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Shaping soil fungal communities: How swine waste treatment systems and geography drive fungal community shifts

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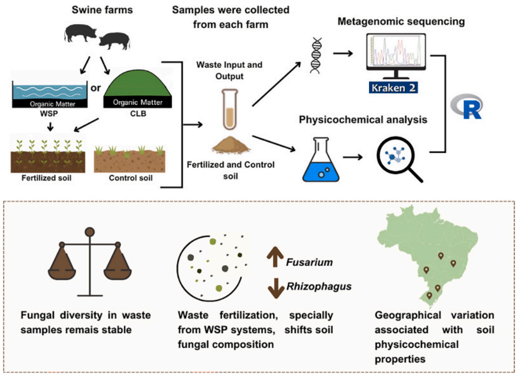
HIGHLIGHTS

- Fertilization altered soil fungal community composition but not diversity.
- Waste treatment systems (CLB vs WSP) minimally impacted fungal communities.
- Geographical region influenced both fungal abundance and community structure in soils.
- The abundances of *Fusarium* and *Rhizophagus* shifted in fertilized soils.

GRAPHICAL ABSTRACT



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ABSTRACT

The use of swine waste as an organic fertilizer is an important practice in sustainable agriculture. This study aims to evaluate the effects of two common swine waste treatment systems, Covered Lagoon Biodigesters (CLB) and Waste Stabilization Ponds (WSP), on fungal community structure in soil. Soil and waste samples were collected from swine farms across five Brazilian states, representing different geographical regions with distinct climate, soil types, and vegetation. A metagenomic approach was employed to analyze the fungal communities present in the samples. Our results revealed that fertilization with swine waste did not significantly affect the overall diversity of fungal communities, although distinct shifts in community composition were observed between fertilized and non-fertilized soils. Notably, reads assigned to *Sugiyamaella lignohabitans* were detected only in

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samples from waste stabilization ponds, suggesting that this environment may favor fungal taxa associated with lignocellulose degradation. Furthermore, the fungal genera *Fusarium* and *Rhizophagus* exhibited contrasting responses to fertilization, with *Fusarium* being more abundant in fertilized soils and *Rhizophagus* decreasing in abundance. Geographic variation in fungal community composition was also observed, correlating with the physicochemical properties of the soil. These findings indicate that, in our dataset, the waste treatment systems had little influence on the fungal diversity of waste samples, whereas soil fertilization with swine waste was associated with marked shifts in fungal community composition, particularly in terms of taxonomic structure.

1. Introduction

The use of swine waste as a fertilizer is a common practice in agriculture, particularly in systems that aim to reduce synthetic fertilizer use and mitigate environmental impacts (Hollas et al., 2023). Swine waste is rich in essential macro- and micronutrients, such as nitrogen, phosphorus, and potassium, which promote plant growth (ASHRAF et al., 2023; Yuan et al., 2024). Additionally, it provides organic matter to the soil, improving its structure, enhancing water retention capacity, and stimulating microbial activity (ASHRAF et al., 2023; Yuan et al., 2024).

In Brazil, two treatment systems are commonly employed for this purpose: Covered Lagoon Biodigesters (CLB) and Waste Stabilization Ponds (WSP) (Kunz et al., 2009). CLB systems are closed structures in which swine waste undergoes anaerobic digestion, a process that converts organic material into biogas and a nutrient-rich solid secondary product (Clarke and Alibardi, 2010). This digestion pathway typically results in reduced oxygen availability and in the transformation of carbon and nitrogen into distinct chemical forms, ultimately yielding a material that can be applied as fertilizer (Giwa et al., 2020). The biogas generated provides an additional benefit as a renewable energy source, contributing to the overall sustainability of the system (Ribeiro et al., 2018). In contrast, WSP systems operate as aerated composting facilities in which waste decomposes under oxygen-rich and temperature-regulated conditions, producing stabilized organic compost that improves soil structure and fertility (Deng et al., 2023). Because WSPs rely on aerobic decomposition, they may favor fungal guilds associated with oxidative organic matter turnover (Bekoe et al., 2018; Semenov et al., 2022). Both systems play a key role in on-farm waste management, reducing environmental contamination risks while supporting more sustainable agricultural practices (Giwa et al., 2020; Kunz et al., 2009).

Fungal communities in the soil play a crucial role in terrestrial ecosystems by decomposing organic matter, cycling nutrients, and forming symbiotic associations that contribute to soil structuring (Frac et al., 2018; Jin et al., 2024). When soil is enriched with organic fertilizers, such as organic matter derived from swine waste, significant changes occur in the composition and diversity of microbial communities, including fungi (Schlatter et al., 2023; Yuan et al., 2024). Although the impact of waste on fungal communities is not fully understood, it is known that it can alter the structure of these communities, favoring certain fungal genera over others. This dynamic is important because fungi not only decompose organic matter but also form symbiotic relationships with plants, facilitating the exchange of essential nutrients, such as phosphorus and nitrogen (Ashraf et al., 2023). Therefore, maintaining a balanced relationship between fungal communities and other microorganisms is critical for ensuring soil sustainability and fertility (Han et al., 2022; Sun et al., 2017). Despite the growing interest in sustainable waste treatment management, most studies investigating microbial responses to swine waste have focused primarily on bacterial communities, with far fewer examining fungal dynamics. Moreover, comparative assessments of fungal communities between distinct waste treatment systems remain scarce, particularly when combined with a broad and environmentally heterogeneous sampling design.

The comparison between swine waste treatment systems is grounded in their distinct decomposition dynamics, which shape the physicochemical properties of the resulting effluents and, consequently, the soil environments that receive them (Cheng et al., 2020; Liu et al., 2024). Different treatment processes generate characteristic nutrient profiles, redox conditions, organic matter composition, and residual microbial inputs, all of which act as ecological filters influencing fungal assembly (Cheng et al., 2020). Aerobic and anaerobic waste treatment systems differ fundamentally in their oxygen availability, decomposition pathways, and microbial consortia, which in turn shape the biochemical environment to which soil microbial communities, including fungi, are exposed. Anaerobic systems favor strictly anaerobic bacterial and archaeal groups that drive hydrolysis, acidogenesis, acetogenesis, and methanogenesis, transforming organic matter into reduced end-products such as volatile fatty acids, CO_2, and methane (Cheng et al., 2018). These processes typically lead to the accumulation of partially stabilized organic compounds, lower redox potential, and shifts in nitrogen forms, conditions known to alter downstream microbial colonization once the organic material is applied to soil (Cheng et al., 2020; Clarke and Alibardi, 2010). In contrast, aerobic treatment relies on oxygen-dependent microbial pathways that promote more complete oxidation of organic matter, greater degradation of complex polymers, and reduced accumulation of inhibitory intermediates (Bekoe et al., 2018; Deng et al., 2023). In addition to treatment-derived effects, we hypothesized that the two waste treatment systems would impose divergent selective pressures on soil fungal communities, leading to measurable shifts in taxonomic structure even if overall diversity remained stable. Additionally, we expected that geographic variation would further modulate fungal composition across sites. Wherefore, in this study, we assessed the effects of soil fertilization with swine waste derived from different treatment approaches – CLB and WSP - on fungal communities. A metagenomic approach was employed to analyze fungal communities in soil samples from swine farms across different regions of Brazil, aiming to examine how factors such as climate, soil type, and vegetation influence microbial community structure in response to these organic fertilizers. Furthermore, we investigated how each waste treatment method affected the fungal community structure in waste samples from these farms, correlating these effects with soil fertilization outcomes. This integrative design allowed us to evaluate both treatment-driven and biogeographic influences on fungal community dynamics across a large and environmentally heterogeneous dataset.

2. Material and methods

2.1. Sample collection

Waste and soil samples were collected from 43 swine farms across three different geographical regions, being 20 farms using WSP located in Brazilian South Region, comprehending Rio Grande do Sul (RS) and Santa Catarina (SC) states, and 23 farms using CLB located in Midwest and Southeast Regions, comprehending Mato Grosso do Sul (MS) and Goiás (GO) states, and Southeast region, with Minas Gerais (MG) state (Fig. 1). In total, 80 samples originated from farms using WSP systems and 92 from farms using CLB systems (Supplementary Table 1).

