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Biochar-Induced Shifts in Fungal Community Structure and Their Association With Soil Physical Properties in Degraded Soil From the Brazilian Semiarid

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ABSTRACT

Soil degradation compromises ecosystem functioning. Biochar, a carbon-rich amendment, has gained attention as a promising strategy to enhance soil structure and restore microbial balance. This study investigated the effects of two biochars, cashew bagasse biochar (CBB) and a co-pyrolyzed biochar produced from sewage sludge and cashew pruning residues (SPB), on the physical properties and the fungal community structure in a severely degraded semiarid soil. A greenhouse experiment was conducted with four biochar application rates (5, 10, 20, and 40 $Mg\,ha^{-1}$) and a control. The fungal community was characterized using 18S rRNA gene sequencing and evaluated through diversity metrics, correlation analyses, and co-occurrence network modeling. CBB preserved the dominance of *Ascomycota* and promoted gradual diversification, whereas SPB induced more pronounced taxonomic shifts, increasing the relative abundance of *Mucoromycota* and *Basidiomycota*. Fungal α-diversity and network complexity peaked at 20 $Mg\,ha^{-1}$, suggesting that intermediate dosages enhanced habitat heterogeneity and nutrient availability. At higher doses, both indices declined, likely due to environmental stress or nutrient overload. Overall, biochar application shaped fungal community composition and showed selective links with soil physical attributes, with CBB increasing macroporosity and contributing to shifts in aggregate-size distribution. In contrast, SPB exerted stronger chemical influences, notably elevating soil Zn, thereby creating a trace-metal gradient that filtered fungal taxa. Correlation analyses further revealed that key fungal groups responded strongly to soil structural domains, particularly pore-size distribution and aggregate fractions, highlighting that each biochar operates through distinct mechanistic pathways that modulate both physical habitat and fungal ecological assembly.

1 | Introduction

As the largest endemic biome in Brazil, the Caatinga is situated within a semiarid region characterized by seasonally dry tropical forests and spiny savannas, harboring high levels of endemism and ecological uniqueness (Fernandes et al. 2020). This ecosystem faces harsh climatic conditions with rainfall, high temperatures, and limited water retention capacity, associated with fragile soils increasingly affected by desertification (Souza et al. 2015; Bieluczyk et al. 2025). The degradation process has been accelerated by intensive land use, recurrent droughts, and climate change, leading to declines in soil stability, water availability, and key ecosystem functions such as nutrient cycling and carbon sequestration (AbdelRahman 2023; Magalhães et al. 2023; Lima et al. 2024; Santos, Sousa, et al. 2025). Vegetation loss and soil erosion are the main causes of soil degradation in semiarid areas, depleting soil organic matter and drastically reducing soil fertility and microbial diversity (Matos et al. 2021). Several strategies have been tested to restore these soils, including green manuring (Pereira et al. 2022) and agroforestry (Fahad et al. 2022; Araujo et al. 2025), yet the effectiveness of external organic amendments such as biochar in reestablishing fungal communities remains poorly understood. Moreover, the feedstock type used for biochar production can drive distinct responses due to its specific physicochemical traits, which influence the composition and structure of soil fungal communities.

Biochar, a carbonaceous material obtained through the pyrolysis of diverse biomasses (Hou et al. 2022; Li et al. 2023), has emerged as a promising tool for restoring degraded soils, especially in semiarid regions (Zhang et al. 2022; Xu et al. 2024; Barbosa et al. 2024; Moniz et al. 2025; Santos, Pereira, et al. 2025). Numerous studies have documented its capacity to improve soil physical (Islam et al. 2021; Li et al. 2023; Moniz et al. 2025), chemical (Chagas et al. 2022; Lucon et al. 2024), and biological properties (Zhang et al. 2023; Barbosa et al. 2024), while also enhancing soil fertility and mitigating greenhouse gas emissions. For instance, Ali et al. (2025) showed that applying 10 t ha^{-1} of biochar with 135 kg N ha^{-1} increased rice productivity by 20%–30% while reducing N_2O emissions. Similarly, Santos, Pereira, et al. (2025) found that biochar addition to degraded semiarid soils enhanced soil carbon stocks and reduced CO_2 fluxes, contributing to climate mitigation. Mechanistically, biochar modifies the structure and activity of soil microbial communities (Xu et al. 2020; Ji et al. 2022; Zhao et al. 2022; Zhao et al. 2024), particularly fungi (Dai et al. 2021; Ma et al. 2023), which play essential roles in organic matter decomposition, nutrient cycling (Pinzari et al. 2016), and beneficial symbioses such as mycorrhizae (Pandey 2019; Warnasuriya et al. 2023). By providing porous habitats and stabilizing soil microclimates, biochar can favor fungal colonization (Saffari et al. 2020; Wang et al. 2023), enhance soil aggregation and structure (Filialuna and Cripps 2021), and thereby restore critical ecosystem functions (Morris et al. 2019).

Despite the recognized potential of biochar to improve soil properties and influence microbial communities, there is limited understanding of how biochars derived from cashew bagasse (CBB) and from the co-pyrolysis of sewage sludge with cashew pruning residues (SPB) affect fungal communities in degraded semiarid soils. The contrasting chemical and physical properties of these biochars suggest that their impacts on soil mycobiota and soil structure are likely dose-dependent, yet the optimal rates for promoting beneficial fungal colonization and improving soil physical conditions remain unknown. Addressing this knowledge gap, we hypothesized that there exists a biochar dose that, when incorporated into degraded semiarid soils, could create favorable microsites that enhance fungal colonization, thereby modifying fungal community structure and improving soil physical properties. To test this, we evaluated different application doses of CBB and SPB, as varying doses are expected to differentially influence soil–fungal interactions due to trade-offs among nutrient supply, carbon input, and potential toxic elements. Consequently, this study aimed not only to assess whether these biochars alter fungal community structure and related soil physical properties, but also to identify which biochar type and application dose most effectively promote fungal community reorganization under degraded semiarid soil conditions.

2 | Material and Methods

2.1 | Sample Collection

The soil used in this study was collected from the 0–10 cm layer of a planosol at 10 randomly distributed points within the experimental area. Subsamples from each point were combined to form a composite sample. This composite sample was then used to prepare 36 experimental replicates for each treatment in the incubation experiment, ensuring representative and reproducible results (IUSS Working Group WRB 2022) in the municipality of Irauçuba, Ceará, Brazil, in an area affected by desertification due to intensive overgrazing (Figure 1). The region is characterized by low annual rainfall (~540 mm), concentrated mainly between January and April (Pereira et al. 2021). The climate is classified as hot semi-arid tropical according to the Köppen–Geiger system, with mean annual temperatures ranging from 26°C to 28°C over the past two decades and an altitude of approximately 152 m above sea level (IPECE 2017). The area has a long history of intensive livestock grazing, particularly during the rainy season. The native vegetation serves as the primary source of forage for smallholder farmers who raise goats, cattle, and sheep in the region.

The soil was sieved through a 4 mm mesh to remove debris while preserving the native microbial community by minimizing excessive disruption of soil aggregates, which could compromise microbial activity. Subsequently, a portion of the sample was air-dried and passed through a 2 mm mesh to obtain the air-dried fine earth fraction, which was used for physical and chemical analyses according to the protocol described by Teixeira et al. (2017). The physical and chemical properties of the soil are presented in Table S1.

