



Research article

Biodiversity of fungi in Rhizosphere of *Imperata cylindrica* on Toposequential landslide areas under dryland agriculture and agroforestry land use

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Abstract

Importance of the work: Soil erosion and land use affect fungal diversity, influencing soil fertility and ecosystem resilience in erosion-prone agricultural areas.

Objectives: To assess fungal diversity in the rhizosphere of *Imperata cylindrica* (L.) P.Beauv. across erosion zones and land use systems on Sumbing Volcano, Central Java, Indonesia.

Materials and Methods: Fungal communities were analyzed using DNA extraction, polymerase chain reaction, Illumina sequencing and glomalin-related soil protein quantification. The soil properties measured included the pH and nitrogen, organic carbon and phosphorus contents across agroforestry and dryland agricultural systems in different erosion zones.

Results: In total, 164,221 high-quality sequences (99.7% of 164,650) identified an average of 359 operational taxonomic units per sample, grouped into the Ascomycota, Basidiomycota, Mortierellomycota and Glomeromycota. Agroforestry had higher levels of pH, nitrogen, organic carbon and phosphorus, whereas phosphorus was lower in dryland agriculture, particularly in depositional zones. Fungal diversity was higher in agroforestry (Chao index approximately 400, Simpson index approximately 0.88) than in dryland agriculture (Chao approximately 350, Simpson approximately 0.65). Clustering analysis showed the depositional zone samples (Ab and Cb) were distinct from the residual zone samples (Aa and Ca), reflecting soil and land use differences.

Main finding: Agroforestry had enhanced fungal diversity and soil fertility, supporting sustainable agriculture in erosion-prone landscapes. These findings highlighted the role of land use in shaping microbial communities and ecosystem resilience.

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Introduction

Soil erosion, particularly by water, is a major factor affecting agricultural productivity, as it leads to nutrient depletion, decreased soil organic carbon, reduced water availability and alterations in microbial communities (Chen et al., 2024). Erosion is influenced by factors including rainfall (Zhao et al., 2021) and land surface variations (topography, soil type) and land use systems (Gong et al., 2022). Landslides, a common erosion phenomenon, redistribute soil from upper to lower slopes, creating residual, erosional and depositional zones (Sartohadi et al., 2018; Purwaningsih et al., 2020). While soil distribution impacts microbial communities and agricultural productivity, few studies have examined the simultaneous effects of land use and erosion on fungal communities (Ballauff et al., 2021).

Kajoran, in Magelang Regency, Central Java, Indonesia, is an important cassava-producing area, facing challenges from periodic landslides, high rainfall and steep slopes. The current research site, located in a former landslide area (13 ha), has a complex soil structure, particularly altered clay minerals, which complicate crop cultivation. The area is divided into agroforestry and dryland agricultural systems, with agroforestry supporting diverse crops (sengon, coconut, teak, petai, rambutan, coffee) and dryland mainly supporting cassava (Purwaningsih et al., 2020; Hadini et al., 2021).

Fungi play essential roles in nitrogen fixation, hormone production, biological control and soil organic matter stabilization (Meng et al., 2020; Zou et al., 2021; Yu et al., 2022). Their diversity is influenced by both biotic (plants, other organisms) and abiotic factors (soil pH, moisture, structure). Soil erosion and land use substantially affect fungal diversity (Ballauff et al., 2021), with vegetation variation impacting fungal composition through microclimatic conditions and plant-microbe interactions. Soil erosion by water such as in landslide phenomenon, is composed of four stages: 1) detachment; 2) splash; 3) transport and redistribution; and 4) deposition and burial of the soil (Olson et al., 2016). These stages create three distinct erosional zones (residual, erosional, depositional) that influence fungal communities (Purwaningsih et al., 2020).

While other research has focused on fungal diversity in erosional and depositional zones, the current study aimed to compare fungal communities in residual and depositional zones under different land uses (agroforestry and dryland

agriculture). The hypotheses to be tested were: 1) fungal communities exhibit greater variation in agroforestry than in dryland agriculture; and 2) fungal distribution differs across landslide-affected zones.

