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Soil fungal communities under plantations of different *Eucalyptus* species in Ethiopia: Insights for evidence-based management

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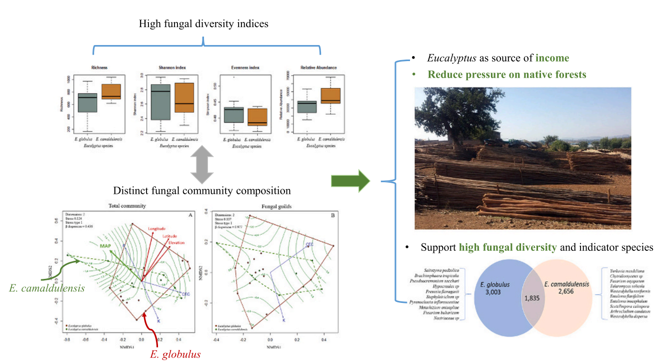
HIGHLIGHTS

- Soil fungal communities studied in Ethiopian *Eucalyptus* plantations
- Fungal communities differ between *E. globulus* and *E. camaldulensis* stands.
- Elevation, precipitation and temperature influence fungal composition.
- Plantations provide products and income, reducing pressure on native forests.
- A mosaic *Eucalyptus* species provide fungal diversity at the landscape level.

GRAPHICAL ABSTRACT



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ABSTRACT

The rapid expansion of *Eucalyptus* plantations in Ethiopia is driven by the increasing demand for woody products, raising concerns about their ecological impact. While conserving native forests remains a priority, *Eucalyptus* plantations provide alternative sources of forest products and income, helping to reduce pressure on native ecosystems. However, the ecological implications of these plantations, particularly their impact on soil fungal communities, key players in nutrient cycling and ecosystem functioning, remain poorly understood. This study investigates soil fungal community dynamics in *Eucalyptus globulus* and *Eucalyptus camaldulensis* plantations across diverse environmental gradients in Ethiopia. Soil samples were collected from 24 plots, and fungal DNA was extracted and sequenced using Illumina MiSeq technology, targeting the ITS2 region. Taxonomic classification and functional guild assignment were performed. Although both plantation types supported a high level of fungal richness and diversity, fungal community composition significantly varied by the *Eucalyptus* species. Environmental factors, including elevation, precipitation, and temperature, were linked to variations in fungal community composition, creating distinct ecological niches. The main indicator taxa under *E. camaldulensis* were the species *Yurkovia mendeliana*, *Fusarium oxysporum*, *Talaromyces solicola*, and *Westerdykella reniformis*, as well as an unidentified member of the class Chytridiomycetes. Under *E. globulus*, the main indicator taxa were the species *Saitozyma podzolica*, *Brachiosphaera tropicalis*, *Pseudoacremonium sacchari*, and *Preussia flanaganii*, along with an unidentified member of the order Hypocreales. Although the species *Archaeorhizomyces finlayi* and members of

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the families Hydnangiaceae and Chaetomiaceae and the order Sordariales were present in both plantation types, their relative abundances differed significantly between the two species. Our findings highlight that expanding *Eucalyptus* plantations support soil fungal diversity. A mosaic landscape combining the two species at the landscape level could enhance fungal biodiversity and ecosystem functionality. Understanding these fungal associations provides valuable insights for evidence-based plantation management and sustainable forestry practices in Ethiopia.

1. Introduction

Ethiopia has a long history of deforestation and land degradation (Mosisa et al., 2024), which has led to severe environmental challenges, particularly in regions where indigenous forests were once abundant. These challenges have been exacerbated by rapid population growth, agricultural land expansion, and the overexploitation of natural resources (Zerga et al., 2021) (Sisay et al., 2024; Tekalign et al., 2018). The extensive deforestation and degradation of natural vegetation have resulted in loss biodiversity loss and declining ecosystem services (EBI, 2022). To meet the increasing demand for forest products while mitigating deforestation, large-scale plantations of fast-growing exotic tree species, particularly *Eucalyptus*, have been widely established across Ethiopia. *Eucalyptus* was first introduced to Ethiopia in 1895 (Belachew and Minale, 2025) and has since become the most dominant plantation species in the country (Abebe and Tadesse, 2014).