From each farm, waste samples were collected from swine waste treatment input (43 samples) and output points (43 samples); and soil samples from non-fertilized (43 samples) and fertilized (43 samples) with waste output areas were collected, resulting in a total of 172 samples (Supplementary Table 1). Non-fertilized soils were collected exclusively from areas within each farm that had no history of organic or mineral fertilizer application. Samples were stored in a portable freezer (−20 °C) until transferred to −80 °C in the laboratory. Samples were treated as independent observational units, with farm identity included as a grouping factor in downstream statistical analyses to avoid pseudoreplication and to account for hierarchical structure.

2.2. DNA isolation and shotgun metagenomic sequencing

Metagenomic DNA isolation was performed by the DNeasy® PowerSoil® kit (Qiagen, Germany) following the manufacturer's instruction. DNA quality and quantity were assessed using NanoDrop One spectrophotometer (Thermo Fisher Scientific, USA) and Qubit™ fluorometer (Thermo Fisher Scientific, USA), respectively. Shotgun sequencing was performed by Illumina NovaSeq 6000 platform (Illumina, USA), 2 × 150 bp, with 30 GB/sample depth.

2.3. Statistical and comparative analyses

Metagenomic analyses were based as described in (Chen et al., 2021). Briefly, sequencing reads were quality-checked using FastQC and MultiQC, followed by trimming with Trimmomatic to remove short and low-quality bases (length < 50 nt; Phred <30), and adapters. High-quality paired-end reads were then analyzed using Kraken2 (v2.1.2) (Wood et al., 2019) for taxonomic classification, with the standard PlusPF database. The resulting reports were used to generate a BIOM file for downstream microbial community analysis.

Microbial community composition and diversity were analyzed using a combination of alpha and beta diversity metrics, differential abundance testing, and core taxa analysis. All statistical analyses and data visualization were conducted using R (version 4.3.2) with packages including *phyloseq*, *microbiome*, *microeco*, and *ggpubr*. Shannon diversity indices were calculated, and non-parametric tests (Wilcoxon and Kruskal–Wallis; *p-value* = 0.05) were applied based on results from the Shapiro–Wilk test (*p-value* = 0.05) and permutational multivariate analysis of variance (PERMANOVA). PERMANOVA models included sample type, treatment (non-fertilized vs. fertilized), waste treatment system (CLB vs. WSP), and geographic region as fixed factors, with Bray–Curtis dissimilarities calculated on relative abundance data. To visualize and identify relationships within the fungal community structures of the samples, we performed Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarities. Taxonomic differential abundance at the phylum, genus, and species levels was evaluated using the *microeco* package, applying the Wilcoxon test (*p-value* = 0.05) and a relative abundance threshold of 0.001 to filter out rare taxa. Core microbiome composition was examined using prevalence cutoffs, and Venn diagrams were generated to visualize shared and exclusive taxa among groups; only taxa with a prevalence above 30% were considered. These thresholds were chosen to minimize noise from very low-abundance and rarely detected taxa, which can disproportionately influence dissimilarity measures and compromise the reproducibility of shotgun metagenomic analyses (Quince et al., 2017). For co-occurrence network analysis, rare taxa were filtered and aggregated by sample groups. Spearman correlations ($|\rho| \geq 0.6$, FDR-adjusted *p value* < 0.05) were then calculated between these groups to assess co-abundance patterns, and the resulting correlation matrix was visualized as a network using *igraph* package, with nodes representing sample groups and edges weighted according to correlation strength. All analyses were based on sample metadata, which included grouping variables such as sample type and treatment conditions (Supplementary Table 1). Raw metagenomic sequencing data have been deposited in the NCBI under BioProject number PRJNA1321884 (BioSamples SAMN51227481-SAMN51227652).

2.4. Physicochemical characterization and multivariate analysis of samples

Physicochemical properties of soil and waste output samples were evaluated to investigate nutrient dynamics and compositional differences between treatment groups (Supplementary Table 2). Soil samples were analyzed for pH (Soil_pH), macronutrients (calcium [Soil_Ca], magnesium [Soil_Mg], potassium [Soil_K], phosphorus [Soil_P], sulfur [Soil_S]), and micronutrients (copper [Soil_Cu], zinc [Soil_Zn]), alongside indicators of soil acidity including exchangeable aluminum (Soil_Al), potential acidity (Soil_H + Al), and aluminum saturation

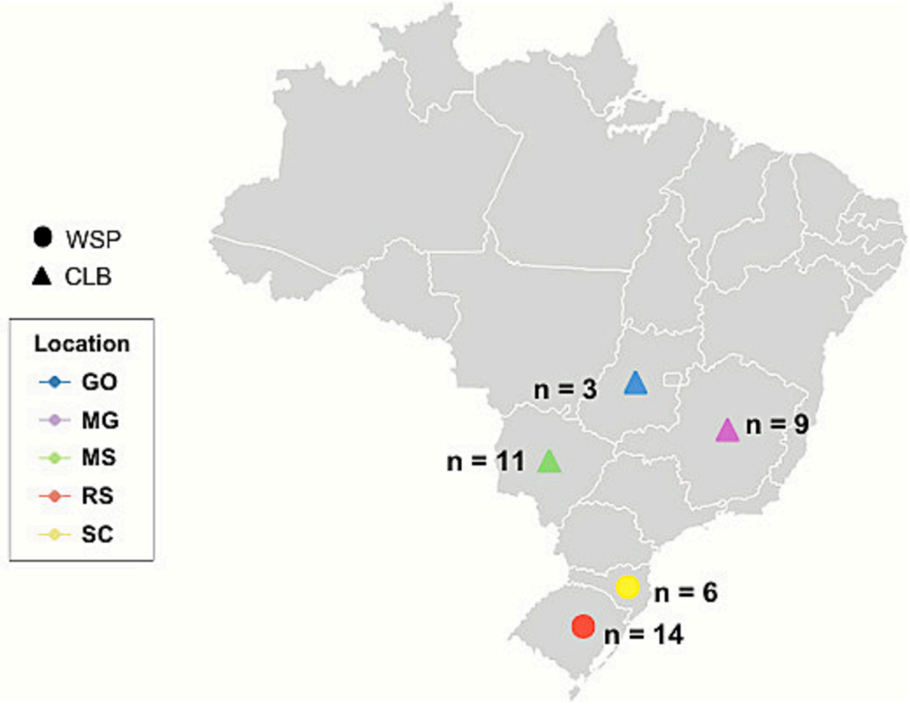

Fig. 1. Schematic map of the regions in Brazil where swine waste and soil samples were collected, their respective sample sizes and waste management system.

(Soil_Sat_Al). Additional metrics included base saturation ratios (Soil_Ca/Mg, Soil_K/CTC, Soil_Ca/CTC, Soil_ Mg/CTC), cation exchange capacity at pH 7 (Soil_ CTCpH7) and effective CEC (Soil_CTCef), clay content (Soil_Clay), total organic carbon (Soil_ COT), total nitrogen (Soil_NT), and the carbon-to-nitrogen ratio (Soil_COT/NT). These chemical variables were used to construct Euclidean distance matrices and perform Principal Coordinates Analysis (PCoA) for each sample group (control vs. fertilized soil), and the different waste management systems (WSP vs. CLB). Ellipses were added to the PCoA plots to indicate group dispersions. All analyses were based on sample metadata, which included grouping variables such as sample type, treatment condition, and the concentration (ppm) of all chemical elements analyzed (Supplementary Table 2).

The physicochemical analysis of waste output samples focused on quantifying macro- and micronutrients as well as organic matter components. Specifically, the following parameters were measured: total nitrogen (Waste_output_N), potassium (Waste_output_K), phosphorus (Waste_output_P), calcium (Waste_output_Ca), magnesium (Waste_output_Mg), copper (Waste_output_Cu), zinc (Waste_output_Zn), total solids (Waste_output_ST), fixed solids (Waste_output_SF), volatile solids (Waste_output_SV), total organic carbon (Waste_output_COT), and total nitrogen content (Waste_output_NT). These chemical data were incorporated into the analysis as sample metadata (Supplementary Table 2) and used to compute Euclidean distance matrices for subsequent multivariate ordination (PCoA), enabling the identification of compositional patterns among samples based on waste treatment group and system.