Materials and Methods

Sampling areas

This study was conducted on the southern slope of Mount Sumbing, within the Kaliwungu Sub-watershed in Central Java, Indonesia, covering 13 ha across agroforestry and dryland agriculture systems. The site spans three erosion zones—residual, erosional and depositional. *Imperata cylindrica* (L.) P.Beauv. and rhizosphere soil samples were collected from both land use types across all zones.

Table 1 Coordinates of sampling locations

Zone type	Dryland agriculture	Agroforestry
Residual	7.548957° N U, 110.057593° S	7.550408 ° N, 110.059338° S
	7.547813 ° N, 110.057567 S	7.551232 ° N, 110.059130° S
Erosional	7.546640 ° N, 110.058065 S	7.551098 ° N, 110.058557° S
	7.547427 ° N, 110.058378 S	7.549968 ° N, 110.058287° S
Depositional	7.547980 ° N, 110.059325 S	7.549893 ° N, 110.057960° S
	7.548527 ° N, 110.059510 S	7.551075 ° N, 110.058033° S

Soil chemical analysis

Chemical analysis of the soil samples was conducted at the Soil Science Laboratory, Faculty of Agriculture, Universitas Gadjah Mada, Indonesia. The soil pH was determined using a pH meter in a soil-to-water suspension ratio of 1:2.5. The total nitrogen (N) content was quantified using the Kjeldahl method (Raimondi et al., 2025), while organic carbon (organic C) was measured using the Walkley-Black wet oxidation procedure (Shamrikova et al., 2023). Available phosphorus (P) was extracted using the Bray I method (Silva et al., 2024). The cation exchange capacity (CEC) was assessed using the ammonium acetate method at a pH of 7.0. (Nafi’ah et al., 2025).

Glomalin-related soil protein content

Measurement of the easily extractable fraction-glomalin related soil protein (EE-GRSP) and total glomalin-related soil protein (T-GRSP) used the method of Qiu et al. (2020).