2.2 | Preparation and Characterization of Biochars

We used cashew bagasse (CBB) and a 1:1 co-pyrolyzed mixture of sewage sludge and cashew pruning residue (SPB) as feedstocks for biochar production. Cashew bagasse was selected due to its local abundance and the challenges of waste

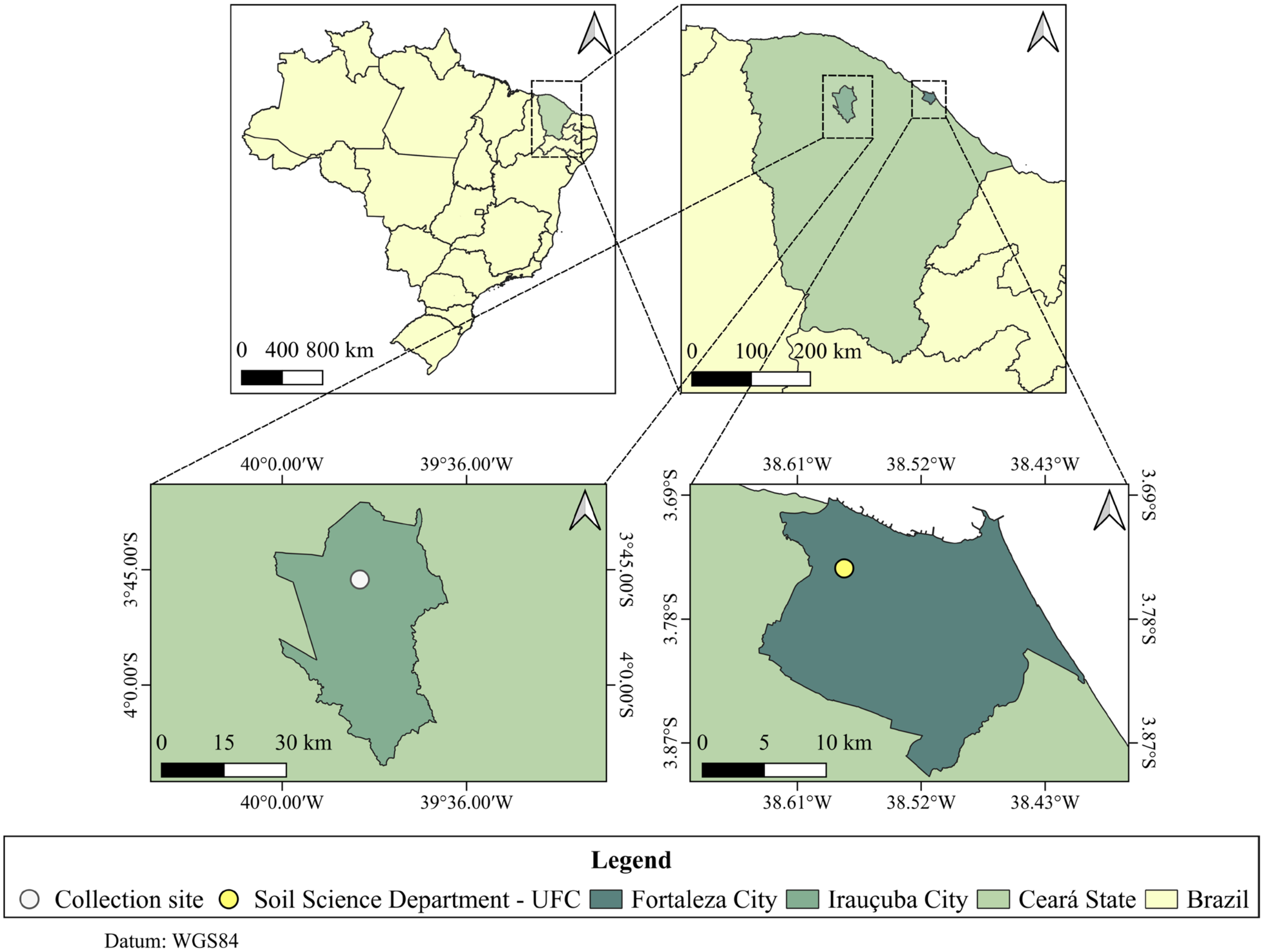

FIGURE 1 | Geographic location map of the soil collection site and greenhouse experiment setup in Fortaleza city, Ceará state, Brazil. [Colour figure can be viewed at wileyonlinelibrary.com]

management in the cashew industry of Northeast Brazil (Oliveira and Ipiranga 2011; Nascimento et al. 2024). The co-pyrolysis of sewage sludge with pruning residues aims at sustainable sludge disposal (Sugurbekova et al. 2023) and reduces the carbon footprint of pruning waste (Carvalho et al. 2019), while also diluting heavy metals to improve the biochar's suitability for soil application.

The cashew bagasse was collected from a cashew-producing farm in Aquiraz, Ceará, Brazil, and the sewage sludge was obtained from a domestic wastewater-treatment plant in Fortaleza, Ceará, Brazil, originating from a UASB (upflow anaerobic sludge blanket) reactor. Both biomasses were pyrolyzed at 500°C, with a heating rate of 10°C min^{-1} under a moderate nitrogen flow. The co-pyrolysis treatment lasted 1 h 37 min, whereas the pyrolysis of cashew bagasse alone continued for 3 h 10 min. The obtained material was analyzed in terms of its granulometric and chemical properties (Table S2).

2.3 | Greenhouse Experiment

The study was conducted in a greenhouse in Fortaleza, Ceará, Brazil (Figure 1). The experiment followed a completely randomized design, with a 2 × 4 + 1 factorial arrangement, including two types of biochar (CBB and SPB), four doses (5, 10, 20, and 40 Mg ha^{-1}), a control treatment (without biochar application), and four replications, totaling 36 experimental units. Each experimental unit was represented by a PVC column (20 cm in diameter and 55 cm in height). The top 5 cm of each column was left open to allow water addition during irrigation. The irrigation was performed manually using distilled water, based on the maize plants' water demand as determined by readings from mercury tensiometers installed in the soil.

The biochar doses were applied to the soil and homogenized. Importantly, the control treatment (soil only) was subjected to the same homogenization procedure, in which the solids (soil+biochar or soil alone) were manually mixed in a plastic container to avoid bias due to aggregate disruption. Based on the chemical characterization of the soil, the need for fertilization was identified, and the guidelines for maize cultivation (*Zea mays* L.) were followed, as outlined in the Manual of Fertilization and Soil Correction for the State of Ceará (Aquino et al. 1993). Fertilization was carried out in two stages. The first, referred to as planting, involved the use of single superphosphate (4.436 mg), potassium chloride (421 mg), and urea (840 mg) per column. The supplementary fertilization was done on 25 and 45 days after maize plant emergence, applying potassium chloride (210 mg) and urea (838 mg) per column. To correct the calcium-to-magnesium ratio, magnesium sulfate was used as a magnesium source, due to the high calcium concentration relative to magnesium.

Under field conditions, the bulk density of the soil used in this study is 1.80 g cm^{-3} (Lima et al. 2024). However, due to the incorporation of biochar, the plowing and harrowing processes result in a reduction of this density. In this context, the PVC columns were set up with a bulk density of 1.55 g cm^{-3}, a value below the threshold considered non-limiting for plant growth (USDA-ARS 2001). After setup, the columns were incubated for 30 days, always maintaining field capacity, with distilled water used to meet the water requirements.

After the incubation period, seeds of the BRS2022 maize cultivar were sown in the soil at a depth of 5 cm, which is considered adequate to ensure uniform seedling emergence (Molatudi and Mariga 2009), maize (*Zea mays* L.) was chosen as the indicator crop because its growth and root development are sensitive to changes in soil properties and microbial activity, making it suitable for evaluating the effects of biochar on soil fungal communities. Additionally, its fast growth, high nutrient demand, and wide cultivation in the region enhance the practical relevance of the study. Two thinning operations were performed, 5 and 8 days after emergence, leaving one maize plant per column. Matric potential and soil moisture were monitored using tensiometers with mercury manometers, installed at a depth of 20 cm. Soil moisture was maintained between field capacity and 30% of the available water capacity (AWC).

At the end of the 90-day experiment (30 days of incubation and 60 days of maize growth), disturbed and undisturbed soil samples were collected from the 0–20 cm layer of each of the 36 experimental units, totaling 72 samples (36 disturbed and 36 undisturbed). Disturbed samples were used to determine particle density, total organic carbon (TOC), soil respiration basal (SRB), microbial biomass carbon (MBC), and β-glucosidase activity. Undisturbed samples (5 cm in height and 5 cm in diameter) were used to evaluate bulk density, microporosity, and the pore continuity index. Additional soil aggregates were collected to assess aggregate stability. Rhizosphere soil from maize roots was obtained for DNA extraction and subsequent sequencing, with one composite sample per experimental unit stored in 2 mL Eppendorf tubes at −20°C until DNA extraction.

2.4 | Soil and Plant Analysis

Bulk density (ρs) was determined using the volumetric ring method, and particle density (ρp) by the volumetric flask method (Blake and Hartge 1986a, 1986b). Total porosity (α) was calculated from ρs and ρp ($\alpha = 1 — \rho s/\rho p$). Microporosity was measured at 6 kPa on a tension table, and macroporosity was obtained as the difference between total and microporosity (Klute 1986). Aggregate stability was evaluated by the wet-sieving method using a vertical oscillating apparatus with sieves of 4.76–0.25 mm to determine the proportion and size distribution of water-stable aggregates (Kemper and Rosenau 1986). Pore continuity indices (log M and N) were derived from the relationship between soil air permeability (Kar) and air-filled porosity (εar) in undisturbed samples using a constant-head permeameter, fitted to the logarithmic Kozeny–Carman equation ($\log Kar = \log M + N \log \varepsilon ar$) (Kirkham 1947; Ahuja et al. 1984; Neves et al. 2007; Silva et al. 2009; Silveira et al. 2011).

