390/soilsystems7010022>
- Guimarães PTG, Garcia AWR, Alvarez VVH et al (1999) Cafeeiro. In: Ribeiro AC, Guimarães PTG, Alvarez VVH (eds) *Recomendações para o uso de corretivos e fertilizantes em Minas Gerais, 5ª Aproximação*. UFV, Viçosa, pp 289–302
- IPCC (2021) Assessment report 6 climate change 2021: The physical science basis
- Jiang J, Yuan M, Xu R, Bish DL (2015) Mobilization of phosphate in variable-charge soils amended with biochars derived from crop straws. *Soil Tillage Res* 146:139–147. <https://doi.org/10.1016/j.still.2014.10.009>

- Kavamura VN, Santos SN, da Silva JL et al (2013) Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. *Microbiol Res* 168:183–191. <https://doi.org/10.1016/j.micres.2012.12.002>
- Knight CG, Nicolitch O, Griffiths RI et al (2024) Soil microbiomes show consistent and predictable responses to extreme events. *Nature* 636:690–696. <https://doi.org/10.1038/s41586-024-08185-3>
- Köhl J, van der Plas CH, Molhoek WML, Fokkema NJ (1995) Effect of interrupted leaf wetness periods on suppression of sporulation of *Botrytis allii* and *B. cinerea* by antagonists on dead onion leaves. *Eur J Plant Pathol* 101:627–637. <https://doi.org/10.1007/BF01874867>
- Kost E, Kundel D, Feola Conz R, Mäder P, Krause H-M, Six J, Mayer J, Hartmann M (2024) Soil microbial resistance and resilience to drought under organic and conventional farming. *Eur J Soil Biol* 123:103690. <https://doi.org/10.1016/j.ejsobi.2024.103690>
- Kutos S, Bennett RE, Rao MV, Fleischer RC, Rice RA, Muletz-Wolz CR (2024) Farm management and shade tree species influence coffee soil microbiomes in Central and South America. *Appl Soil Ecol* 202:105571. <https://doi.org/10.1016/j.apsoil.2024.105571>
- Laborde CMF, dos Botelho DMS, Rodríguez GAA et al (2019) *Phialomyces macrosporus* reduces cercospora coffeicola survival on symptomatic coffee leaves. *Coffee Sci* 14:1–11
- Lal R (2020a) Regenerative agriculture for food and climate. *J Soil Water Conserv* 75:123A–124A. <https://doi.org/10.2489/jswc.2020.0620A>
- Lal R (2020b) Soil organic matter content and crop yield. *J Soil Water Conserv* 75:27–32. <https://doi.org/10.2489/JSWC.75.2.27A>
- Lau JA, Lennon JT (2011) Evolutionary ecology of plant-microbe interactions: soil microbial structure alters selection on plant traits. *New Phytol* 192:215–224. <https://doi.org/10.1111/j.1469-8137.2011.03790.x>
- Lavallee JM, Soong JL, Cotrufo MF (2020) Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Glob Chang Biol* 26:261–273. <https://doi.org/10.1111/GCB.14859>
- Lehman R, Osborne S, McGraw K (2019) Stacking agricultural management tactics to promote improvements in soil structure and microbial activities. *Agronomy* 9:539. <https://doi.org/10.3390/agronomy9090539>
- Lehmann J, Kleber M (2015) The contentious nature of soil organic matter. *Nature* 528:60–68. <https://doi.org/10.1038/nature16069>
- Lehmann J, Bossio DA, Kögel-Knabner I, Rillig MC (2020) The concept and future prospects of soil health. *Nat Rev Earth Environ* 1:544–553. <https://doi.org/10.1038/s43017-020-0080-8>
- Li J, Wan X, Liu X et al (2019) Changes in soil physical and chemical characteristics in intensively cultivated greenhouse vegetable fields in North China. *Soil Tillage Res* 195:104366. <https://doi.org/10.1016/j.still.2019.104366>
- Liu C, Cui Y, Li X, Yao M (2021) Microeco: an R package for data mining in microbial community ecology. *FEMS Microbiol Ecol* 97:fiiaa255. <https://doi.org/10.1093/femsec/fiaa255>
- Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. *Embnetjournal* 17:10–12. <https://doi.org/10.14806/ej.17.1.200>
- Martinez HEP, Clemente JM, De Lacerda JS et al (2014) Nutrição mineral do cafeeiro e qualidade da bebida. *Rev Ceres* 61:838–848. <https://doi.org/10.1590/0034-737X201461000009>