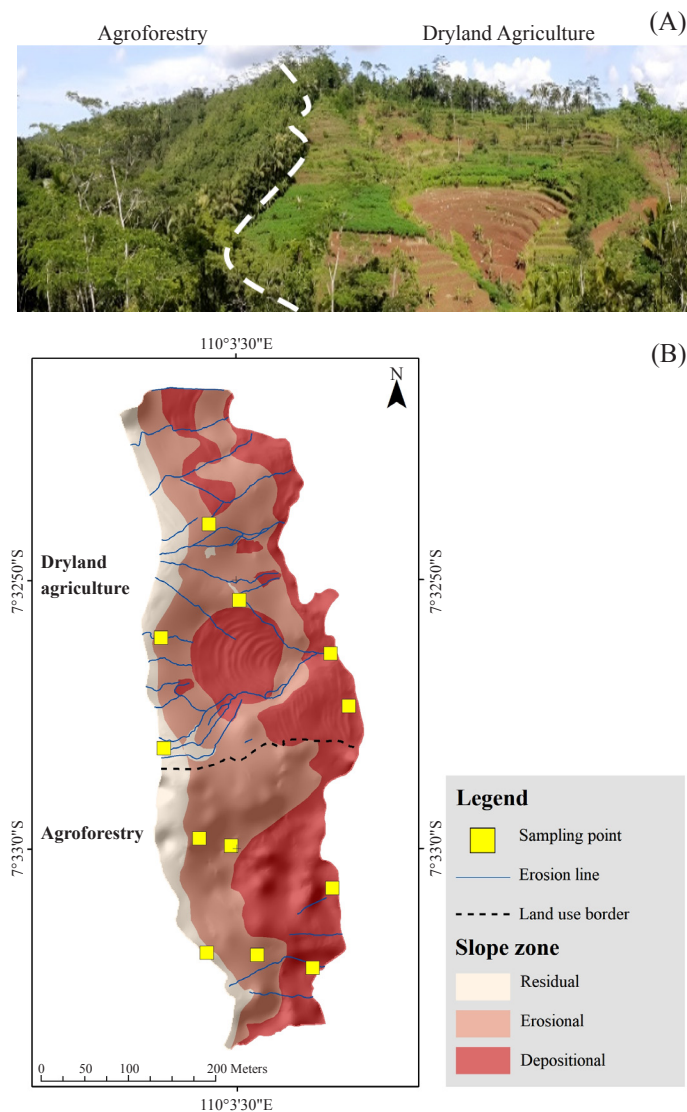


Fig. 1 Sampling locations: (A) photograph illustrating two different land uses; (B) mapped within land use systems and slope zones

DNA extraction, Illumina sequencing and data processing

Root samples (50–100 mg) of *I. cylindrica* were cleaned and DNA was extracted using a FavorPrep™ Plant Genomic DNA Maxi kit and the CTAB/SDS method (Krishnan et al., 2024)) and then quantified and diluted to 1 ng/μL. Fungal internal transcribed space (ITS) regions were amplified using ITS1-1F-F and ITS1-1FR primers with Phusion® High-Fidelity Master Mix and products were verified via 2% agarose gel. Libraries were prepared following Wang et al. (2019) using the NEBNext® Ultra™ DNA Library Prep Kit and assessed using the Qubit 2.0 and Agilent Bioanalyzer 2100 system. Sequencing was performed on the Illumina platform with 250 bp paired-end reads.

Raw reads were merged using FLASH (Magoč and Salzberg, 2011), quality-filtered and then chimeras were removed using UCHIME (Edgar et al., 2011) against the Silva database (Haas et al., 2011). OTUs were clustered at 97% similarity using Uparse (Edgar, 2011), taxonomically annotated using the GreenGene database (DeSantis et al., 2006) and RDP Classifier (Wang et al., 2007) and aligned using MUSCLE (Edgar, 2004). OTU counts were normalized and alpha/beta diversity was analyzed in QIIME v1.7.0 (Caporaso et al., 2010) and visualized using the R language and environment for statistical computing (v2.15.3) .R Core Team, (2013).).

Alpha diversity by land use

The influence of fungal alpha diversity on land cover was determined based on the Chao index and Simpson index (Chernov et al., 2015).

Statistical analysis

A nested design was used, with land use types (agroforestry and dryland agriculture) and erosion zone (residual and depositional) as independent variables and arbuscular mycorrhizal fungi (AMF) diversity indices as the dependent variables. Data were analyzed using analysis of variance, followed by Tukey's honest significant difference test for multiple comparisons at a test level for significance of $p < 0.05$, where applicable. Results were presented as mean $\pm$ SD values. The experimental design is summarized in Table 2. A summary of the experimental design is presented in Table 2.

Table 2 Experiment design used for this study

Erosion soil topography	Land area			
	Agroforestry (A)		Dryland agriculture (C)	
	1	2	1	2
Residual zone (A)	AA1	AA2	CA1	CA2
Erosional zone (T)	AT1	AT2	CT1	CT2
Deposisional zone (B)	AB1	AB2	CB1	CB2

Results

Chemical properties of agroforestry and dryland agriculture

Across the studied land use types and topographic positions, variations were observed in soil chemical properties: total N, organic C, available P and cation exchange capacity (CEC).

In agroforestry soils, the residual zone had mean total N and organic C values of $1.38 \pm 0.43\%$ and $1.67 \pm 0.47\%$, respectively, while in the dryland agriculture residual zone, the values were $0.87 \pm 0.04\%$ and $1.49 \pm 0.47\%$, respectively. The CEC values were in the range from 60.4 ± 3.39 cmolc/kg (agroforestry residual) to 73.4 ± 12.16 cmolc/kg (dryland agriculture erosional). Available P ranged from 0.75 ± 0.39 ppm (agroforestry residual) to 4.19 ± 1.34 ppm (dryland agriculture depositional). Although numerical differences were observed among topographic zones and land use types, none of these differences were statistically significant (Table 3).