3. Results

3.1. *Effects of fertilization and waste treatment systems on fungal diversity and community composition*

We conducted a comprehensive analysis of the overall structure of our samples. We found no significant differences in the Shannon diversity index for alpha-diversity between waste input and output samples (*p-value* = 0.77; Fig. 2a). Similarly, no significant change was observed in the overall fungal community structure between non-fertilized and fertilized soils (*p-value* = 0.29; Fig. 2b), suggesting that soil fertilization did not significantly affect the fungal community structure. We observed that both soil and waste samples formed distinct clusters, with similar distribution between control and fertilized soil samples, as well as waste input and output samples (Fig. 2c).

We performed a Venn diagram analysis to identify common fungal taxa across the samples, considering only those with at least 30% prevalence. This analysis revealed a total of nine, four, 26, and 35 core

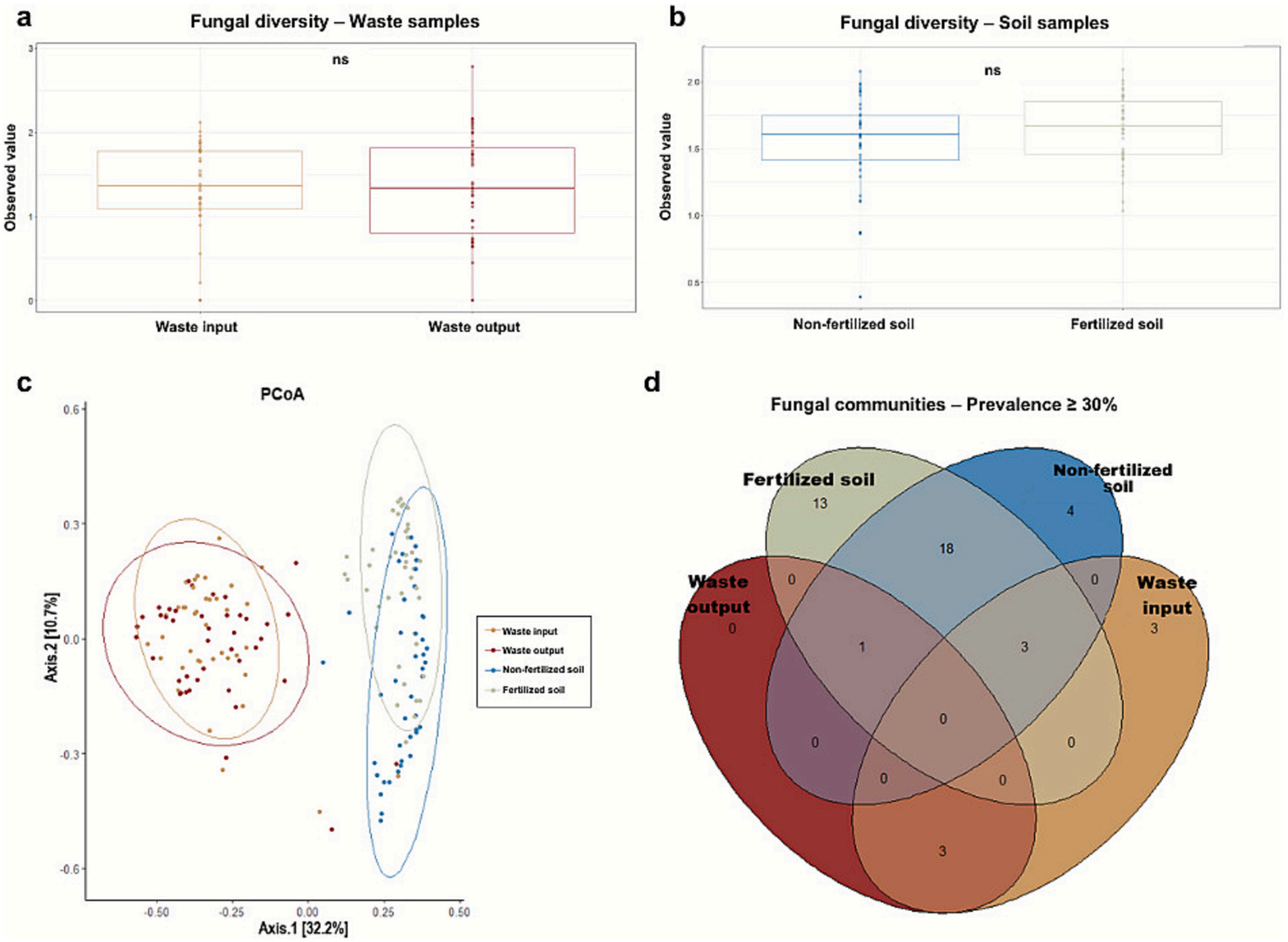

Fig. 2. Fungal diversity in swine waste and soil samples collected from different regions of Brazil. **(a)** Shannon alpha-diversity richness indices comparing waste samples (input and output). **(b)** Shannon alpha-diversity richness indices comparing soil samples (non-fertilized and fertilized). Statistical analysis was performed using the Wilcoxon rank-sum test (*p-value* = 0.05); ns = non-significant. **(c)** Principal Coordinate Analysis (PCoA) of fungal diversity based on Bray-Curtis dissimilarities from waste input and output samples, and non-fertilized and fertilized soil samples. **(d)** Venn diagram showing the relationships between the fungal communities present in all samples.

fungal taxa in waste input, waste output, non-fertilized soil, and fertilized soil samples, respectively, with no taxa shared across all sample groups (Fig. 2d).

The influence of geographical region (South, Southeast, or Central-West), location (GO, MS, MG, SC or RS), and manipulation of both soil and waste samples were analyzed as potential influencing experimental factors to fungal composition, according to the waste treatment system from each farm. The Kruskal-Wallis test was performed on the full set of soil and waste samples, irrespective of treatment group (non-fertilized or fertilized; input or output), and indicated differences in the fungal alpha-diversity based on the experimental factors. In CLB farms, significant differences were observed by location for waste samples (*p-value* = 0.001, Table 1) and by region for soil samples (*p-value* = 0.0302, Table 2). To assess how experimental factors structured fungal community composition, we performed PERMANOVA analyses and examined associated R^2 values, which indicate the proportion of variation explained by each factor. For waste samples from CLB, PERMANOVA indicated that fungal community composition differed significantly between waste input and output samples (*p-value* = 0.032, R^2 = 0.0459, Table 3). Significant differences were also detected across locations (*p-value* = 0.001, R^2 = 0.1671) and between regions (*p-value* = 0.005, R^2 = 0.0602, Table 3). In contrast, for waste samples from WSP, no significant differences were observed for any evaluated factor. The waste treatment group showed no effect on community composition (*p-value* = 0.710, R^2 = 0.0144), and location was also non-significant (*p-value* = 0.076, R^2 = 0.0419, Table 3). Regional comparisons were not applicable for WSP, as all samples originated from the same region. For soil samples, we found significant differences in fungal community composition between non-fertilized and fertilized soils in both waste treatment systems (CLB: *p-value* = 0.001, R^2 = 0.0975; WSP: *p-value* = 0.001, R^2 = 0.3030, Table 4). In CLB farms, an additional effect of location was detected (*p-value* = 0.048, R^2 = 0.0830), whereas no other experimental factors showed significant influence on soil community structure (Table 4). These indicate that although alpha diversity remained stable, fertilization with swine waste and geographic factors significantly shaped fungal beta-diversity, indicating shifts in community composition rather than richness.

3.2. Relative abundance and changes in fungal communities in soil and waste samples

We analyzed the relative abundance of the top 10 most abundant fungal communities in individual samples, comparing non-fertilized and fertilized soils, as well waste input and output. We performed a relative abundance analysis on waste samples, comparing waste input and output. The fungal community profiles were highly variable in waste samples, exhibiting homogeneity in the distribution of fungal genera across the samples (Fig. 3a). Notably, the relative abundance of fungal genera was more pronounced in waste input samples from farms using CLB systems for treatment, and this diversity profile was sustained in the waste output samples (Fig. 3a). No detectable counts of the top 10 fungal taxa included in the analysis were found in three waste input samples.