Total organic carbon (TOC) was measured by dichromate oxidation and titration with ammoniacal ferrous sulfate (Yeomans and Bremner 1988). β-glucosidase activity was determined using ρ-nitrophenyl β-D-glucopyranoside as substrate, incubated for 1 h at 37°C, and the released ρ-nitrophenol quantified at 400 nm (Eivazi and Tabatabai 1988). Soil basal respiration (SBR) was quantified by capturing CO_2 evolved from microbial activity in 1 M NaOH and titrating with 0.5 M HCl (Jenkison and Powlson 1976). Microbial biomass carbon (MBC) was obtained by the fumigation–extraction method (Vance et al. 1987; Anderson and Domsch 1990; Joergensen and Mueller 1996), and the metabolic quotient (qCO_2) was calculated as the ratio between SBR and MBC (Anderson and Domsch 1990). The determination of soil pH (in water), electrical conductivity (EC), and Zn content was carried out following the procedures described by Teixeira et al. (2017).

Maize plants were evaluated for growth traits and biomass production. Plant height (cm) and stem diameter (mm) were measured using a graduated ruler and a digital caliper, respectively. After harvest, plant material was separated into shoots and roots and dried in a forced-air oven to constant weight. Based on these measurements, shoot dry mass, root dry mass, and total dry mass were determined.

Soil physical, chemical, biological, and plant growth variables were analyzed using ANOVA, and treatment means were compared using Tukey's test at $p \leq 0.05$. Before ANOVA, all datasets were checked for normality and homogeneity of variances, and when assumptions were not met, Box–Cox transformations were applied to stabilize variance. These procedures correspond to the analyses presented in Tables 1–4. All analyses were performed on the SAS Studio environment.

2.5 | Analysis of the Soil Fungal Community Structure

2.5.1 | DNA Extraction, 18S Amplification and Illumina Miseq Sequencing

Genomic DNA was extracted from 0.25 g of soil per sample using the DNeasy PowerSoil Pro Kit (QIAGEN, Germany), following the manufacturer's instructions. The V9 region of the 18S rRNA gene was amplified using the universal eukaryotic primers 1391f (5′-GTACACACCGCCCGTC-3′) and EukBr (5′-TGATCCTTCTGCAGGTTCACCTAC-3′). The choice of the 18S rRNA V9 region, instead of the more commonly used ITS region for fungal community profiling, was motivated by its ability to provide a broader coverage of eukaryotic diversity, including fungal taxa, and to reduce amplification biases in highly degraded soils. Although ITS is widely applied for detailed fungal taxonomic resolution, V9 offers a more consistent amplification across diverse fungal lineages and is particularly useful in studies where both fungal and non-fungal eukaryotes are considered. The resulting amplicons (~150 bp) were purified, and PCR

TABLE 1 | Soil physical properties under different doses of cashew bagasse biochar (CBB) and sewage sludge biochar supplemented with cashew residues (SPB).

	g cm³	Porosity (cm³)		Pore index (mμ²)		Aggregates by classes (mm)				
Treatments	BD	Macro	Micro	Log M	*N*	> 4.76	2.00–4.76	1.00–2.00	0.50–1.00	0.25–0.50
Control	1.59 a	0.0944 a	0.2666abc	2.94a	1.35a	83.27a	7.05a	1.59a	1.02a	0.63a
CBB5	1.54 a	0.1325 a	0.2420bc	2.40ab	0.86ab	70.12b	10.66a	3.20a	2.27a	1.24a
CBB10	1.54 a	0.1342 a	0.2301c	2.66ab	1.03ab	61.00c	12.66a	4.35a	3.10a	1.47a
CBB20	1.59 a	0.1075 a	0.2461abc	2.10b	0.66b	62.04c	12.94a	4.50a	2.68a	1.83a
CBB40	1.55 a	0.1195 a	0.2783ab	2.01b	0.57b	65.02c	11.26a	2.91a	1.98a	1.33a
SPB5	1.57 a	0.0775 a	0.2836ab	2.27b	0.67b	89.10a	3.59a	0.71a	0.96a	0.52a
SPB10	1.56 a	0.0738 a	0.2859a	2.22b	0.55b	91.59a	4.08a	0.76a	0.57a	0.23b
SPB20	1.46 a	0.1342 a	0.2596abc	2.16b	0.66b	80.95ab	7.57a	2.07a	1.21a	0.66a
SPB40	1.57 a	0.0953 a	0.2660abc	2.65ab	1.06ab	83.12a	6.14a	1.39a	1.21a	0.62a

Note: Means followed by the same lowercase letter in the column do not differ from each other by the Tukey test ($p \leq 0.05$). BD: Bulk density.

TABLE 2 | Biological properties and total organic carbon content in soils treated with different doses of cashew bagasse biochar (CBB) and sewage sludge biochar supplemented with cashew residues (SPB).

Treatments	SBR (mg of CO_2-C of soil^{-1} day^{-1})	MBC (mg C g soil^{-1})	qCO_2 (mg $CO_2$$^{h-1}$ BMC g soil^{-1})	TOC (g kg^{-1})	β-glucosidase (mg of p-nitrophenol kg soil^{-1} h^{-1})
Control	0.0157g	0.0146a	1.13b	8.28de	22.90ab
CBB5	0.0293cd	0.0176a	1.83ab	11.79abc	5.96d
CBB10	0.0328bc	0.0195a	1.72ab	9.35cd	21.54bc
CBB20	0.0373b	0.0174a	2.54ab	9.17de	10.46cd
CBB40	0.0434a	0.0174a	2.70a	12.26ab	16.03bcd
SPB5	0.0195fg	0.0159a	1.24ab	14.05a	35.32a
SPB10	0.0230ef	0.0204a	1.19ab	6.67e	28.12ab
SPB20	0.0265de	0.0204a	1.34ab	9.82bcd	19.23bcd
SPB40	0.0291cd	0.0258a	1.74ab	13.04a	18.20bcd

Note: Means followed by the same lowercase letter in the column do not differ from each other by the Tukey test ($p \leq 0.05$).
Abbreviations: MBC, microbial biomass carbon; qCO_2, metabolic quotient; SBR, soil basal respiration; TOC, total organic carbon.

products were submitted for paired-end sequencing (2×150 bp) on the Illumina MiSeq platform at Genomics and Bioinformatics Center from Federal University of Ceará.

2.5.2 | Bioinformatics Data Processing and Statistical Analyses

Data processing was initially performed using QIIME 2 (Bolyen et al. 2019). Briefly, raw sequences were imported and quality filtered with Cutadapt to remove adapters and primers. Denoising and chimera removal were conducted using the DADA2 plugin within QIIME 2. The taxonomic assignment was performed using the Silva v. 138 (Quast et al. 2013) database. Subsequent analyses were carried out in RStudio via a phyloseq object (McMurdie and Holmes 2013). The taxonomic composition of fungal communities was visualized using bar plots at the phylum and class levels, based on amplicon sequence variant (ASV) counts normalized to relative abundance. Only fungal taxa with relative abundance ≥1% in at least one treatment were included in the barplots and correlation analyses. A total of 32,254,858 high-quality reads were obtained from the sequencing run across 36 samples. After filtering, chimera removal, and ASV assignment, the dataset comprised 16,572 features (ASVs). The sequencing depth per sample ranged from 539,216 to 1,159,546 reads, with a mean of 895,968 reads per sample (median = 900,187). To standardize sampling effort across all libraries, rarefaction was applied to the minimum sequencing depth (539,216 reads per sample), ensuring that downstream analyses were performed using normalized sequencing effort.

TABLE 3 | Height, diameter, and biomass production of maize plants in soils treated with different doses of cashew bagasse biochar (CBB) and sewage sludge biochar supplemented with cashew residues (SPB).