Statistical analysis revealed that only the soil pH and available P were significantly different between land use systems (Fig. 2A and Fig. 2B). Agroforestry systems had higher pH levels than dryland agriculture. In contrast, available P was lower for agroforestry than dryland agriculture. However, there were no significant differences among the different topographic zones (residual, erosional, depositional) for any of the measured parameters, within or across land use systems. Additionally, no significant interaction effects between land use system and topographic position were detected for total N, organic C, or CEC (Table 3).

Soil fungal diversity and community composition

In total, 164,221 high-quality ITS sequences were analyzed, yielding an average of 359 OTUs per sample. At the phylum level (Fig. 3A), the Ascomycota dominated across all samples, representing 94.8% in agroforestry residual, 94.3% in agroforestry depositional and 97.8% in dryland agriculture residual, but dropping to 36% in dryland agriculture depositional, where Basidiomycota sharply increased to 63.8%. The Mortierellomycota and Glomeromycota were present in minor proportions.

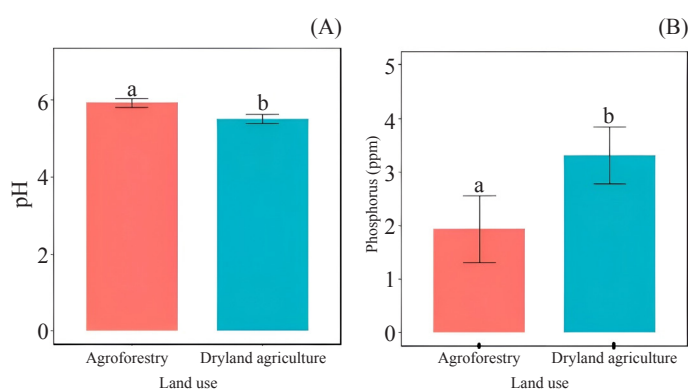


Fig. 2 Comparison of mean values between agroforestry and dryland agriculture systems for: (A) soil pH; (B) available phosphorus. Different lowercase letters above columns indicate significant ($p < 0.05$) differences between treatments. Error bars = $\pm$ SD; ppm = parts per million.

Table 3 Chemical properties of agroforestry and dryland agriculture soil

Sample		pH	Total N (%)	Organic C (%)	Available P (ppm)	CEC (cmolc/kg)
Agroforestry	Residual	5.95 ± 0.20	1.38 ± 0.43	1.67 ± 0.47	0.75 ± 0.39	60.4 ± 3.39
	Erosional	6.15 ± 0.01	1.23 ± 0.64	1.28 ± 0.87	1.53 ± 1.46	67.2 ± 9.05
	Depositional	5.68 ± 0.3	0.98 ± 0.35	0.92 ± 0.35	3.54 ± 1.14	67.6 ± 2.82
Dryland agriculture	Residual	5.73 ± 0.42	0.87 ± 0.04	1.49 ± 0.47	2.75 ± 1.44	65.4 ± 5.37
	Erosional	5.50 ± 0.23	0.95 ± 0.04	1.16 ± 0.23	2.98 ± 1.47	73.4 ± 12.16
	Depositional	5.31 ± 0.07	0.73 ± 0.36	0.84 ± 0.21	4.19 ± 1.34	63.4 ± 3.68

CEC = cation exchange capacity.

Values are presented as mean $\pm$ SD; no significant differences were observed among them ($p > 0.05$).