More than 0.5 million ha of *Eucalyptus* plantations exist in Ethiopia due to its rapid growth, adaptability to various environmental conditions, and short rotation cycles (Bekele, 2011; Jaleta et al., 2016). More than 55 *Eucalyptus* species are grown in Ethiopia across diverse ecological zones, with *E. globulus* and *E. camaldulensis* being the most widely planted. These species provide essential forest products, contribute to afforestation and soil conservation, and serve as a crucial source of income for local communities (Belachew, 2025; Gil et al., 2010). Additionally, *Eucalyptus* plantations help reduce pressure on native forests by serving as alternative wood sources (Belachew and Minale, 2025). Despite these perspectives, the knowledge and status of soil fungal communities in *Eucalyptus* plantations across different agroecological zones in Ethiopia remain largely unexplored. Understanding these fungal dynamics is crucial for developing sustainable plantation forest management strategies, which can support the integration of fungal biodiversity conservation and mushroom production in *Eucalyptus*-dominated landscapes through a mycosilvicultural approach (Castaño et al., 2019; Dejene et al., 2017a). This approach could also foster ecological resilience while enhancing the economic output of plantation forests in the country (Dejene et al., 2017b).

Despite their economic benefits, the rapid expansion of *Eucalyptus* plantations has raised debates over their ecological effects (Belay et al., 2025; Molla et al., 2023) (Aklilu et al., 2019; Birara Dessie et al., 2019; Getnet et al., 2024; Gil et al., 2010; Kassa et al., 2019; Zerga, 2015). While some studies report negative impacts, including reduced biodiversity, altered soil properties and excessive water drainage, others highlight their potential to support ecological functions when properly managed. A growing body of research suggests that *Eucalyptus* plantations can sustain biodiversity, particularly soil microbial communities, which play fundamental roles in nutrient cycling, organic matter decomposition, and tree resilience (Bekele, 2011; Jaleta et al., 2016; Zhu et al., 2024). However, the influence of different plantations of *Eucalyptus* species on soil fungal communities across different environmental gradients in Ethiopia remains poorly understood.

Soil fungi are key drivers of ecosystem stability and forest productivity, influencing soil nutrient dynamics and plant health (Lombard et al., 2011). The soil fungal composition is strongly shaped by the type of tree species, edaphic and environmental variables which make fungi as an important indicators of ecosystem health and functioning (Tedersoo et al., 2014). Understanding fungal dynamics in *Eucalyptus* plantations is therefore essential for informed management practices. Studies suggest that *Eucalyptus grandis* plantations in Ethiopia enhance fungal diversity and alter community composition, contributing to belowground biodiversity (Castaño et al., 2019; Dejene et al., 2017b). Moreover, soil fungal communities in plantation forests serve as key indicators of soil quality assessment, as higher fungal diversity is often associated with well-functioning ecosystems (Wu et al., 2019). Despite this, the complex interactions between soil fungi, tree species, and environmental factors remain underexplored, particularly in comparison to aboveground ecosystem components. While some research highlights the role of *Eucalyptus* plantations in biodiversity rehabilitation (Moges et al., 2010), the extent to which different *Eucalyptus* species influence fungal diversity and composition is largely unknown. Studying the soil fungal diversity can provide valuable insights into the overall health and sustainability of plantation forests (Hereira-Pacheco et al., 2025). Addressing this gap is crucial for ensuring the sustainable management of plantation forests in Ethiopia (Dejene et al., 2017a; Kewessa et al., 2022; Moges et al., 2010).

Given the ecological importance of soil fungi and the increasing expansion of *Eucalyptus* plantations in Ethiopia, it is essential to explore how *Eucalyptus* species and environmental factors influence soil fungal communities across different site conditions. We aim to address this gap by examining the composition and diversity of soil fungi associated with two species of *Eucalyptus* that are commonly planted in Ethiopia: *E. globulus* and *E. camaldulensis*. We hypothesize that: (i) both *Eucalyptus* species support similar levels of fungal diversity owing to shared ecological traits, such as plantation structure and leaf litter production. The overall diversity levels are likely to be comparable owing to similar resource availability and plantation management practices. Despite this, we anticipate that: (ii) fungal community composition among *Eucalyptus* species varies because the composition is driven by species-specific traits, such as leaf chemistry, root architecture, or nutrient cycling. Finally, we hypothesize that: (iii) environmental factors such as mean annual precipitation (MAP), mean annual temperature (MAT), and site variables (i.e., elevation, longitude, and latitude) shape fungal communities by affecting soil parameters. Thus, the specific objectives of this study are: (i) to determine the soil fungal diversity associated with *E. globulus* and *E. camaldulensis*; (ii) to analyze and compare the composition of soil fungal taxa in areas planted with *E. globulus* and *E. camaldulensis*; and (iii) to elucidate environmental variables shaping the fungal communities associated with these *Eucalyptus* plantations. Such a comprehensive assessment of soil fungal communities in *Eucalyptus* plantations should contribute to a deeper understanding of the ecological implications of planting *Eucalyptus* plantations in Ethiopia. Our findings should inform sustainable forest management practices and guide policymakers in the development of strategies to mitigate potential negative impacts on soil health and biodiversity while maximizing the ecological and economic benefits of *Eucalyptus* plantations.