Treatments	Height (cm)	Diameter (mm)	Dry mass of the aerial part (g/plant)	Dry mass of the roots (g/plant)	Total dry mass (g/plant)
Control	238.5a	18.29b	274.8a	228.6a	175.6a
CBB5	206.7a	21.18ab	245.1a	222.0a	171.8a
CBB10	214.5a	19.61ab	222.3a	225.2a	189.6a
CBB20	212.7a	21.11ab	239.6a	220.1a	178.8a
CBB40	229.2a	20.58ab	295.9a	228.8a	169.2a
SPB5	228.7a	20.44ab	273.3a	232.3a	197.1a
SPB10	224.5a	19.75ab	286.1a	225.3a	187.1a
SPB20	211.2a	22.31a	308.4a	238.9a	204.3a
SPB40	187.0a	20.01ab	268.9a	222.5a	169.1a

Note: Means followed by the same lowercase letter in the column do not differ from each other by the Tukey test ($p \leq 0.05$). Part of the data was published by Moniz et al. (2025).

TABLE 4 | Soil pH, electrical conductivity (EC) and Zn in soils treated with different doses of cashew bagasse biochar (CBB) and sewage sludge biochar supplemented with cashew residues (SPB).

Treatments	pH (in water)	EC ($dS\,m^{-1}$)	Zn ($mg\,kg^{-1}$)
Control	5.09c	0.1275ab	1.50e
CBB5	5.06c	0.0925ab	1.07e
CBB10	5.11c	0.0975ab	1.20e
CBB20	5.45abc	0.0700b	1.10e
CBB40	5.67ab	0.1350a	1.00e
SPB5	5.23bc	0.0875ab	2.58d
SPB10	5.40abc	0.1100ab	3.66c
SPB20	5.58ab	0.0950ab	5.15b
SPB40	5.70a	0.1225ab	10.21a

Note: Means followed by the same lowercase letter in the column do not differ from each other by the Tukey test ($p \leq 0.05$).

Alpha diversity was assessed using the Shannon index and observed richness and differences in alpha diversity among treatments were evaluated using Kruskal–Wallis. Beta diversity was evaluated based on Bray–Curtis dissimilarity and visualized through non-metric multidimensional scaling (NMDS) using the vegan package (Oksanen et al. 2020), and differences were assessed using PERMANOVA. Spearman correlations between fungal taxa and environmental variables were computed, and the results were visualized as a correlation heatmap adopting $p < 0.05$ as the significance threshold. Co-occurrence networks were constructed using significant ($p < 0.05$) and strong ($\rho > 0.6$) Spearman correlations among taxa. Network visualization and topological metrics were computed using Gephi (Bastian et al. 2009). Network complexity was evaluated based on key topological features, including the number of nodes (microbial taxa), edges (interactions among taxa), and the balance of positive and negative associations. Biologically, an increase in nodes and edges reflects a more diverse and interconnected microbial community, where a greater number of taxa engage in ecological interactions such as cooperation, competition, or metabolite exchange, indicating enhanced functional integration and potential stability of the soil microbiome. The Classification Method (CLAM) applies to a multinomial probabilistic model to the relative abundance and frequency of each ASV across two habitats, assigning taxa to one of four categories: specialists of habitat A, specialists of habitat B, generalists that occur proportionally in both habitats, or rare taxa with insufficient information for classification. This method does not rely on pairwise significance testing but on probabilistic thresholds for habitat association. The CLAM was applied using the clamtest function from the ecolTest R package (Chazdon et al. 2011).

3 | Results

3.1 | Soil and Plant Attributes Associated With Fungal Responses

Spearman's correlations revealed distinct association patterns between fungal taxa and soil attributes (Figure 2). *Ascomycota* showed positive correlations with MBC and with the coarse aggregate fraction (> 4.76 mm), even though the proportion of this size class declined in some treatments, and a negative correlation with qCO_2 (Figure 2A). *Basidiomycota*, in contrast, exhibited predominantly negative correlations with microporosity and qCO_2, while showing a positive association with MBC (Figure 2A).

To avoid overgeneralization of physical outcomes, it is important to note that soil structural responses to biochar were selective.

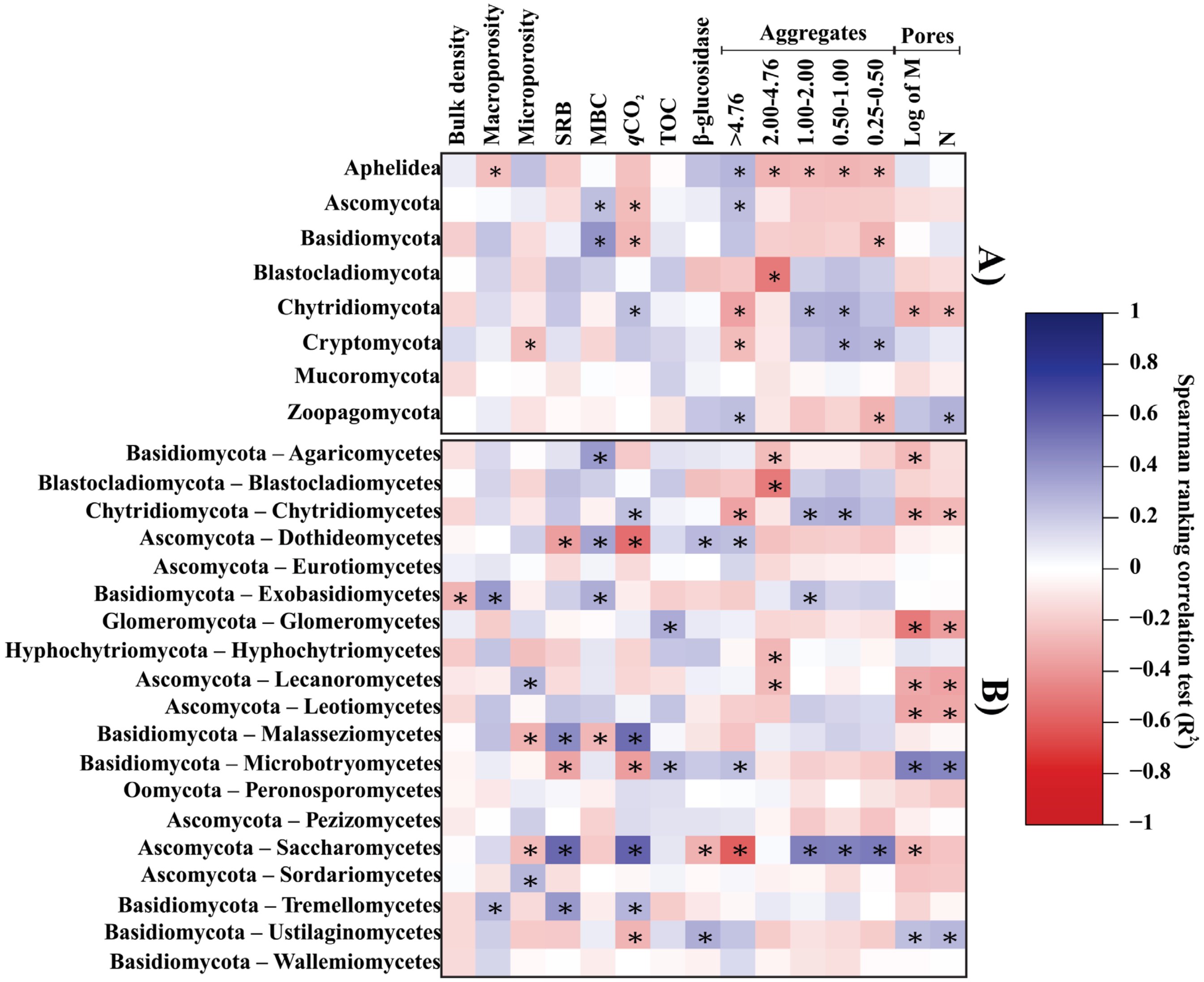

FIGURE 2 | Heatmap of Spearman correlations (ρ) between the relative abundance of fungal phylum (A) and classes (B) and soil attributes. The color intensity reflects the value of ρ (blue = positive correlation, red = negative correlation), and asterisks indicate statistical significance ($p < 0.05$). MBC, microbial biomass carbon; qCO_2, metabolic quotient; SBR: soil basal respiration; TOC, total organic carbon. [Colour figure can be viewed at wileyonlinelibrary.com]

The clearest and most consistent effect was the increase in macroporosity under CBB (Table 1), particularly at intermediate and higher application rates. In contrast, air-permeability parameters (LogM and N; Table 1) exhibited only modest variation across treatments and did not follow the same directional trend observed for macroporosity. Aggregate-size distribution also responded heterogeneously: intermediate-size classes shifted depending on dose and biochar type, whereas the largest fraction (> 4.76 mm) decreased in some treatments, indicating that structural changes were not uniform across size classes or biochar types.