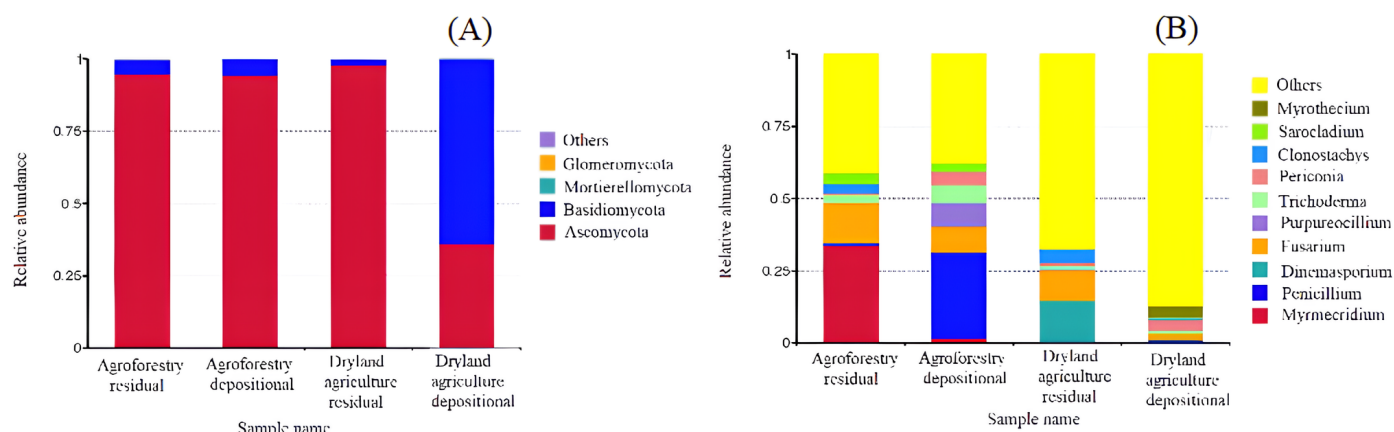


Fig. 3 Relative abundance of fungal communities at: (A) phylum level; (B) genus level, across different land use types and erosion zones.

At the genus level (Fig. 3B), ‘Others’ accounted for the largest proportion in all zones, particularly in dryland agriculture depositional, indicating diverse low-abundance genera. *Myrmecridium* was the most abundant named genus, especially in agroforestry residual. *Penicillium* dominated agroforestry depositional samples, while *Dinemasporium* was prevalent in dryland agriculture residual. In addition, *Trichoderma* and *Sarocladium* appeared consistently across land use types.

Alpha diversity by land use

Land cover can influence fungal alpha diversity, as observed through the Chao index and the Simpson index. Based on the current results, agroforestry land supports significantly higher fungal diversity compared to dryland agriculture, as evidenced by the Chao index, which was significantly higher in agroforestry (approximately 400) than in dryland agriculture (around 350), as shown in Fig. 4A. Similarly, the values for the Simpson index were significantly different (agroforestry scoring around 0.88 compared to 0.65 for dryland agriculture), as shown in Fig. 4B. Furthermore, there were changes in fungal alpha diversity before and after erosion events; in both land use systems, the residual zone had higher alpha diversity than the depositional zone (Figs. 5A and 5B).

Beta diversity across slope zones

The T-GRSP and EE-GRSP levels were highest in the residual and depositional zones, with no significant differences between them, while the erosional zone had significantly lower values (Figs. 6A and 6B), suggesting that glomalin accumulation was reduced under erosion stress. As a mycorrhizal glycoprotein,

glomalin contributes to soil structure stability, carbon storage and nutrient cycling (Šarapatka et al., 2019), highlighting its importance in maintaining soil health (Figs. 6A and 6B).