2. Materials and methods

2.1. The study area

This study was conducted in *Eucalyptus*-dominated plantations in Ethiopia, selected for their ecological and economic significance. A preliminary survey identified areas with extensive *Eucalyptus* plantations, leading to the selection of *E. globulus* and *E. camaldulensis* as the focus species. The chosen plantations share similar climatic conditions, minimizing environmental variability and allowing for meaningful comparisons of fungal communities.

Detailed site-specific characteristics, including geographic coordinates, elevation, climate, and soil properties, are provided in Table 1, while the study area map (Fig. 1) highlights the exact locations of the sampled sites, offering a visual representation of the study's spatial context.

2.2. Sampling procedure and environmental data collection

Eight plantations (i.e., three *E. camaldulensis* plantations and five *E. globulus* plantations) were selected for soil fungal sampling, with three transects established in each plantation. Each transect was spaced 200 m apart, and rectangular plots (2 m × 50 m) were laid out systematically at 100-m intervals to avoid spatial confounding (Dejene et al., 2017b; Hiiesalu et al., 2017; Rudolph et al., 2018). A total of 24 plots (three plots per plantation) were established for soil sampling. Soil samples were collected between August 24 and 26, 2023. The litter layer was removed before sampling to focus on soil fungal communities (Vořiškova et al., 2014). Five soil cores (0–15 cm depth) were collected from the corners and center of each plot using a soil corer (radius, 2 cm; depth, 20 cm) as described in previous studies (Alem et al., 2020; Castaño et al., 2019; Chen et al., 2022; Dejene et al., 2017a; Kewessa et al., 2022; Liu et al., 2021; Zhang et al., 2021). These cores were pooled to form composite samples comprising approximately 500 g of soil per plot. The systematic sampling design ensured consistency while accounting for site-specific variations.

The composite soil samples were dried, sieved (2-mm mesh), and ground into a fine powder for chemical analysis and were frozen immediately and kept at −20 °C until DNA was extracted. Key soil properties, including organic carbon (OC), total nitrogen (N), available phosphorus (P), and pH, were analyzed using standard methods. Specifically, soil OC was assessed using wet digestion (Walkley and Black, 1934). N was measured using the Kjeldahl method (Kim et al., 2005). P was calculated following the standard procedure described by Tan (2005). A pH meter was used to analyze a soil: water (1:2.5) suspension to determine the pH of the soil samples (Reeuwijk, 2002).

Climate data, including temperature and precipitation, were obtained from nearby meteorological stations, while geographical coordinates (latitude and longitude), elevation, and aspect were recorded in the field using a GPS device at each sampled plot (Table 1). These climate variables, combined with site-specific topographical data, provided valuable insights into the environmental factors shaping fungal community dynamics.

2.3. DNA extraction and metagenomic sequencing

To analyze the soil fungal communities, DNA was extracted from the collected composite soil samples using the DNeasy PowerSoil kit (Qiagen) and following the manufacturer's protocol. For each extraction, 0.25 g of soil was used. The extracted DNA was subsequently used for fungal metagenomic analysis, focusing on the amplification of the Internal Transcribed Spacer 1 (ITS1) region, which is a widely accepted marker for fungal community studies, ensuring comprehensive coverage of diverse fungal taxa. Metagenomic sequencing was conducted on the Illumina iSeq 100 platform, utilizing a 2 × 150 bp configuration. The ITS1 region was amplified using a set of forward and reverse primers designed for this region, which allowed for robust amplification of diverse fungal taxa. The forward primer set consisted of the following sequences:

- ITS_fwd_1 with the sequence CTTGGTCATTTAGAGGAAGTAA;
- ITS_fwd_2 with the sequence CTCGGTCATTTAGAGGAAGTAA;
- ITS_fwd_3 with the sequence CTTGGTCATTTAGAGGAACTAA;
- ITS_fwd_4 with the sequence CCCGGTCATTTAGAGGAAGTAA;
- ITS_fwd_5 with the sequence CTAGGCTATTTAGAGGAAGTAA;
- ITS_fwd_6 with the sequence CTTAGTTATTTAGAGGAAGTAA;
- ITS_fwd_7 with the sequence CTACGTCATTTAGAGGAAGTAA;
- ITS_fwd_8 with the sequence CTTGGTATTTAGAGGTCGTAA.

The reverse primer set consisted of the following sequences:

- ITS_rev_1 with the sequence GCTGCGTTCTTCATCGATGC;
- ITS_rev_2 with the sequence GCTGCGTTCATCGATGG;
- ITS_rev_3 with the sequence GCTACGTTCTTCATCGATGC;
- ITS_rev_4 with the sequence GCTGCGTTCTTCATCGATGT;
- ITS_rev_5 with the sequence ACTGTGTTCTTCATCGATGC;
- ITS_rev_6 with the sequence GCTGCGTTCTTCATCGTTGC;
- ITS_rev_7 with the sequence GCGTTCTTCATCGATGC.

Following initial amplification, a second PCR was performed to incorporate Illumina sequencing adapters and dual-index barcodes using Nextera™ XT v2 indices. AMPure XP beads were used after both PCR steps to clean the amplicons, ensuring high-quality DNA libraries.

Table 1
The mean values of environmental data and soil characteristics of each study site.

	Plantation species							
	Eucalyptus globulus					*Eucalyptus camaldulensis*		
Site	Gafarsa	Ciri	Dabana 1	Dabana 2	Sidisa	Birbirsa	Odabari	Kality
Elevation (m asl)	2604.33	2397.33	1883.00	1649.67	2010.00	2156.33	2006.00	2174.67
Latitude (N)	9°04′	9°03′	8°41′	8°42′	8°45′	8°54′	8°57′	8°54′
Longitude (E)	38°37′	38°25′	36°30′	36°42′	36°34′	37°44′	37°45′	38°46′
MAP (mm)	1188.00	1100.00	1100.00	1100.00	1100.00	950.00	950.00	1874.00
MAT (°C)	14.00	18.50	15.39	15.39	15.39	19.50	19.50	15.60
Sand (%)	61.00	59.67	66.33	69.00	56.33	47.00	43.67	55.00
Silt (%)	25.67	28.33	19.67	19.00	29.67	34.33	35.67	27.67
Clay (%)	13.33	12.00	14.00	12.00	14.00	18.67	20.67	17.33
pH	5.76	5.82	5.58	5.42	5.16	5.52	5.13	5.48
EC (ppm)	0.66	0.88	0.79	1.31	0.92	0.53	0.43	0.54
Na (ppm)	2.07	2.21	1.98	2.31	2.13	2.29	2.48	2.10
K (ppm)	0.69	0.66	0.98	0.67	0.66	0.85	0.59	0.53
Ca (ppm)	12.74	13.97	13.52	13.13	7.77	11.12	9.21	7.83
Mg (ppm)	5.40	5.65	5.21	5.12	4.25	5.75	4.42	3.90
CEC (ppm)	44.24	44.27	41.13	40.47	41.20	47.13	34.95	32.33
OC (ppm)	2.35	2.61	2.61	2.57	2.13	2.12	1.19	2.16
N (ppm)	0.16	0.19	0.23	0.19	0.16	0.14	0.07	0.13
P (ppm)	7.86	7.55	5.84	6.44	8.48	8.81	8.17	1036

Abbreviations: MAP, mean annual precipitation; mean annual temperature, MAT; EC, exchange capacity; CEC, cation exchange capacity; OC, organic carbon.