In soil samples, the analysis of the top 10 most abundant fungal genera revealed a balance between the most abundant genus, *Fusarium*, and the second most abundant genus, *Rhizophagus*, along with other less abundant fungal communities (Fig. 3b). Interestingly, the fungal community profile in fertilized soils changed, with an increase in *Fusarium* abundance, while other fungal communities decreased (Fig. 3b). The presence of *Rhizophagus* declined, while *Pichia* increased, suggesting that fertilization impacted the soil microbiota (Fig. 3b).

Table 1
Kruskal-Wallis statistical analysis of Shannon richness and diversity in total waste samples.

Covered Lagoon Biodigesters			Waste Stabilization Ponds		
Experimental factor	*p-value*		Experimental factor	*p-value*	
Location	0.001	***	**Location**	0.103	ns
Region	0.787	ns	**Region**	–	#

*** *p-value* < 0.001; ns = non-significant. # All samples are from the same region.

Table 2
Kruskal-Wallis statistical analysis of Shannon richness and diversity in total soil samples.

Covered Lagoon Biodigester			Waste Stabilization Ponds		
Experimental factor	*p-value*		Experimental factor	*p-value*	
Location	0.346	ns	**Location**	0.194	ns
Region	0.030	*	**Region**	–	#
Soil use	0.749	ns	**Soil use**	0.348	ns
Addition of organic fertilizers	0.140	ns	**Addition of organic fertilizers**	0.229	ns
Addition of mineral fertilizers	0.533	ns	**Addition of mineral fertilizers**	0.246	ns

#All samples are from the same region.
* *p-value* < 0.05; ns = non-significant.

Table 3
PERMANOVA analysis among experimental factors on fungal community composition in waste samples.

Covered Lagoon Biodigester					
Experimental factor	Df	R2	F	Pr (>F)	
Waste treatment group	1	0.0459	2.1188	0.032	*
Location	2	0.1671	4.3153	0.001	***
Region	1	0.0602	2.8206	0.005	**
Waste Stabilization Ponds					
Experimental factor	**Df**	**R2**	**F**	**Pr (>F)**	
Waste treatment group	1	0.0144	0.6290	0.710	ns
Location	1	0.0419	1.8826	0.076	ns
Region	–	–	–	–	#

#All samples are from the same region.
* *p-value* < 0.05.
** *p-value* < 0.01.
*** *p-value* < 0.001; ns = non-significant.

Table 4
PERMANOVA analysis among experimental factors on fungal community composition in soil samples.

Covered Lagoon Biodigesters					
Experimental factor	Df	R2	F	Pr (>F)	
Soil treatment group	1	0.0975	4.6452	0.001	***
Location	2	0.0830	1.9018	0.048	*
Region	1	0.0144	0.6290	0.710	ns
Soil use	1	0.0419	1.8826	0.076	ns
Addition of organic fertilizers	1	0.0447	2.0157	0.075	ns
Addition of mineral fertilizers	1	0.0208	0.9156	0.490	ns
Waste Stabilization Ponds					
Experimental factor	**Df**	**R2**	**F**	**Pr (>F)**	
Soil treatment group	1	0.3030	16.5210	0.001	***
Location	1	0.0284	1.1137	0.309	ns
Region	–	–	–	–	#
Soil use	4	0.0499	0.4605	0.953	ns
Addition of organic fertilizers	2	0.0281	0.5364	0.800	ns
Addition of mineral fertilizers	2	0.0468	0.9095	0.512	ns

* *p-value* < 0.05.
*** *p-value* < 0.001; ns = non-significant. #All samples are from the same region.

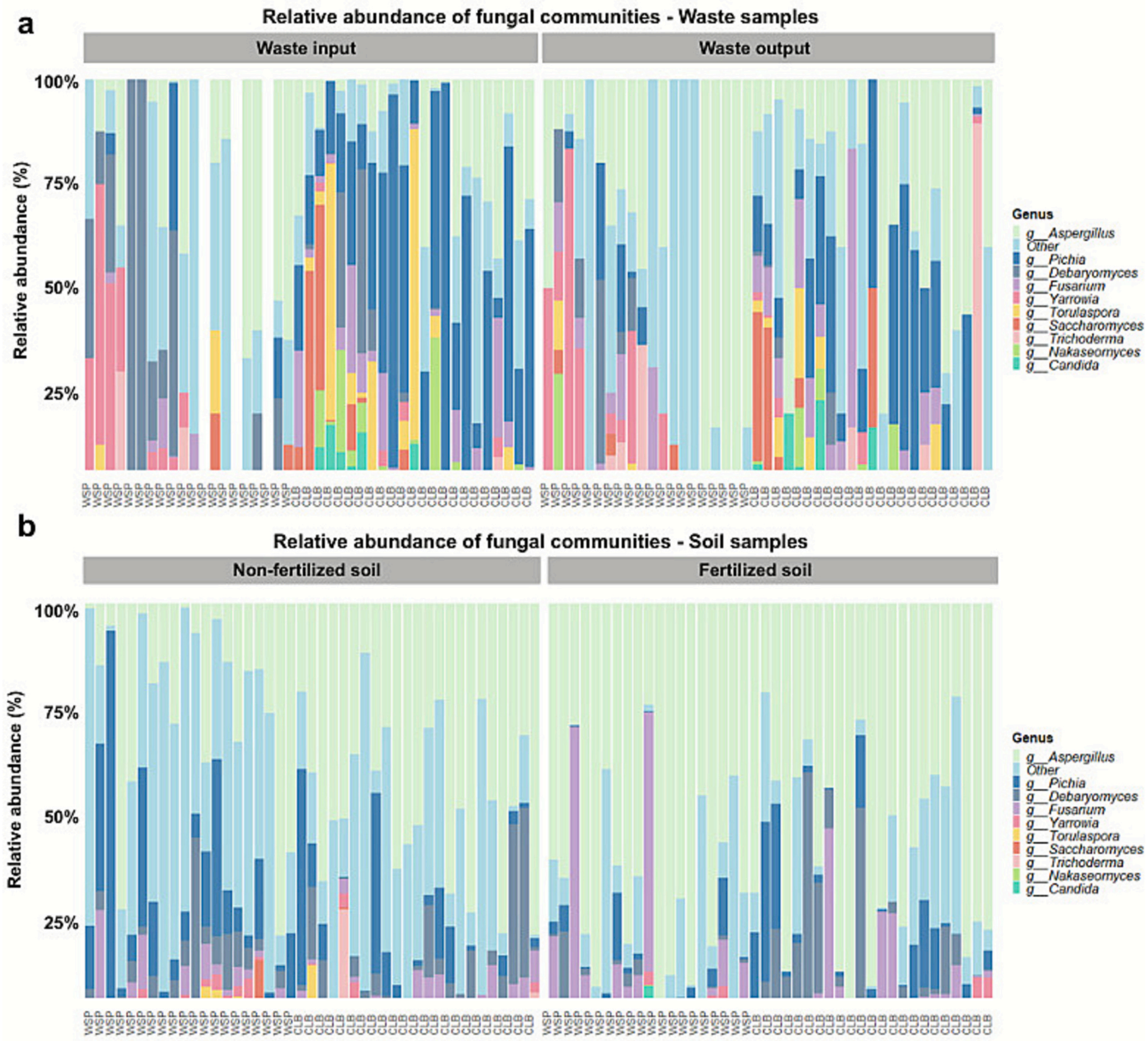

Fig. 3. Relative abundance in bar plots based on Amplicon Sequence Variants (ASVs) richness, showing the 10 most abundant fungal genera found in waste samples **(a)** and soil samples **(b)**.

3.3. Waste treatment system has no influence on fungal communities

We assessed the differences in fungal communities present in waste input and output, considering samples from wastewater treated either by WSP or CLB systems. The *Ascomycota* was the most abundant phylum followed by *Basidiomycota* and *Mucoromycota* in both waste treatment systems (Fig. 4a and b). However, differential abundance analysis between waste input and output samples revealed no significant variation in either treatment, indicating that the phylum profile remained largely unchanged (Fig. 4a and b). Additionally, similar clustering patterns were observed between the sample groups, with minimal or no distinction between swine waste treated with the CLB or WSP systems (Fig. 4c). These results suggest that the treatment systems had a minimal impact on the fungal communities present in swine waste.