At the class level (Figure 2B), *Sordariomycetes* correlated only with microporosity and were most abundant under 20 Mg ha^{-1} CBB. *Eurotiomycetes* showed no significant correlations with any measured attribute but increased under CBB and decreased under SPB. *Glomeromycetes* did not correlate with aggregate-size fractions; instead, they showed a positive correlation only with TOC. *Malasseziomycetes* exhibited a negative correlation with MBC, whereas *Dothideomycete*s showed a negative correlation with SBR. *Saccharomycete*s presented negative correlations with β-glucosidase activity and with the > 4.76 mm aggregate fraction, together with a strong positive correlation with soil respiration (Figure 2B).

TOC showed a non-linear response to biochar, with no consistent increase across doses, whereas both MBC and SBR increased under several treatments (Table 2). Plant growth indicators, including maize height, stem diameter, and biomass, remained stable across treatments (Table 3), indicating that contrasting chemical inputs did not impair plant development. Soil pH increased moderately across biochar doses, whereas EC differences remained subtle. In contrast, Zn concentrations increased markedly under SPB, rising from 1.50 mg kg^{-1} in the control to 10.21 mg kg^{-1} under SPB40 (Table 4).

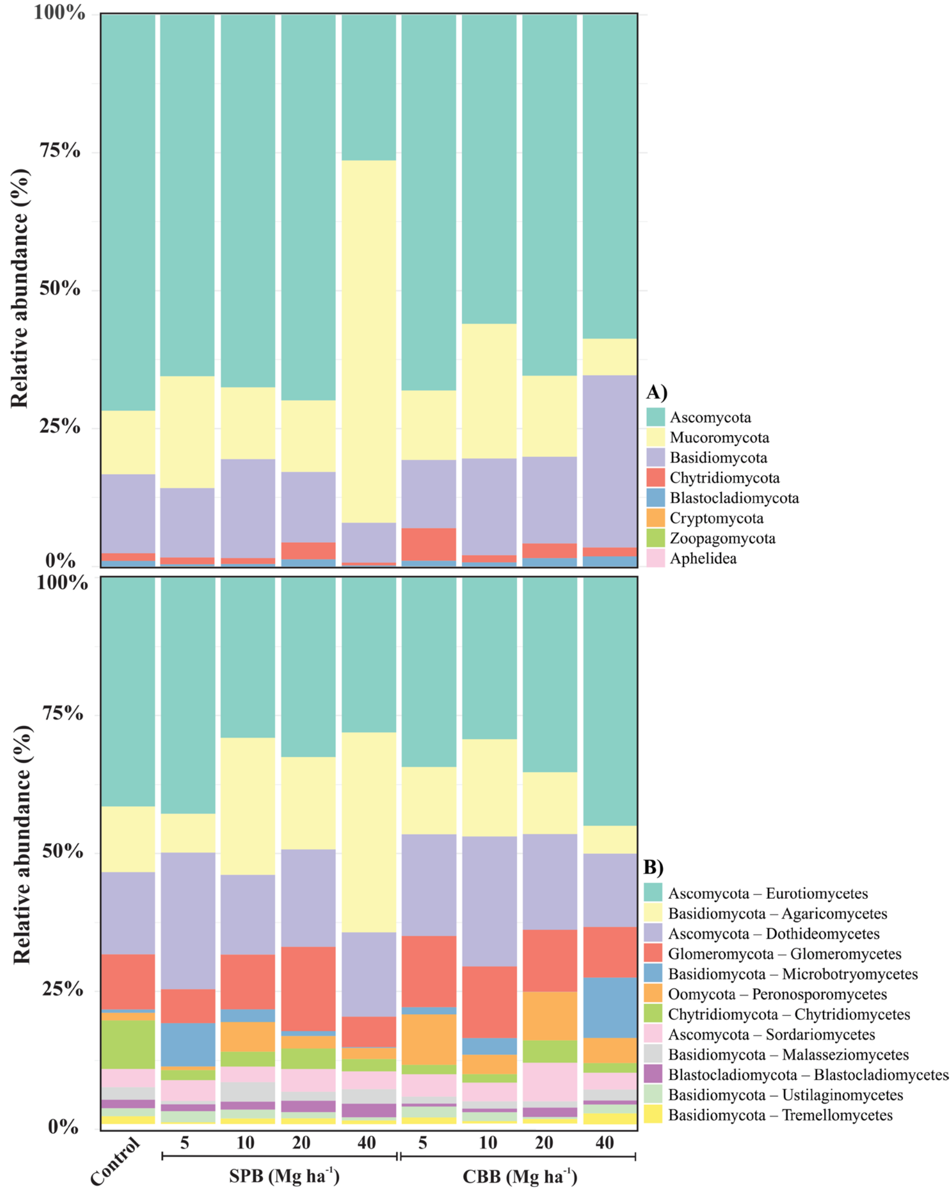

FIGURE 3 | Effects of cashew bagasse biochar and sewage sludge supplemented with cashew pruning residues, at different doses, on the composition of the soil fungal community: (A) phylum and (B) classes. Differences among treatments were significant at $p < 0.05$. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Biochar-Induced Changes in Fungal Taxonomic Composition

The application of cashew bagasse biochar (CBB) and sewage sludge supplemented with cashew residue (SPB) induced substantial changes in fungal community composition and structure. At the phylum level, Ascomycota remained dominant across all treatments, yet its relative abundance declined markedly under SPB at 40 Mg ha^{-1}, with a partial increase at intermediate doses (Figure 3A). This contrasted with CBB, which maintained high Ascomycota levels even at the highest dose. Also, Mucoromycota increased markedly under SPB but remained low under CBB. Basidiomycota showed moderate increases under both biochars, with the largest rise under CBB. At the class level, Eurotiomycetes consistently dominated, whereas Dothideomycetes and Agaricomycetes remained relatively stable. Glomeromycetes responded positively to SPB at 20 Mg ha^{-1} (Figure 3B).

3.3 | Effects of Biochar Type and Dose on Fungal α- and β-Diversity

Alpha diversity indices reflected biochar-driven community restructuring. Taxon richness increased in the biochar-amended treatments compared to the control, with higher values under CBB at the greater application rate and intermediate values under SPB, showing a pattern like that observed for the Shannon index (Figure 4A,B). Beta diversity (NMDS) revealed treatment-specific clustering, with SPB and CBB causing clear separation from the control, while PERMANOVA indicated a significant effect of biochar dose and a marginal effect of biochar type (Figure 5).

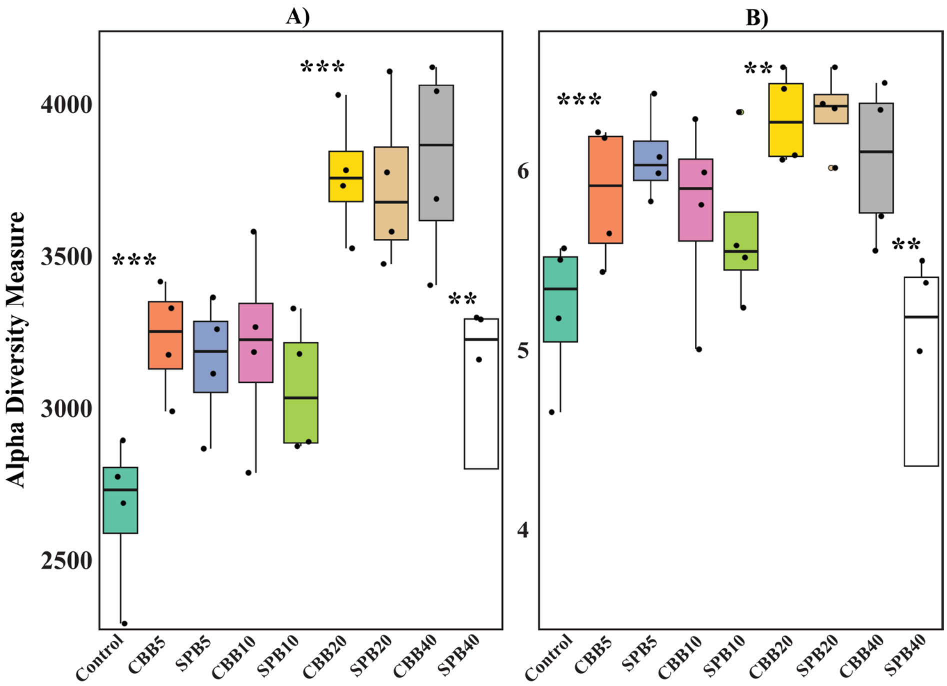

FIGURE 4 | Effects of cashew bagasse biochar and sewage sludge supplemented with cashew pruning residues, at different doses, on the soil fungal α-diversity: (A) observed species and (B) Shannon index. Differences among treatments were significant at $p < 0.05$. [Colour figure can be viewed at wileyonlinelibrary.com]