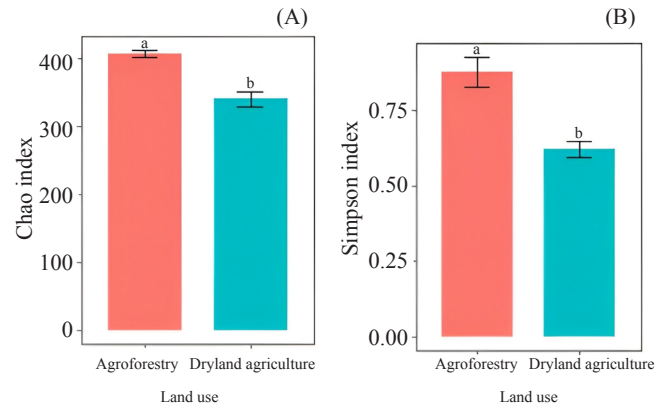


Fig. 4 Comparison of land use types based on (A) Chao index and (B) Simpson index. Different lowercase letters above the columns indicate significant differences ($p < 0.05$) between treatments. Error bars = $\pm$ SD.

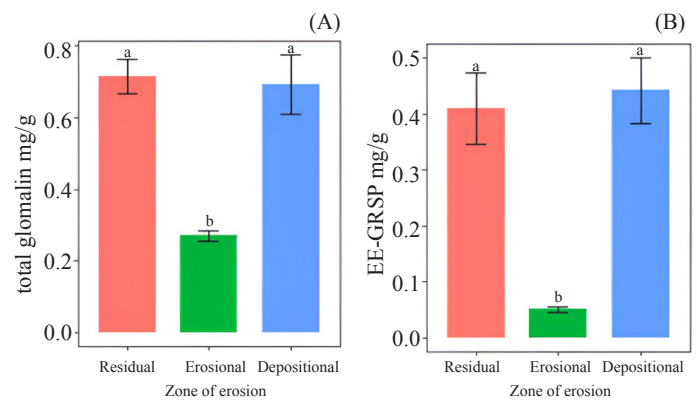


Fig. 6 Fungal glomalin indices across erosion zones: (A) total glomalin; (B) easily extractable glomalin-related soil protein (EE-GRSP). Different lowercase letters above columns indicate significant differences ($p < 0.05$) among zones of erosion. Error bars = $\pm$ SD.

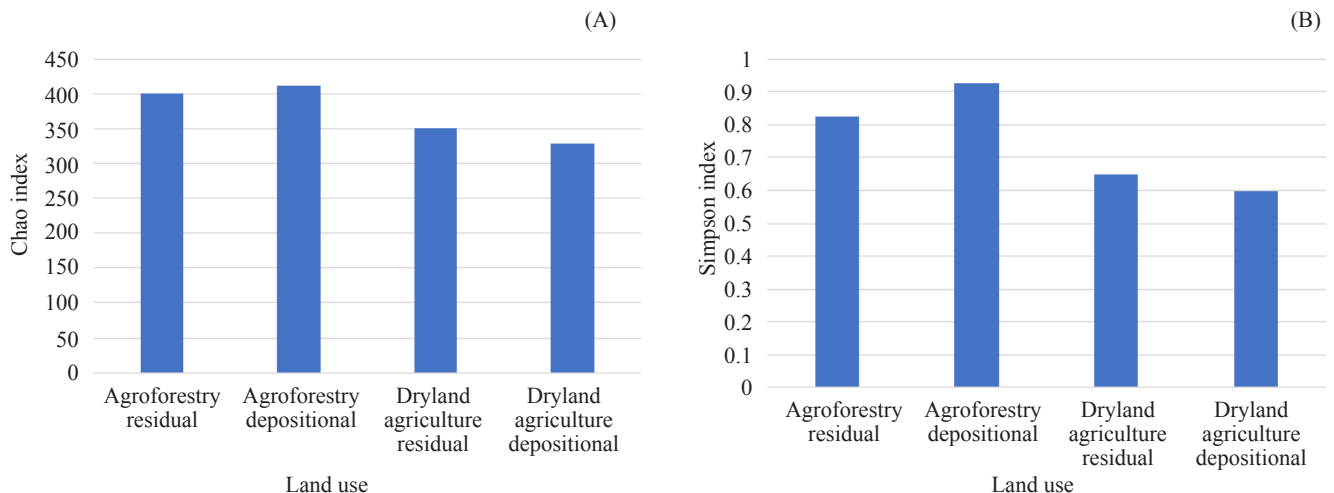


Fig. 5 Index values of fungal communities across different land use types and erosion zones: (A) Chao index; (B) Simpson index.