The two most abundant fungal genera found were *Aspergillus* in WSP samples and *Pichia* in CLB samples (Fig. 4d and e). No statistical differences in fungal genus abundance were observed between waste input and output samples in both treatment systems (Fig. 4d and e, **Supplementary Fig. 1**). PCoA analysis was performed using Euclidean distance matrices calculated from the physicochemical properties of post-treatment waste samples, including nutrients like nitrogen, phosphorus, potassium, calcium, and magnesium, as well as organic matter and solids content. The ordination revealed that the physicochemical properties of waste output formed closely grouped clusters, indicating the homogeneity of these conditions (Fig. 4f).

3.4. Geographical variations in soil physicochemical properties and their influence on fungal diversity in different waste treatments

The soil sample group used for comparative fungal diversity analyses was obtained from different regions of Brazil, which exhibit significant differences in their physicochemical properties due to variations in climate, soil types, and vegetation. We evaluated the physicochemical properties of the soil samples used in our analysis to establish a relationship with the fungal diversity observed in these samples.

To perform a multivariate assessment of how fertilization and waste management strategies influence soil chemistry and potential microbial community drivers, we analyzed 156 soil samples out of a total of 172 collected samples. Soil samples were analyzed for nutrient levels, acidity indicators, organic matter, pH, macro- and micronutrients, and aluminum content, cation exchange capacity, clay percentage, and the balance between carbon and nitrogen. The PCoA, based on Euclidean

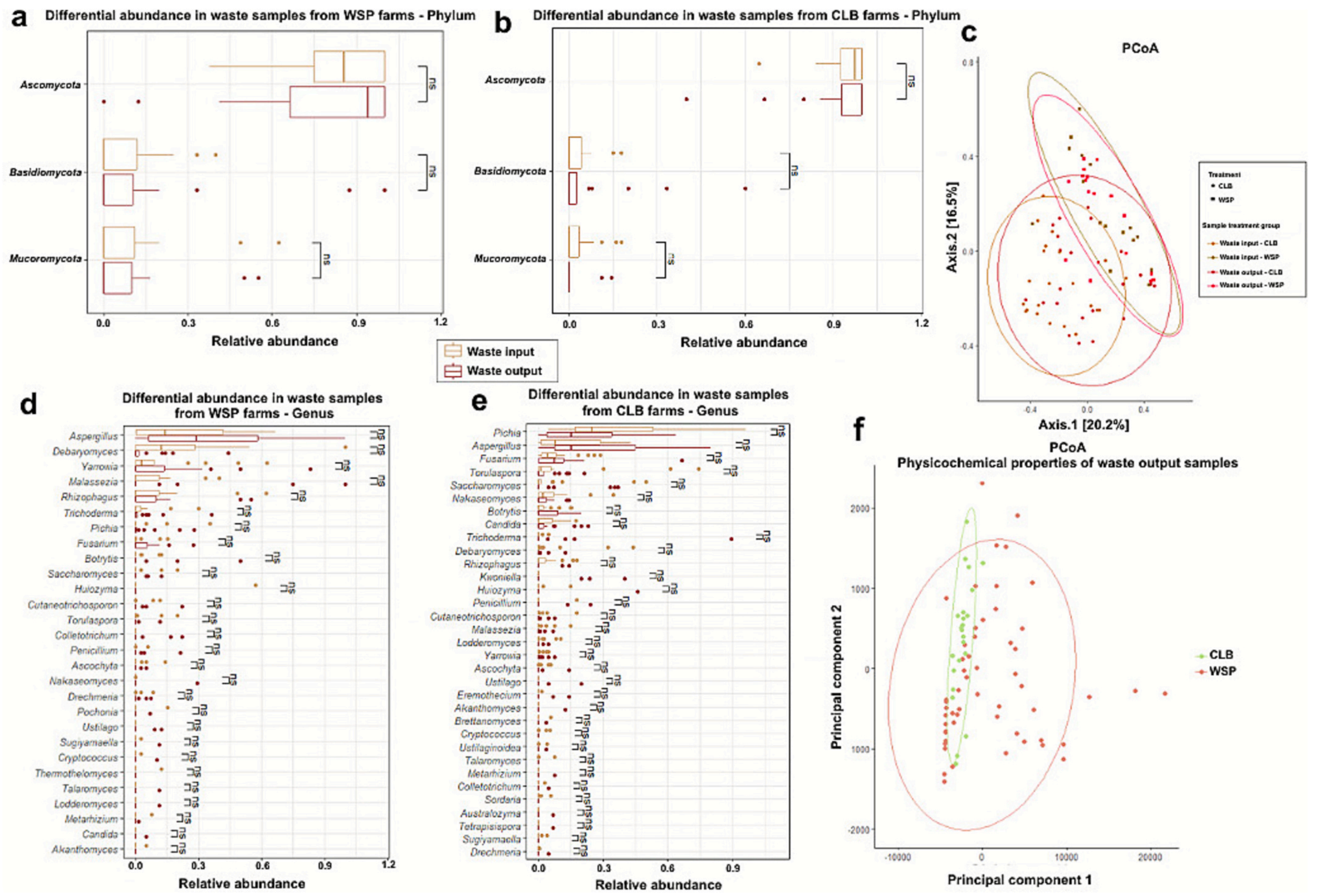

Fig. 4. Fungal abundance and diversity in waste treated by waste stabilization ponds (WSP) and covered lagoon biodigesters (CLB) systems. Differential abundance of fungal phyla between input and output samples of waste after treatment using the WSP **(a)** and CLB **(b)** systems. **(c)** Principal Coordinate Analysis (PCoA) of fungal diversity based on Bray-Curtis dissimilarities from waste input and output samples from farms that use WSP or CLB. Differential abundance of fungal genera between input and output samples of waste after treatment using WSP **(d)** and CLB **(e)** systems. **(f)** PCoA based on the Euclidean distance matrices from physicochemical properties of waste after treatment in WSP and CLB systems. Statistical analysis was performed using the Wilcoxon test (*p-value* = 0.05); ns = non-significant.

distance matrices, revealed that the non-fertilized soils - those that did not receive any addition of waste or fertilizers - from the different geographical regions tended to cluster closely, indicating a region-specific signature in soil chemistry (Fig. 5a). The partial overlap observed between clusters implies some shared characteristics among soil samples (Fig. 5a). Notably, the non-fertilized samples were collected from distinct locations within the farms, including both native forest and garden areas.

Samples collected from the southern region (RS and SC) use the WSP systems for waste treatment, while the central-west and southeastern regions (MS, MG, and GO) utilize CLB systems. We divided the non-fertilized soil samples according to these two treatment conditions and assessed the differential abundance of fungal genera between them. The genera *Fusarium*, *Malassezia*, and *Aspergillus* were enriched in non-fertilized soils from CLB systems, whereas *Metarhizium* was differentially abundant in non-fertilized soils from WSP (Fig. 5b). These results suggest that, despite maintaining similar fungal community structures, soil samples collected from different regions of Brazil exhibit intrinsic differences in the abundance of fungal communities. When we analyzed the physicochemical properties, we observed clustering of the fertilized soil samples derived from WSP and CLB (Fig. 5c).

3.5. Swine waste soil fertilization promotes a fungal communities balance on soil

To assess the impact of fertilization with treated swine waste on soil fungal communities, we analyzed differential abundance by comparing non-fertilized soils and fertilized soils for both treatment systems. *Ascomycota* was the most prevalent phylum, with an increase in its presence in fertilized soils. In contrast, the presence of *Mucoromycota* decreased in the fertilized soil samples (Fig. 6a and b). Unlike the findings for waste samples, the Bray-Curtis dissimilarity analysis for soil samples showed distinct clustering between CLB and WSP treatments, indicating significant differences in fungal ASVs distribution between these two treatment systems (Fig. 6c). *Fusarium* was the most abundant fungal genus in soil samples and was enriched in soils fertilized with waste from WSP systems, while *Rhizophagus*, the second most abundant genus identified, showed a decrease in fertilized soils (Fig. 6d). *Metarhizium*, *Pochonia*, and *Sugiyamaella* also exhibited a reduction in abundance in fertilized soils compared to non-fertilized soils (Fig. 6d). On the other hand, *Cuteneotricosporum*, *Cercospora*, and *Neurospora*, which were present in low abundance, showed an increase in fertilized soils compared to non-fertilized (Fig. 6d).