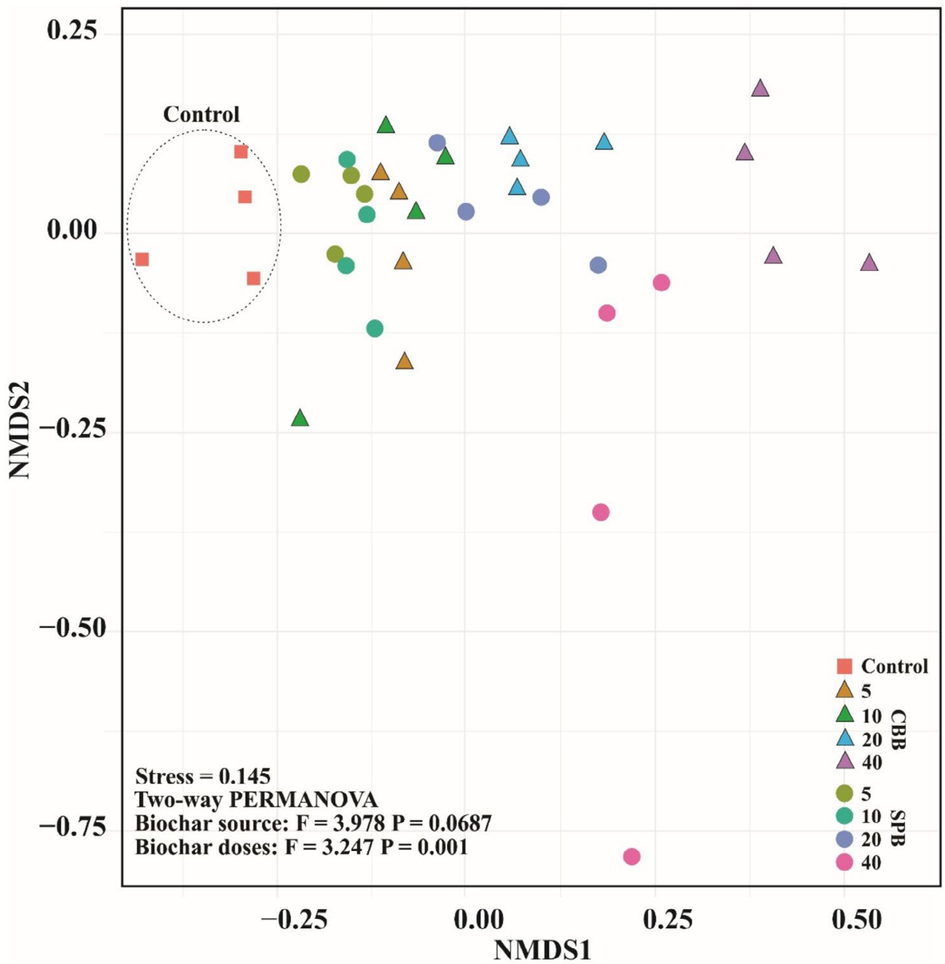

FIGURE 5 | Effects of cashew bagasse biochar and sewage sludge supplemented with cashew pruning residues, at different doses, on soil fungal beta diversity. Differences among treatments were significant at $p < 0.05$. [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Network Complexity and Niche Specialization in Fungal Communities

Co-occurrence network analyses demonstrated that both biochars reshaped fungal interactions. SPB increased network complexity at 20 Mg ha^{-1}, but this declined at 40 Mg ha^{-1}, whereas CBB peaked at 20 Mg ha^{-1} and retained high cooperative connectivity at 40 Mg ha^{-1} (Figure 6). Niche occupancy patterns further confirmed that CBB promoted specialist fungi more strongly than SPB, with linear increases up to 20 Mg ha^{-1} followed by reductions at 40 Mg ha^{-1}, while generalists remained relatively stable and rare species were consistently low (Figure 7).

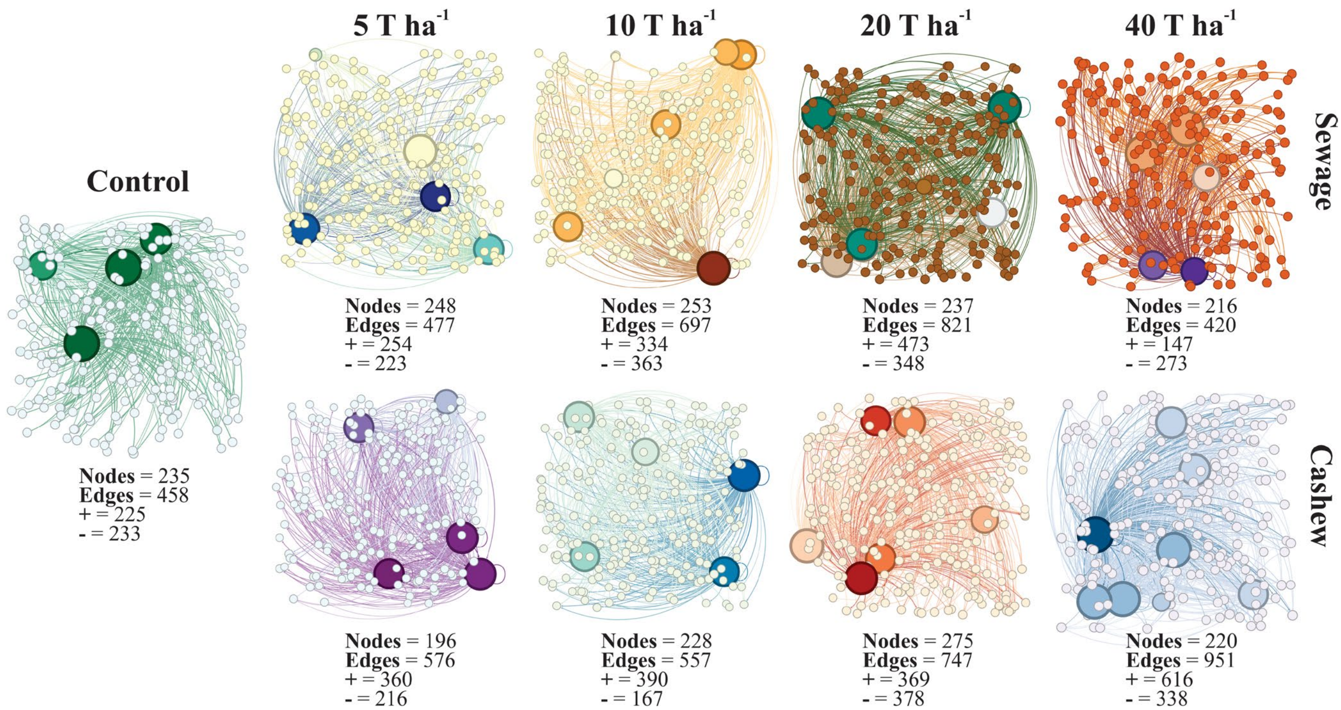

FIGURE 6 | Effects of cashew bagasse biochar and sewage sludge supplemented with cashew tree residues, at different doses, on soil fungal co-occurrence networks. Each network represents the structure of the fungal community; nodes indicate microbial taxa, and edges represent significant correlations among them. The numbers of nodes, connections (edges), and positive (+) and negative (–) interactions are indicated below each network. [Colour figure can be viewed at wileyonlinelibrary.com]