- Moreira SG, Hoogenboom G, Nunes MR et al (2023) Circular agriculture increases food production and can reduce N fertilizer use of commercial farms for tropical environments. *Sci Total Environ* 879:163031. <https://doi.org/10.1016/j.scitotenv.2023.163031>
- Naylor D, Coleman-Derr D (2018) Drought stress and root-associated bacterial communities. *Front Plant Sci* 8:1–16. <https://doi.org/10.3389/fpls.2017.02223>
- Nilsson RH, Larsson K-H, Taylor AFS et al (2018) The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res* 47:D259–64. <https://doi.org/10.1093/nar/gky102>
- Nunes MR, Karlen DL, Veum KS et al (2020) Biological soil health indicators respond to tillage intensity: a US meta-analysis. *Geoderma* 369:114335. <https://doi.org/10.1016/j.geoderma.2020.114335>
- Orwin KH, Wardle DA (2004) New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. 36:1907–1912. <https://doi.org/10.1016/j.soilbio.2004.04.036>
- Paula FS, Rodrigues JLM, Zhou J et al (2014) Land use change alters functional gene diversity, composition and abundance in Amazon forest soil microbial communities. *Mol Ecol* 23:2988–2999. <https://doi.org/10.1111/mec.12786>
- Paulson J, Stine O, Bravo HC, Pop M (2013) Differential abundance analysis for microbial marker-gene surveys. *Nat Methods*. <https://doi.org/10.1038/nmeth.2658>
- Pessoa TN, Bovi RC, Nunes MR, et al (2024) Clay mineral composition drives soil structure behavior and the associated physical properties in Brazilian Oxisols. *Geoderma Reg* 38. <https://doi.org/10.1016/j.geodrs.2024.e00837>
- Petermann BJ, Lewis K, Acosta-Martinez V, et al (2024) Soil health influenced more by conservation tillage and cropping practice than irrigation level in a sandy semiarid cotton system. *Soil Sci Soc Am J* 1–19. <https://doi.org/10.1002/saj2.20737>
- Pfenning LH, Martins MF (2000) Espécies de *Fusarium* associados ao cafeeiro na região sul de Minas Gerais. Poços de Caldas, MG
- Quast C, Priesse 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>
- R Development Core Team R (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing
- Ramos BZ, Toledo JPVF, de Lima JM et al (2013) Gypsum applications to coffee: influence on calcium, magnesium and potassium contents and pH of the solution of a dystrophic red latosol. *Rev Bras Ciência Do Solo* 37:1018–1026. <https://doi.org/10.1590/S0100-06832013000400019>
- Reis PR, Cunha RL (2010) Café arábica: do plantio à colheita, 1st edn. EPAMIG, Lavras

- Resende LS, Botrel ÉP, Pozza EA et al (2022a) Effect of soil moisture, organic matter and fertilizer application on brown eye spot disease in coffee plantations. *Eur J Plant Pathol*. <https://doi.org/10.1007/s10658-022-02481-2>
- Resende LS, Pozza EA, Luz ALF, et al (2022b) Brown eye spot incidence during the vegetative stage of coffee grown in soil under sustainable management. *Pesqui Agropecu Bras* 57. <https://doi.org/10.1590/S1678-3921.pab2022.v57.02477>
- Rocha OC, Guerra AF, Ramos MLG et al (2014) Physical-hydric quality of oxisol under irrigation and brachiaria in farming of coffee in the Cerrado region. *Coffee Sci* 9:516–526
- Sá Júnior A de, Carvalho LG de, Silva FF da, Alves M de C (2011) Application of the Köppen classification for climatic zoning in the state of Minas Gerais, Brazil. *Theor Appl Climatol* 101 1081 108:1–7. <https://doi.org/10.1007/S00704-011-0507-8>
- Saiya-Cork KR, Sinsabaugh RL, Zak DR (2002) The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. *Soil Biol Biochem* 34:1309–1315. [https://doi.org/10.1016/S0038-0717\(02\)00074-3](https://doi.org/10.1016/S0038-0717(02)00074-3)
- Sanchez PA (2019) Properties and management of soils in the Tropics. Cambridge University Press., London
- Santos H, Jacomine P, Anjos L, et al (2018) Sistema Brasileiro de Classificação de Solos. In: Embrapa Solos, 5 ed. Brasília, DF