The principal component analysis (Fig. 7) showed that axis 1 explained 43.6% of the variation and separating the fungal communities primarily based on erosion zone. The residual samples from both agroforestry and dryland agriculture are clustered on the right side of the plot, while dryland agriculture depositional samples are distinctly separate on the far left, indicating a different fungal community composition. The agroforestry depositional samples are located near the center, having a partial overlap with the residual samples. In contrast, axis 2 explained 35.9% of the variation and does not separate the samples into distinct land use types. Based on these results, the erosion zone exerted a stronger influence on fungal community structure than land use type.

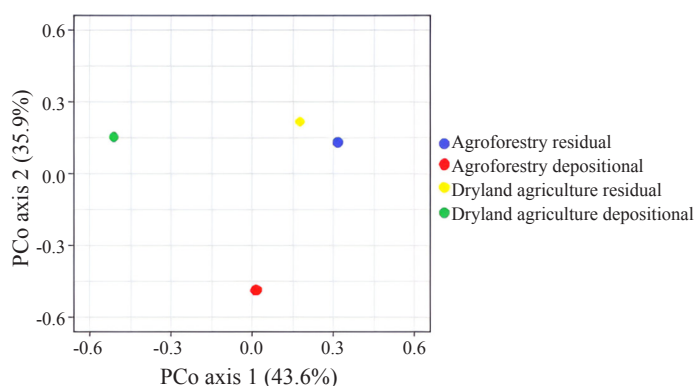


Fig. 7 Principal coordinate analysis (PCo) of arbuscular mycorrhizal fungi (AMF) communities based on land use type (agroforestry and dryland agriculture) and erosion zones (residual and depositional).

Discussion

I. cylindrica was selected as a model species due to its exceptional ecological adaptability as it thrives in nutrient-poor, dry and saline soils, making it effective for land rehabilitation and erosion control (Syahrudin et al., 2020; Rusdy, 2020). In addition, its occurrence in both agroforestry and dryland agriculture settings provided a consistent basis for investigating rhizosphere interactions and soil fungal communities (Ahmad et al., 2020; Mao et al., 2024; Shi et al., 2024).

Based on the current results, land use systems significantly influenced soil properties. For example, the agroforestry sites had higher levels of total N, organic C and CEC, aligning with another study reporting that diverse plant inputs enhanced soil fertility (Fahad et al., 2022). Similarly, the soil pH and available P were higher in agroforestry, likely due to the decomposition of the diverse sources of plant litter that could buffer acidity and increase P bioavailability (Nahon et al., 2024;

Zoungrana et al., 2024). However, even within the agroforestry systems, nutrient concentrations were lower in depositional zones, possibly due to slower organic matter turnover and site-specific environmental constraints (Amoakwah et al., 2022; Fahad et al., 2022). Notably, land use exerted a greater influence on soil fertility than slope position, as there were no significant differences in the values for N, organic C or CEC across the topographic zones.

These findings contrasted with other studies reporting increased nutrient accumulation on lower slopes due to erosion and deposition processes (Haile et al., 2024; Zhou et al., 2024). However, in the current study, there were no significant differences in these soil parameters between residual, erosional and depositional zones or between land use types, suggesting that other factors, such as past land use history or spatial heterogeneity, may have played a more dominant role in shaping soil properties on the study sites.

The analysis of the 164,221 ITS sequences revealed higher fungal diversity in agroforestry systems, attributed to better plant cover and soil structure that enhance fungal roles in soil aggregation and erosion control (Olson et al., 2016; Smith et al., 2021). This supports studies showing reduced diversity in monocultures due to limited organic inputs and altered nutrient cycling (Turley et al., 2020; Guo et al., 2022).