Overall, nine fungal genera showed significant differences in their abundances when comparing non-fertilized with fertilized soils. Interestingly, we found significant modifications in the abundance of fungal genera only in soil samples from WSP farms, but not in soil samples from CLB farms (Fig. 6d and e). We applied the same physicochemical analyses described above and observed partial clustering between non-fertilized and fertilized soils. However, fertilized samples, whether treated with organic matter from WSP or CLB, showed distinct chemical profiles (Fig. 6f). Notably, the fungal composition also differed between

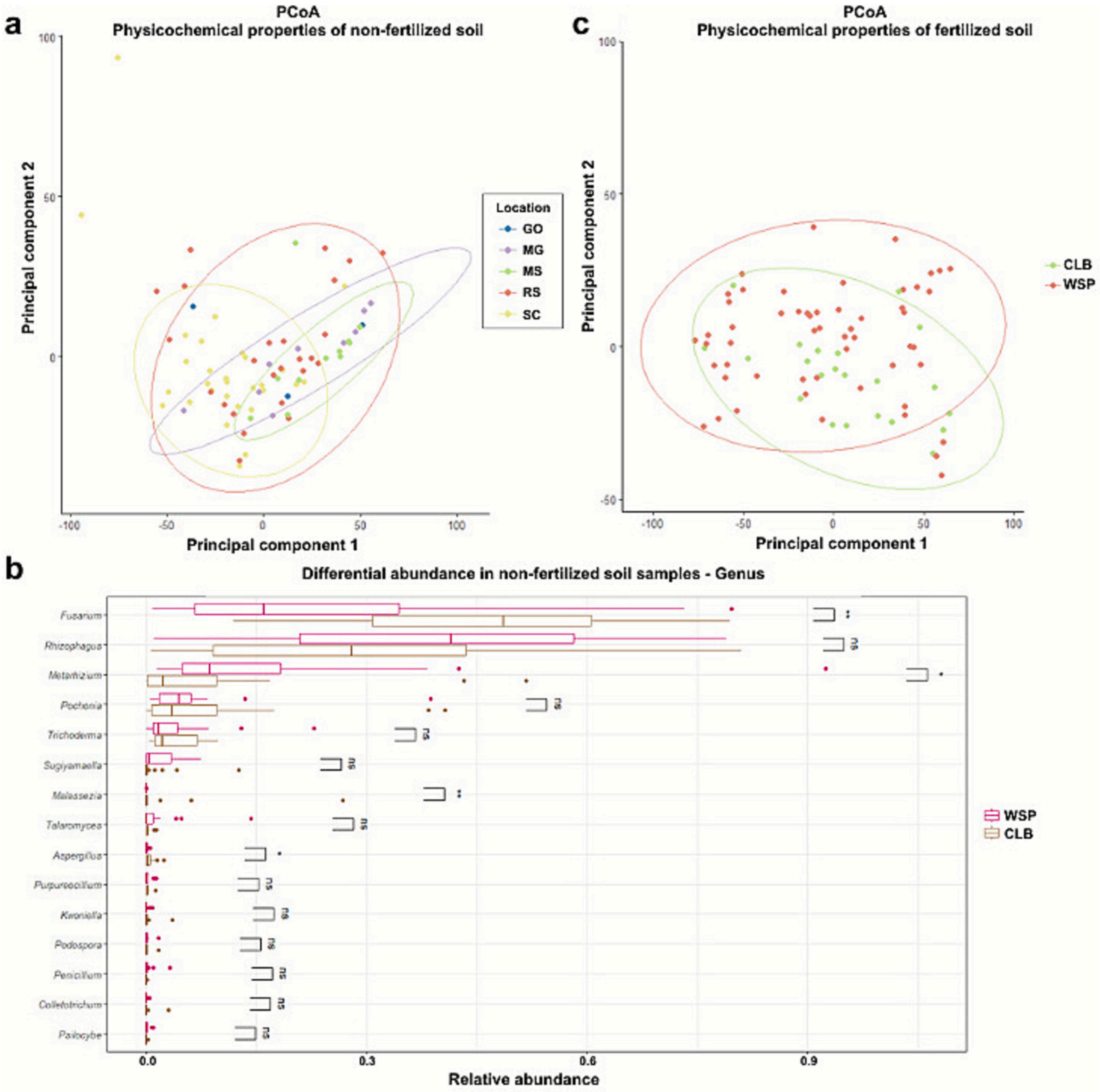

Fig. 5. Fungal diversity and physicochemical properties of non-fertilized and fertilized soils. **(a)** Principal Coordinate Analysis (PCoA) based on Euclidean distance matrices from physicochemical properties of non-fertilized soil samples, divided by locations (Supplementary Table 2). **(b)** Differential abundance of fungal genera between control soil samples from farms that use waste stabilization ponds (WSP) and covered lagoon biodigesters (CLB). **(c)** PCoA based on the Euclidean distance matrices from physicochemical properties of fertilized soil samples comparing fertilization with waste treated in WSP vs CLB systems. Statistical analysis was performed using the Wilcoxon test; *p value < 0.05; **p value < 0.01; ns = non-significant.

these treatments, with certain species found exclusively in one system. For example, *Sugiyamaella lignohabitans*, a saprotrophic fungus capable of degrading cellulose and lignin (Šuchová, Chyba, Hegyi, Rebroš and Puchart, 2022), was found only in samples from the WSP treatment (Fig. 6d **and Supplementary Fig. 2**). The PCoA of physicochemical variables demonstrated clear differentiation of soil chemical profiles between regions and treatment systems (Fig. 5a and c **and** Fig. 6f). These chemical gradients corresponded to shifts in fungal community composition identified in the PERMANOVA and differential abundance analyses.

We analyzed the co-occurrence patterns of fungal taxa across our sample groups. Spearman correlation revealed strong associations between fungal taxa in waste input and output samples, as well as between non-fertilized and fertilized soil samples (Fig. 7a). A similar correlation pattern was observed when comparing samples from CLB and WSP farms (Fig. 7b and c), indicating that the overall structure of fungal communities in these two environments remains largely consistent. In contrast, co-occurrence of fungal taxa between waste and soil samples was negatively correlated, even when assessing correlations between waste outputs and fertilized soils amended with organic matter derived from these wastes (Fig. 7b and c).

4. Discussion

Although numerous studies have demonstrated significant shifts in bacterial diversity in soil and swine waste environments (He et al., 2019; Torres et al., 2024; Zheng et al., 2022), fungal communities remain relatively overlooked despite their ecological significance. The results obtained in this study revealed significant variability in fungal communities across soil and swine waste samples, with distinct patterns observed between different types of waste treatment systems, and geographic locations. The Venn diagram analysis indicated no common fungal taxa shared across all sample groups, suggesting that fungal diversity was partially specific to each sample type. The presence of shared