- SCAA (2013) Cupping protocols. Specialty Coffee Association of America. Available at:<http://www.scaa.org/PDF/resources/cupping-protocols.pdf>. Accessed 3 Feb 2025
- Serafim ME, de Oliveira GC, de Lima JM et al (2013) Disponibilidade hídrica e distinção de ambientes para cultivo de cafeeiros. *Rev Bras Eng Agrícola e Ambient* 17:362–370. <https://doi.org/10.1590/s1415-43662013000400002>
- Silva BM, Oliveira GC, Serafim ME et al (2015) Critical soil moisture range for a coffee crop in an oxidic latosol as affected by soil management. *Soil Tillage Res* 154:103–113
- Silva BM, Oliveira GC, Serafim ME et al (2019) Soil moisture associated with least limiting water range, leaf water potential, initial growth and yield of coffee as affected by soil management system. *Soil Tillage Res* 189:36–43. <https://doi.org/10.1016/j.still.2018.12.016>
- Singh S, Singh S, Lukas SB, et al (2023) Long-term agro-management strategies shape soil bacterial community structure in dryland wheat systems. *Sci Rep* 1–14. <https://doi.org/10.1038/s41598-023-41216-z>
- Soil Survey Staff (2022) Keys to soil taxonomy, 13th edn. United States Department of Agriculture, Natural Resources Conservation Service
- Teixeira P, Donagemma G, Fontana A, Teixeira W (2017) Manual de Métodos de Análise de Solo, 3 edição r. Embrapa, Brasília, DF
- Veloso TGR, da Silva MCS, Moreira TR et al (2023) Microbiomes associated with *Coffea arabica* and *Coffea canephora* in four different floristic domains of Brazil. *Sci Rep* 13:1–12. <https://doi.org/10.1038/s41598-023-45465-w>
- Vilela MS, Toledo Castanheira D, José Guimarães R et al (2023) Behavior of coffee plants under different cropping systems with a focus on mitigating water scarcity. *Arch Agron Soil Sci* 00:1–20. <https://doi.org/10.1080/03650340.2023.2278901>
- Vilela MS, Castanheira DT, Carvalho MAdeF et al (2024) Contribution of soil sustainable management to improve coffee nutrition and mitigate water scarcity. *J Plant Nutr* 47:1–11. <https://doi.org/10.1080/01904167.2024.2342357>
- Vilela MS (2024) Conservative long term cropping systems mitigating drought stresses and improving soil health. Universidade Federal de Lavras (UFLA)
- Voltolini GB, Vilela MS, Alecrim ADO et al (2022) Techniques for sustainable coffee crop management: impacts on growth and yield. *Arch Agron Soil Sci* 00:1–17. <https://doi.org/10.1080/03650340.2022.2157406>
- Voltolini GB, da Silva LC, de Alecrim AO, et al (2020) Soil chemical attributes in coffee growing with different agronomic techniques. *Coffee Sci* 15. <https://doi.org/10.25186/V15I.1689>
- Wan Q, Li L, Liu B et al (2023) Different and unified responses of soil bacterial and fungal community composition and predicted functional potential to 3 years' drought stress in a semiarid alpine grassland. *Front Microbiol* 14:1–14. <https://doi.org/10.3389/fmicb.2023.1104944>
- Wang S, Hoang TTD, Luu TA et al (2023) Environmental memory of microbes regulates the response of soil enzyme kinetics to extreme water events: drought-rewetting-flooding. *Geoderma*. <https://doi.org/10.1016/j.geoderma.2023.116593>
- Withers PJA, Rodrigues M, Soltangheisi A et al (2018) Transitions to sustainable management of phosphorus in Brazilian agriculture. *Sci Rep* 8:1–13. <https://doi.org/10.1038/s41598-018-20887-z>
- Wulannityas HS, Gong Y, Li P, et al (2020) A cover crop and no-tillage system for enhancing soil health by increasing soil organic matter in soybean cultivation. *Soil Tillage Res* 205. <https://doi.org/10.1016/j.still.2020.104749>
- Zavaschi E, de Abreu FL, Ferraz-Almeida R et al (2020) Dynamic of P flux in tropical acid soils fertilized with humic acid-complexed phosphate. *J Soil Sci Plant Nutr* 20:1937–1948. <https://doi.org/10.1007/s42729-020-00265-3>