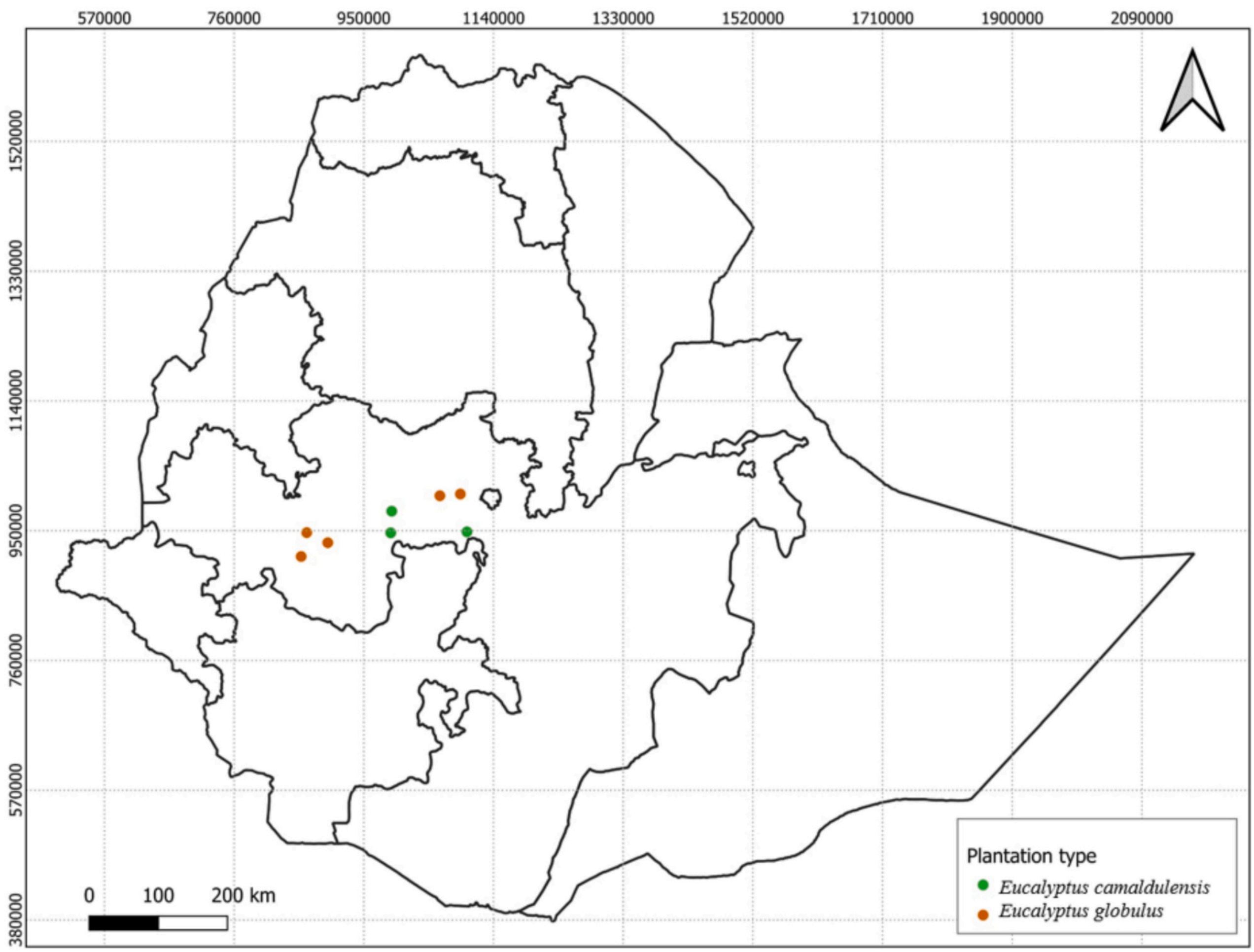

Fig. 1. Map of Ethiopia showing the location of the study areas.

Libraries were quantified, normalized, and pooled before sequencing. To enhance data quality, 20 % of PhiX sequencing controls were added to the pooled libraries. Sequencing was performed using the iSeq v2 reagent kit (Illumina, CA, USA) at Biotecnología Forestal Aplicada, Palencia, Spain, following the manufacturer's instructions for 300-cycle paired-end sequencing.