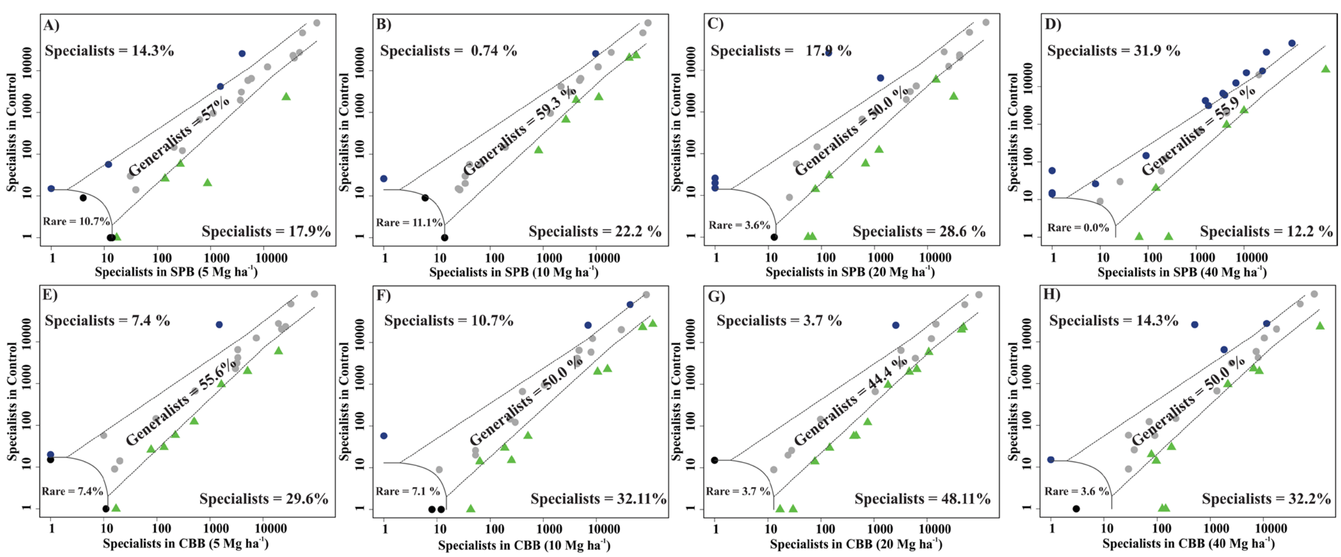

FIGURE 7 | Effects of sewage sludge supplemented with cashew tree residues cashew bagasse biochar (A–D: 5, 10, 20, and 40 Mg ha^{-1}) and cashew bagasse (E–H: 5, 10, 20, and 40 Mg ha^{-1}) on the niche occupation of specialist, generalist, and rare soil fungi. In each panel, the points represent the occurrence rates of specialist (blue), generalist (gray), and rare (black/green) taxa. Dashed and solid lines delimit the niche envelope. Percentages indicate the proportion of specialists in each treatment. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | Discussion

4.1 | Soil and Plant Attributes Associated With Fungal Responses

The integrative patterns revealed by the correlation analysis indicate that biochar-driven shifts in soil physical and chemical conditions acted as key environmental filters governing fungal community assembly. At the phylum level, *Ascomycota* and *Basidiomycota* emerged as primary responders, but through distinct ecological pathways. The association of *Ascomycota* with coarse aggregates (> 4.76 mm) highlights their contribution to structural stabilization, a role supported by their extensive hyphal networks and enzymatic machinery capable of decomposing complex polymers and enhancing organo-mineral bonding (Six et al. 2004; Geiser et al. 2006; Couturier et al. 2016; Zeiner et al. 2016). These mechanisms align with classical models of aggregate formation in semiarid soils (Tisdall et al. 1997) and with the well-documented tendency of biochar to promote lignocellulolytic taxa (Guo et al. 2020; Han et al. 2020; Liao et al. 2024).

Importantly, the structural responses in this study were selective. Although CBB enhanced microporosity, other indicators such as LogM, N, and the abundance of the coarsest aggregates did not exhibit similar gains. This selective pattern suggests that biochar effects do not translate into uniform structural enhancement but instead reshape specific pore domains with functional significance for fungi, particularly those relying on oxygen diffusion and spatial heterogeneity to sustain growth and activity.

Basidiomycota followed a different ecological trajectory, responding more strongly to variations in microporosity, aeration, and microbial activity. Their negative associations with microporosity and qCO_2, together with positive associations with MBC, point to a sensitivity to pore connectivity and oxygen supply, consistent with the metabolic strategies described in Nascimento et al. (2023). In this sense, biochar-induced adjustments in pore architecture may create microsites that either facilitate or constrain the oxidative metabolisms characteristic of many *Basidiomycota*.

The class-level patterns further illustrate how different fungal guilds partition environmental gradients in response to biochar-induced changes in soil conditions. *Sordariomycetes* responded narrowly to microporosity, suggesting dependence on specific pore configurations that facilitate hyphal penetration and microsite aeration (Kravchenko and Guber 2017). *Eurotiomycetes*, despite lacking measurable correlations with the soil attributes evaluated, displayed contrasting abundance patterns under CBB and SPB, indicating sensitivity to substrate quality or chemical composition rather than to physical structure. *Glomeromycota*, classically linked to soil aggregation via hyphal enmeshment and glomalin production (Rillig and Mummey 2006), did not correlate with aggregate-size fractions in this experiment; instead, *Glomeromycetes* aligned with TOC, suggesting that carbon availability, potentially driven by rhizodeposition or microbial turnover, was a stronger determinant of their distribution than structural domains. Negative associations of Malasseziomycetes with MBC and of *Dothideomycetes* with SBR reflect divergent responses to microbial competition and metabolic intensity. *Saccharomycetes*, with fermentative potential (Brussaard et al. 1997), aligned positively with soil respiration and negatively with β-glucosidase activity and coarse aggregates, indicating a preference for labile carbon environments rather than structurally stabilized niches.

Chemical and plant-mediated factors added additional layers of filtering. The moderate increase in pH, coupled with minimal changes in EC, suggests that ionic effects were less influential than shifts in surface chemistry and nutrient availability. The pronounced increase in Zn under SPB introduced a trace-metal gradient capable of selecting for tolerant or metal-responsive taxa (Beesley et al. 2011), contributing to the sharper taxonomic shifts observed under this biochar. Plant growth remained stable across treatments, indicating that rhizosphere-driven carbon inputs did not vary substantially and thus did not confound fungal responses (Moniz et al. 2025). This functional stability reinforces the interpretation that fungal restructuring stemmed chiefly from soil modifications rather than plant stress.

Patterns of TOC, MBC, and SBR point to further interactions between biochar quality and carbon cycling. Non-linear TOC responses, modulated by rhizodeposition and microbial turnover (Santos, Pereira, et al. 2025), indicate that carbon accumulation did not scale directly with dose. Yet increases in MBC and SBR across treatments (Barbosa et al. 2024) suggest enhanced microbial access to organic substrates and improved habitat quality, conditions that promote fungal activity and niche differentiation.

Taken together, these structural, chemical, and plant-mediated shifts demonstrate that biochar acts not as a uniform modifier of soil conditions, but as a selective architect of microhabitats. By reorganizing soil structure, altering trace-metal availability, and modulating carbon pathways, biochar treatments, particularly CBB for physical traits and SPB for chemical gradients, created distinct ecological filters that shaped fungal assembly. This mechanistic perspective helps explain why fungal responses were taxon-specific and dose-dependent, highlighting the tight coupling between soil restoration processes and microbial ecological resilience in semiarid environments.

4.2 | Biochar Effects on Fungal Community Composition

In this study, we investigated the effects of different doses of biochar obtained through the pyrolysis of cashew bagasse and the co-pyrolysis of sewage sludge supplemented with cashew pruning waste on the recovery of fungal community in degraded drylands. Our results supported the hypothesis that biochar changed the structure of the fungal community, increased diversity, and promoted niche specialization. These changes were associated with selective improvements in soil physical conditions, particularly increased macroporosity under CBB, together with shifts in biological attributes. These patterns suggest that the structural and compositional shifts induced by biochar are mechanistically linked to changes in soil physical, chemical, and biological functioning. Beyond serving as carbon sources, biochars act as catalysts that reshape the soil's physicochemical environment, altering nutrient dynamics, porosity, and the configuration of ecological niches available for microbial colonization (Nascimento et al. 2023; Nascimento et al. 2024; Moniz et al. 2025; Mota et al. 2025; Santos, Pereira, et al. 2025). However, the physical effects were limited to specific components rather than the full set of structural indicators.

However, these interpretations should be considered with caution, as the experiment was conducted under greenhouse conditions with controlled water and nutrient inputs, which may not fully represent the environmental variability typical of natural semiarid field conditions. Under field conditions, fluctuations in temperature, soil moisture, and resource availability can significantly alter microbial dynamics, competition, and nutrient turnover. Nonetheless, the results provide valuable mechanistic insights into how biochar promotes fungal niche differentiation, favoring the coexistence of distinct functional groups through changes in soil structure, carbon sources, and nutrient gradients.