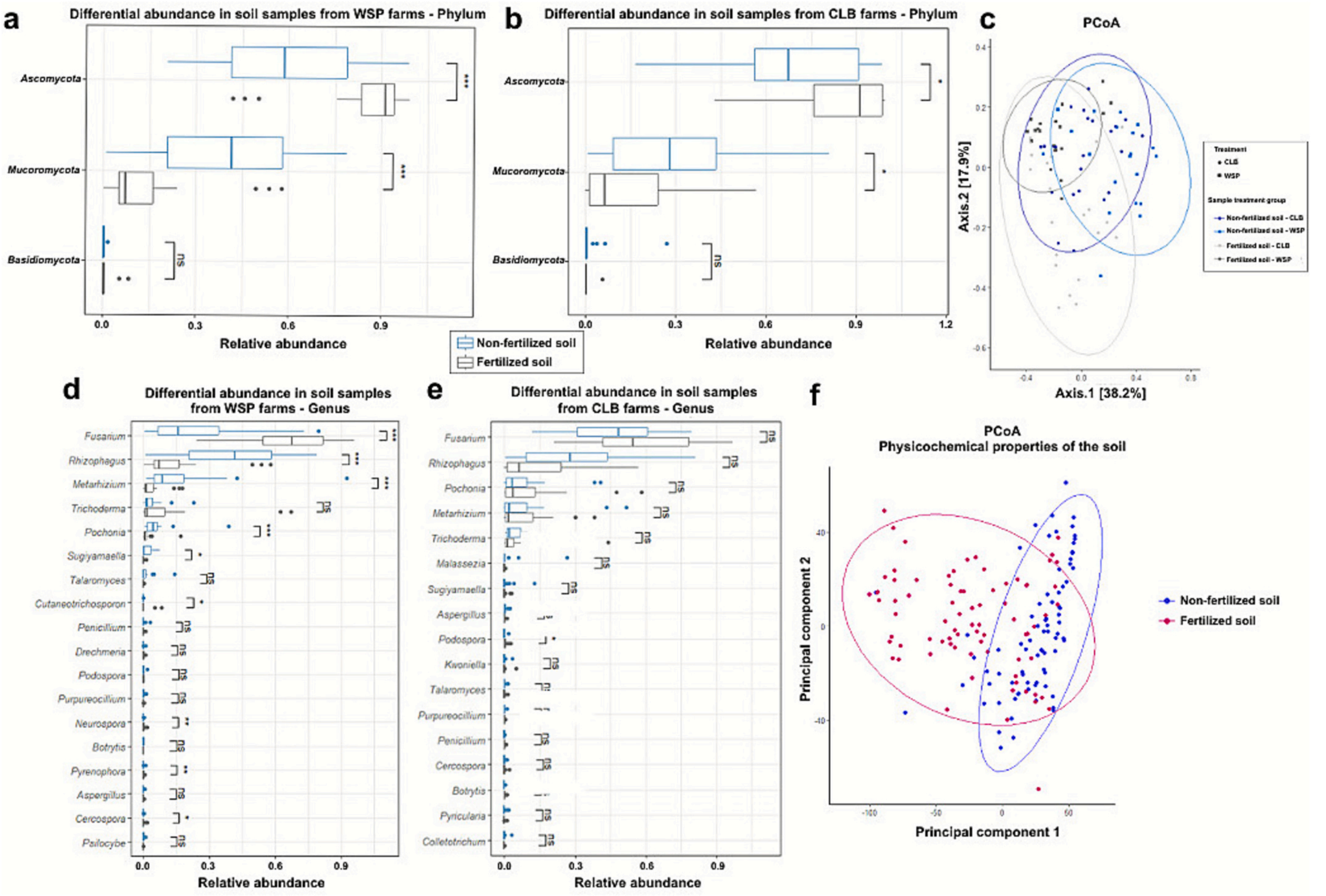

Fig. 6. Fungal abundance and diversity in non-fertilized and fertilized soils with organic matter from waste stabilization ponds (WSP) and covered lagoon biodigester (CLB) systems. Differential abundance of fungal phyla between non-fertilized and fertilized soil samples with organic matter generated from WSP **(a)** and CLB **(b)** farms. **(c)** Principal Coordinate Analysis (PCoA) of fungal diversity based on Bray-Curtis dissimilarities from non-fertilized and fertilized soil samples from farms that use WSP or CLB. Differential abundance of fungal genera between non-fertilized and fertilized soil samples with organic matter generated in WSP **(d)** and CLB **(e)** farms. **(f)** PCoA based on physicochemical properties of non-fertilized and fertilized soil samples. Statistical analysis was performed using the Wilcoxon test; **p value* < 0.05; ***p value* < 0.01; ****p value* < 0.001; ns = non-significant.

fungal taxa in both waste and fertilized soil samples was limited, which may indicate that, despite fertilization and waste treatment, the fungal community composition was not significantly altered, particularly concerning total diversity as measured by the Shannon index.

The PERMANOVA analyses revealed that experimental factors have differential effects on fungal community composition across waste and soil samples. For CLB waste samples, significant differences between waste input and output were detected, indicating that although the effect was statistically significant, the proportion of variance explained was relatively low. This suggests that other unmeasured environmental or stochastic factors may contribute substantially to fungal community variation, consistent with prior studies highlighting the complex and heterogeneous nature of fungal assemblages in waste environments (Assress et al., 2019). Location and region showed moderate explanatory power, emphasizing that spatial factors influence fungal beta-diversity more strongly than treatment effects alone. In contrast, waste samples from WSP systems exhibited no significant effect of treatment or location and low R^2 values, support that fungal communities in these samples are relatively homogeneous. For soil samples, fertilization with swine waste significantly affected fungal composition in both CLB and WSP systems. The higher R^2 in soils fertilized with WSP-waste indicates that fertilization explains a substantial portion of community variation, highlighting the strong impact of organic matter amendment on fungal beta-diversity. Location had a modest but significant effect in soils fertilized with CLB-waste, suggesting spatial heterogeneity also contributes to community structuring. Taken together, these results indicate that while alpha diversity metrics remained stable across treatments, beta-diversity analyses capture shifts in community composition driven by fertilization and spatial factors. The relatively low R^2 values in some comparisons reinforce the notion that fungal community assembly is influenced by multiple interacting factors (Panico et al., 2025).

Fertilization with swine waste had a more pronounced effect on the fungal composition of soil compared to the non-fertilized soils, especially in fertilized soil samples from WSP systems, indicating that soil fertilization with organic matter from WSP systems seems to have a greater impact on the balance of fungal communities in the soil. The genus *Fusarium* was more abundant in soils fertilized with waste from WSP, while *Rhizophagus*, one of the most abundant genera in non-fertilized soils, was reduced in these samples. *Fusarium* species are known to produce bioactive secondary metabolites, some of which have pharmacological relevance, such as antimicrobial activity (Li et al., 2020; Xu et al., 2023). However, it is important to note that *Fusarium* species are also plant pathogens, capable of affecting a wide range of plants and causing diseases that can impact crop safety (Ma et al., 2013; Perincherry et al., 2019). In contrast, *Rhizophagus* species are arbuscular mycorrhizal fungi that form mutualistic relationships with plant roots, promoting nutrient absorption and supporting soil health and plant growth (Kokkoris et al., 2024; McGale and Sanders, 2022). The similar