2.4. Taxonomic classification and functional group assignment

For taxonomic identification, the Illumina BaseSpace 16S Metagenomics App was utilized. This platform employs the UNITE fungal ITS sequence database (v7.2) for taxonomic classification, ensuring the accurate assignment of sequences to taxonomic groups. Sequences were classified by pairwise similarity searches against curated fungal ITS sequences, with taxonomic assignments based on Species Hypothesis (SH) groups, as defined by Kõljalg et al. (2013). The UNITE fungal database includes identified fungal sequences and ecological functions, facilitating robust taxonomic classification and functional group analysis. Operational Taxonomic Units (OTUs) with $\geq$90 % similarity to fungal SHs with known ecological functions were assigned to functional groups using the FungalTraits database (Põlme et al., 2020). The assignment process was facilitated via the PlutoF web workbench (Abarenkov et al., 2010).

2.5. Statistical analysis

We conducted all statistical analyses utilizing the sequence count for each OTU as the abundance value and following the method by Danzeisen et al. (2011) for non-singleton fungal communities. The data used for relative abundance and Shannon diversity index analyses met the parametric criteria of normality and homoscedasticity and, thus, no transformations were necessary. Evenness was log-transformed, and richness was Box-Cox optimum transformed. Differences among treatments were evaluated using linear mixed-effects (LME) models (Pinheiro et al., 2012), with the plot designated as a random effect and the plantation type as a fixed effect. The adequacy of these mixed models was verified through graphical inspections and the Shapiro–Wilk test to confirm the normality and homoscedasticity of residuals. All data analyses were performed using R version 4.2.2 (R Core Team, 2022).

We performed a Permutational Multivariate Analysis of Variance (PerMANOVA) using the *adonis2* function to determine the effect of *Eucalyptus* species on the distribution of the soil fungal community composition, which was determined based on the Bray–Curtis dissimilarity after excluding singleton OTUs. We used a Hellinger transformed community matrix and environmental scaled data for the analysis. Prior to PerMANOVA, we used *betadisper* to avoid misinterpretation of potential differences observed. The distribution was visualized using Non-metric Multidimensional Scaling (NMDS) and the analysis of correlation with environmental data was performed using the *envfit* function in R (R Core Team 2022). We performed NMDS analyses for total fungi and fungal guilds. Finally, we used multilevel pattern analysis using the *multipatt* function in R to assign taxa that were significantly associated with each treatment. Fungal community composition was further visualized through a taxonomic hierarchy using Krona charts (Ondov et al., 2011). We used the *ordisurf* function in R to fit a Generalized Additive Model with a Gaussian error family. This allowed us to represent, within

NMDS, variables that were most statistically correlated with the fungal community composition.

3. Results

3.1. Taxonomic identification

In total, 841,553 high-quality filtered reads that were classified as fungi were obtained from the sequenced soil samples. Between 15,437 and 67,943 high-quality reads were obtained from each soil sample. Across the eight plantations, 3824 fungal species belonging to six distinct fungal phyla were detected. The majority of the identified fungal species belonged to either Ascomycota (58 %) or Basidiomycota (26 %). Other phyla included Mortierellomycota (10 %) and Kickxellomycota (3 %). However, approximately 3 % of the total recorded fungal species could not be assigned to a specific fungal phylum (Fig. 2).

Within the phylum Ascomycota, several genera were particularly abundant, with *Microidium* accounting for 11 % of the community, followed by *Penicillium* (6 %), *Chaetomium* (5 %), and *Trichoderma* (5 %) (Fig. 3). Other notable genera, such as *Fusarium* (4 %), were abundant across the eight plantations. The chart also shows the presence of a large number of lesser-known fungal taxa, many of which remained unidentified (4 %), reflecting the unexpectedly high diversity and complexity of fungal species associated with *Eucalyptus* plantations.

Laccaria was the most abundant genus within the Basidiomycota phylum (Fig. 4), accounting for 24 % of the Basidiomycota community, followed by the genus *Saitozyma* (18 %). The hierarchal analysis also highlighted other diverse types of genera, including *Descomyces* (5 %) and *Boletus* (3 %) (Fig. 5), suggesting a complex fungal community with various ecological roles. However, 17 % of the Basidiomycota taxa remained unidentified (Fig. 4).

3.2. Effect of Eucalyptus species on the abundance and diversity of soil fungal taxa

The soil fungal communities detected in *E. globulus* and *E. camaldulensis* plantations did not differ significantly in terms of fungal relative abundance ($p = 0.108$), the Shannon–Wiener index, (H′) ($p = 0.906$), richness ($p = 0.279$), evenness ($p = 0.352$) (Fig. 5), or fungal guilds (Fig. 6).