The contrasting responses among fungal groups to the two types of biochar suggest that intrinsic characteristics of the material, such as elemental composition, metal content, and porous structure, are key determinants in shaping fungal community assembly (Dai et al. 2018). CBB appears to exert a more modulating effect, possibly due to its higher carbon content and lower mineral complexity (Table S2). In contrast, SPB demonstrated a greater capacity to promote taxonomic reorganizations, which may be attributed to its higher content of nutrients and heavy metals (Table S2), creating more intense environmental filters and favoring fungi with opportunistic strategies or adaptations to nutrient-enriched environments (Dai et al. 2021). The marked increase in Zn content in soil under SPB, from 1.50 $mg\,kg^{-1}$ in the control to 10.21 $mg\,kg^{-1}$ under SPB40 (Table 4), reflects its substantially higher concentration in the material (Supplementary Table S2), establishing a trace-metal gradient capable of selecting for tolerant or metal-responsive taxa (Beesley et al. 2011).

4.3 | Diversity Responses and Ecological Implications of Biochar Addition

The rise in fungal diversity indices, particularly at intermediate application doses, suggests that moderate levels of environmental enrichment create more favorable conditions for the development of a diverse fungal community (Zhang et al. 2021; Chen et al. 2024). This finding is consistent with prior evidence demonstrating that moderate biochar application enhances fungal α-diversity and community evenness over time. Specifically, meta-analytical data indicate that fungal diversity tends to increase in sandy soils with low organic carbon content, particularly under moderate biochar application doses (Deshoux et al. 2023). Moreover, results from long-term field experiments have shown that higher biochar doses can increase the relative abundance of arbuscular mycorrhizal fungi and the AMF-to-saprotrophic fungi ratio, indicating a biochar-induced shift in fungal community composition toward more diverse and functionally distinct assemblages. (Luo et al. 2017; Li et al. 2020).

As a result, better diversity and reorganization of fungal communities may enhance the resilience of the soil–plant system under stress in degraded dry environments (e.g., water deficit and salinity), due to the strengthening of symbiotic interactions and physiological adaptation mechanisms.

However, the structural simplification observed at higher biochar doses may indicate a saturation effect or environmental stress (Yang et al. 2024), possibly associated with the accumulation of potentially toxic compounds (Brtnický et al. 2021; Nissen et al. 2021) or with intensified competition among keystone taxa. In particular, Chen et al. (2019) reported that the fungal genera *Chaetomium* (*Sordariomycetes*) and *Penicillium* (*Eurotiomycetes*) act as central taxa exhibiting antagonistic interactions with other members within their respective modules, indicating a prominent competitive role in reshaping fungal community structure. This prior evidence provides a useful conceptual framework for interpreting the patterns observed in our study.

4.4 | Network Complexity and Functional Specialization in Biochar-Amended Soils

The increased network connectivity observed at intermediate dose points to enhanced functional integration, indicating that biochar stimulates both cooperative and competitive interactions among taxa that stabilize microbial networks and optimize resource use (Oña et al. 2025). Co-occurrence analyses confirmed that biochar altered community composition and reconfigured ecological interactions among fungal groups (Voorde et al. 2014; Chen et al. 2019; Bieluczyk et al. 2025; Lei et al. 2023). The higher connectivity and complexity observed at intermediate doses reflect greater functional redundancy and ecological stability, key attributes for the resilience of degraded soils (Zhang et al. 2023). Conversely, the decline in network complexity at higher doses likely indicates a contraction of ecological niches and the emergence of dominance by a few opportunistic groups, which could constrain overall system functionality (Chen et al. 2019).

The increased proportion of specialist fungi at intermediate doses further reinforces the role of biochar in promoting environmental heterogeneity, facilitating niche partitioning and the establishment of specific functional groups (Zhao et al. 2024). Although often less abundant, specialists perform essential ecological roles such as decomposing recalcitrant compounds, solubilizing nutrients, and forming mycorrhizal associations with plants (Anastasi et al. 2012; Treseder and Lennon 2015). Their reduction at higher biochar doses may therefore impair key ecosystem processes and limit the success of soil regeneration under degraded semiarid conditions.

4.5 | Practical Implications for Soil Restoration and Future Perspectives

This study demonstrates that biochar application represents a promising tool for reshaping the fungal community and restoring microbial functionality in degraded semiarid soils (Nascimento et al. 2023; Barbosa et al. 2024). However, its effects are highly dependent on the dose and type of material used, making it essential to calibrate applications according to specific soil conditions and the objectives of ecological restoration. Thus, biochars derived from agro-industrial residues can substantially reshape fungal communities and enhance soil microbial functionality in semiarid degraded soils. However, limitations include the short-term nature of the experiment and its confinement to a single soil type and climate regime, which may restrict broader generalization. Additionally, while changes in microbial diversity and network structure were observed, direct links to long-term soil restoration outcomes (e.g., plant productivity, erosion control, or organic matter stabilization) require further validation. Despite these constraints, the results highlight the potential of tailored biochar applications, particularly at intermediate doses, as locally available tools to stimulate microbial diversity, carbon cycling, and soil structure recovery. These findings are applicable to restoration practices in dryland agroecosystems, especially where organic waste recycling and microbial rehabilitation are critical. Future work should integrate plant responses, assess temporal dynamics, and explore multi-functional indicators to refine biochar use in large-scale land restoration strategies.

Taken together, our findings support a conceptual framework in which biochar type and dose jointly regulate fungal community structure through interconnected physicochemical and biological pathways. Variations in nutrient and metal contents (Table S2) define the chemical and physical environment that governs fungal colonization, soil–microbe interactions, and the establishment of functional guilds, while biochar-induced changes in porosity, aggregation, and aeration influence oxygen diffusion, water retention, and the spatial distribution of microsites. These interacting mechanisms collectively drive fungal niche differentiation, promoting the coexistence of specialized taxa under moderate enrichment and competitive exclusion under excessive inputs.

This integrative perspective highlights that the composition and application rate of biochar determine the balance between microbial diversity, carbon stabilization, and soil structural recovery. Conceptually, biochar acts as both a habitat physical modifier, linking soil restoration processes to microbial ecological resilience. This framework provides a mechanistic basis for developing sustainable biochar management strategies in semiarid degraded soils and for guiding field-scale applications and long-term monitoring under variable climatic and edaphic conditions.

5 | Conclusions

This study demonstrated that biochar functions as a biophysical catalyst in the rehabilitation of degraded semiarid soils, not merely as a carbon input but as a driver of microhabitat restructuring that shapes fungal colonization, diversity, and ecological interactions. The effects observed were selective rather than uniform: cashew-bagasse biochar (CBB) promoted clear improvements in macroporosity and induced dose-dependent adjustments in aggregate-size distribution, creating more favorable microsites for fungal guilds. In contrast, sewage-sludge biochar (SPB) exerted weaker physical effects but produced distinct chemical shifts, particularly in Zn availability, that acted as environmental filters selecting for metal-responsive taxa.

Moderate biochar applications (around $20\,Mg\,ha^{-1}$) tended to optimize the balance between physical enhancement and microbiological restructuring, promoting both structural development and increased network connectivity among fungal taxa. This pattern suggests a positive feedback mechanism in which improved pore structure enhances fungal diversification and functional activity, which in turn reinforces aggregate stability and soil functioning. Excessive doses, however, may disrupt this balance by intensifying chemical gradients or altering structural domains beyond optimal thresholds.

From a management perspective, these results support the use of biochar, particularly from locally available residues such as cashew bagasse and sewage sludge, as a viable amendment to restore microbial functioning and physical integrity in drylands vulnerable to desertification. Implementing such strategies also reinforces circular bioeconomy approaches by converting regional wastes into soil conditioners. Long-term and field-scale studies integrating plant–microbe–soil interactions and multifunctional indicators are still needed to refine dose recommendations and assess the persistence of these restorative effects under variable semiarid conditions.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **TABLE S1:** Physical and chemical properties of highly degraded Planosol (0–10 cm) from Irauçuba, Ceará, Brazil. **TABLE S2:** Chemical and granulometric properties of cashew bagasse biochar (CBB) and sewage sludge biochar supplemented with cashew pruning residues (SPB).