Ascomycota dominated most zones (94–98%), except in the dryland depositional soils, where its abundance dropped to 36%, while *Basidiomycota* increased to 63.8%—a shift linked to their ability to decompose complex substrates such as lignin (Du et al., 2021; Farooq et al., 2021). Diversity peaked in the residual zones across land uses, likely due to stable conditions and richer organic matter.

Myrmecridium dominated agroforestry residual zones, functioning as a saprotroph involved in decomposition and nutrient cycling (Jie et al., 2013; Freitas et al., 2022). *Penicillium*, also a saprotroph with biocontrol traits, was abundant in agroforestry depositional zones. In the dryland agriculture, *Dinemasporium* dominated residual soils, reflecting adaptation to stress and low nutrients (Hashimoto et al., 2015). A high proportion of the ‘Other’ genera in dryland depositional zones indicated turnover and microhabitat-driven specialization.

Other ecologically relevant fungi included *Fusarium*, a saprotroph and plant pathogen (Nikitin et al., 2023) and *Trichoderma*, which enhances plant growth and pathogen resistance (Valan et al., 2023). *Sarocladium* and *Purpureocillium* contributed to nutrient cycling and pathogen suppression

(Rigobelo et al., 2024). Less abundant, phyla, such as the Mortierellomycota (notably *Mortierella*, a classic saprotroph) and Glomeromycota, play key roles, especially in undisturbed soils (Li et al., 2024).

The fungal communities in the residual zones were similar across land uses, likely due to minimal disturbance and better habitat quality (Polussa et al., 2024). In contrast, the communities in the depositional zones diverged more strongly; agroforestry supported functional and diverse fungi, while dryland monoculture led to erosion, nutrient loss and selection for stress-tolerant, often saprotrophic, taxa (Beule et al., 2022; Koutika et al., 2024).

The differences in fungal composition between residual and depositional zones were further confirmed based on principal component analysis. The residual zones, with stable soil characteristics and limited erosion, supported specialized fungal groups associated with native vegetation. Conversely, the depositional zones accumulated eroded materials that may have altered the soil pH, organic matter or moisture content, thereby fostering different fungal assemblages. These findings highlighted the role of geomorphological processes in shaping microbial biogeography in agroecological landscapes (Corenblit et al., 2024; Bahrami et al., 2025).

AMF also contributed to ecosystem function by producing GRSPs, which enhance soil aggregation and nutrient retention, with GRSP levels reflecting ecological stability and further linking fungal diversity with soil health and functionality (Gałazka et al., 2020).

These findings underscored agroforestry's role in restoring degraded upland soils by improving microbial diversity, fertility, erosion control and productivity, making it a priority for sustainable land management. The lack of significant differences in some parameters may have stemmed from the legacy effects of past land use such as former rice fields or deforestation affecting pH, nutrient pools and microbial communities (Romdhane et al., 2022; Wu et al., 2024). Additional confounding factors, including spatial heterogeneity, seasonal rainfall and varied management practices (fallowing, organic inputs, intercropping), may have further obscured land use effects, emphasizing the need for long-term, site-specific monitoring (Chalchissa and Kuris, 2024; Wan et al., 2024).

Conclusion

This study underscored the critical influence of land use systems and erosion zones on fungal diversity. Agroforestry

systems had significantly higher fungal diversity than dryland agriculture as indicated by the former having higher Chao and Simpson indices. Thus, the hypothesis was supported of greater variation in fungal communities in agroforestry systems. The fungal communities were predominantly classified into four phyla: the Ascomycota, Basidiomycota, Mortierellomycota and Glomeromycota. Additionally, dryland agriculture had a higher abundance of stress-tolerant and P-mobilizing fungi, such as *Fusarium* and *Penicillium*, particularly in depositional zones. These findings highlighted the vital role of agroforestry in promoting soil fertility and microbial diversity, emphasizing its potential to enhance sustainable agricultural practices in erosion-prone areas.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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