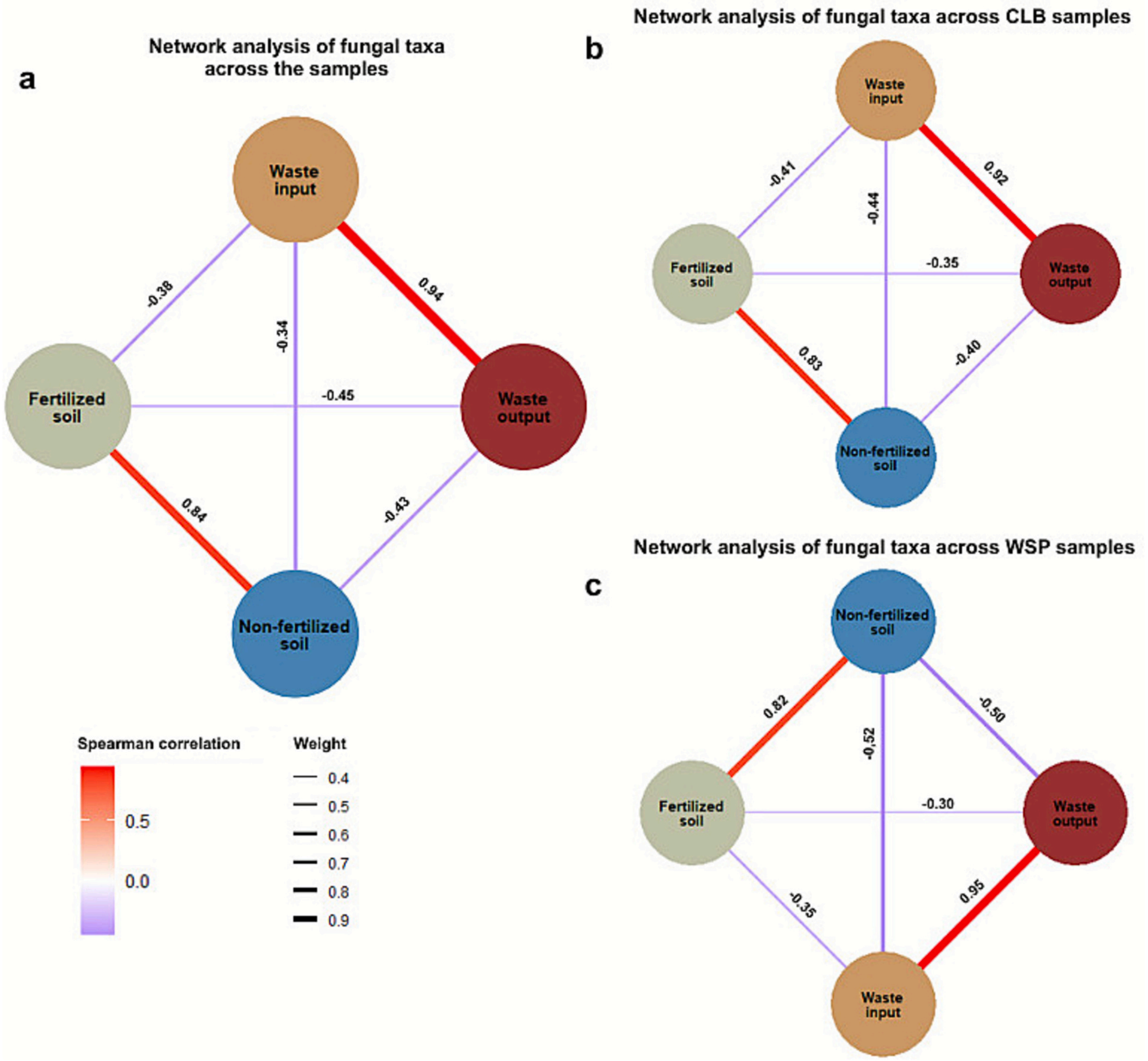

Fig. 7. Co-occurrence networks of fungal taxa across sample groups. Networks correlations among fungal taxa in waste input and output samples, and between non-fertilized and fertilized soils **(a)**, as well as in samples from WSP **(b)** and CLB **(c)** farms. Edge widths represent the strength of Spearman correlations, with positive correlations shown in red and negative correlations in blue. Statistical significance of correlations was assessed using Spearman's rank correlation coefficient.

abundance of *Fusarium* and *Rhizophagus* in non-fertilized soil samples indicates their coexistence in a balanced manner, yet fertilization with waste led to shifts in fungal populations. The enrichment of *Fusarium* species in fertilized soils may be associated with inputs of nitrogen- and carbon-rich organic matter (ASHRAF et al., 2023; Yuan et al., 2024). In contrast, *Rhizophagus* are sensitive to shifts in nutrient balance and soil disturbance, often declining in environments receiving high nutrient inputs (Liu et al., 2024; Semenov et al., 2022).

The network analysis of fungal taxa revealed strong co-occurrence within the sample type (waste input and output or non-fertilized and fertilized soil groups), consistent with the observed community composition patterns. These results suggest that fungal taxa within each environment are tightly associated, forming structured communities that are relatively conserved across different farm systems. Although the application of swine waste promoted the enrichment of specific fungal genera in fertilized soils, cross-habitat sharing between waste and soil communities remained minimal, indicating limited fungal dispersal or establishment between these environments. Consequently, the observed differences in fungal abundances between non-fertilized and fertilized soils can be primarily driven by alterations in soil organic matter content and macro- and micronutrient availability rather than direct transfer of taxa from waste. The consistent co-occurrence of certain taxa across treatments, such as the reciprocal patterns of *Fusarium* and *Rhizophagus*, showed ecological transitions previously documented in soils undergoing organic enrichment (Ashraf et al., 2023; Assunção et al., 2019). The differences in fungal composition between soils fertilized with WSP- and CLB-derived waste are compatible with the distinct biochemical signatures of these treatment systems. WSPs generate more oxidized organic substrates enriched in cellulose- and lignin-derived fractions, which are known to favor oxidative and saprotrophic fungal guilds (Deng et al., 2023). In contrast, the partially reduced compounds produced by anaerobic digestion in CLB systems tend to support a different spectrum of decomposers (Cheng et al., 2020). These functional contrasts align with previous studies showing that organic amendments processed under different redox regimes induce divergent fungal successional dynamics in soil (Assunção et al., 2019; Guo et al., 2025; Schlatter et al., 2023; Semenov et al., 2022).

The presence of lignocellulose-degrading yeasts such as *Sugiyamaella* in WSP-associated soils is consistent with their ability to exploit oxygenated environments enriched in complex plant-derived polymers

(Šuchová et al., 2022). These patterns reinforce the idea that waste treatment systems and fertilization regimes may act as environmental filters, selecting fungal taxa according to their metabolic traits and highlights the potential of WSP systems as a rich environment for fungal species capable of efficiently degrading lignocellulosic materials, offering insights into biotechnological applications for waste management and carbon cycling (Ravn et al., 2021; Šuchová et al., 2022). When we compared waste samples before and after treatment -input and output-, the composition of fungal communities was not significantly altered. Interestingly, *Pichia*, a yeast capable of performing anaerobic fermentation, was likely favored in CLB systems, which carry out anaerobic decomposition of organic matter. However, *Aspergillus* was found in high abundance in waste samples from both treatment systems, highlighting the ability of species such as *Aspergillus chevalieri* to thrive in distinct environments. While many species of *Aspergillus* are harmless or beneficial, some can act as opportunistic pathogens, particularly in immunocompromised individuals, and are known to contaminate crops (Amaike and Keller, 2011; Shabeer et al., 2022). *Pichia* is known for its rapid growth and adaptability, making it ideal for industrial applications such as recombinant protein production and fermentation processes (Barone et al., 2023; Weinacker et al., 2013).

The Central-West region (GO and MS samples) is characterized by drier soils with Cerrado bioma characteristics and high concentrations of minerals such as iron and aluminum (Assunção et al., 2019; Righi et al., 2023), whereas the South region (RS samples) has more fertile soils with higher organic matter content and a temperate climate (Ferreira et al., 2024; Franco et al., 2015). The Southeast region (MG samples) is marked by a high diversity of physicochemical properties resulting from variations in climate and topography (Franco et al., 2015). The PCoA demonstrated that the physicochemical properties of post-treatment waste, such as carbon content, nitrogen, heavy metals, and other covalent ions, formed tightly clustered groups, indicating that the treatments resulted in homogenous conditions across the samples. Although the main conclusions of our study are based on taxonomic patterns, the multivariate structure of the soil chemical data suggests plausible ecological mechanisms underlying the observed fungal distributions. Previous studies have shown that gradients in pH, organic matter content, cation availability, and redox conditions strongly modulate fungal assembly by filtering functional guilds and metabolic strategies (ASHRAF et al., 2023; Assunção et al., 2019; Guo et al., 2025; Semenov et al., 2022). In our dataset, the partial clustering of soils from different regions and treatment systems aligns with these well-established environmental filters, indicating that variation in soil chemistry likely contributes to the compositional shifts observed across samples.

5. Conclusions

This study revealed that waste treatment systems, such as CLB and WSP, have a limited impact on the fungal diversity of waste samples, although the abundance of certain fungal genera may change between systems. On the other hand, fertilization with swine waste, particularly from WSP systems, was more effective in altering the fungal composition of soil. Geographic variations and differences in soil physicochemical properties play a crucial role in shaping fungal community structure. These findings highlight the importance of considering local characteristics and waste treatment types in the management of soil and waste microbiota, as these variables can influence soil fertility, and the ecological processes involved in decomposition and nutrient cycling.

CRediT authorship contribution statement

Camila Diehl: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gabriela Merker Breyer:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Mariana Costa Torres:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Camila Rosana Wuaden:** Resources, Investigation, Conceptualization. **Raquel Rebelatto:** Resources, Investigation, Conceptualization. **Janaina Pastore:** Resources, Investigation, Conceptualization. **Rodrigo da Silveira Nicoloso:** Resources, Investigation, Conceptualization. **Marcio Dorn:** Resources. **Jalusa Deon Kich:** Resources, Investigation, Conceptualization. **Franciele Maboni Siqueira:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.181376.

Data availability

I have shared the public access number at the Methods section

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