3.3. Effect of Eucalyptus species on the soil fungal community composition

The overall fungal community composition detected in *E. globulus* plantations was significantly different from that in *E. camaldulensis* plantations ($F = 1.8752$, $R^2 = 0.07854$, $p = 0.013$) (Fig. 7A). The low-stress value obtained in the NMDS analysis indicated a relatively good fit of the data. Elevation, latitude, longitude, MAP, potassium (K), and cation exchange capacity (CEC) were significantly correlated with fungal composition, while phosphorus (P) exhibited a marginal correlation. By contrast, MAT was not significantly correlated with fungal community composition (Table 2; Fig. 7A).

The distribution of guilds in *E. globulus* plantations did not differ

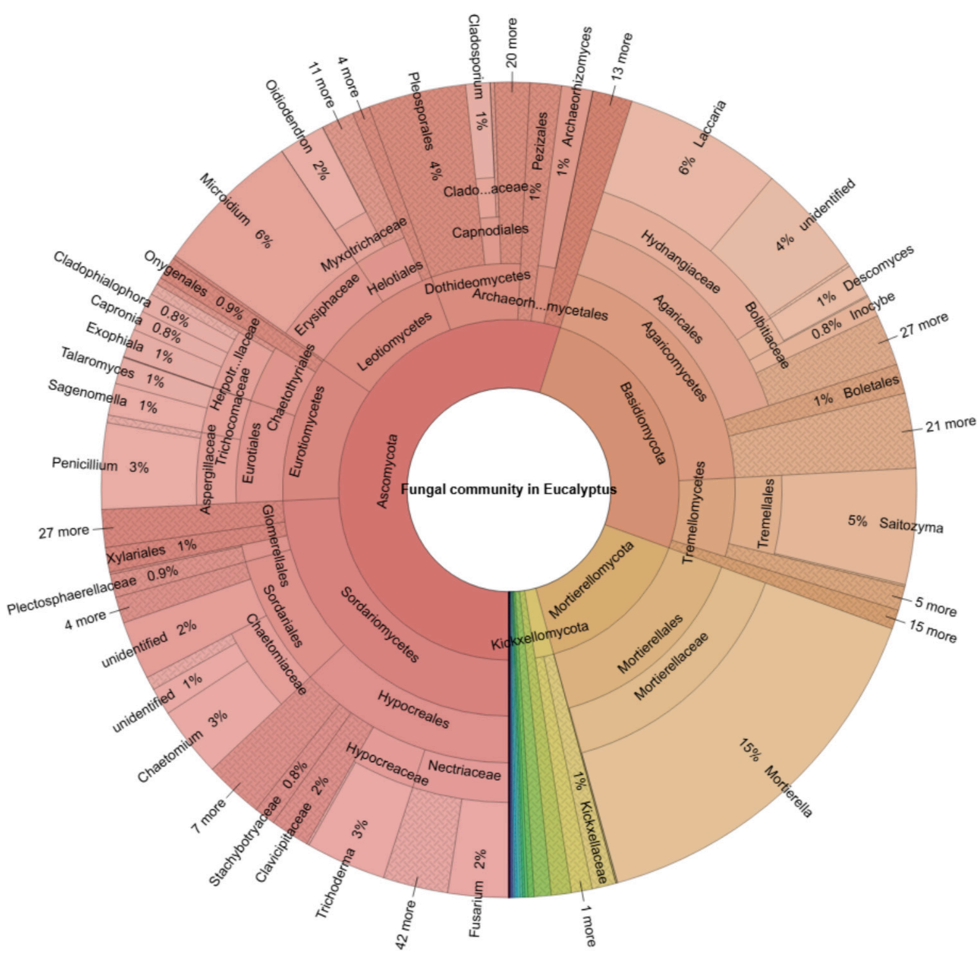

Fig. 2. Taxonomic hierarchy of the soil fungal community associated with plantations of *Eucalyptus* species across different landscapes in Ethiopia. The Krona chart represents the fungal community as a taxonomic hierarchy up to the genus level. The circles and sizes are proportional to the number of fungal species belonging to each phylum, and colors represent absolute taxon abundance (sum of read number).

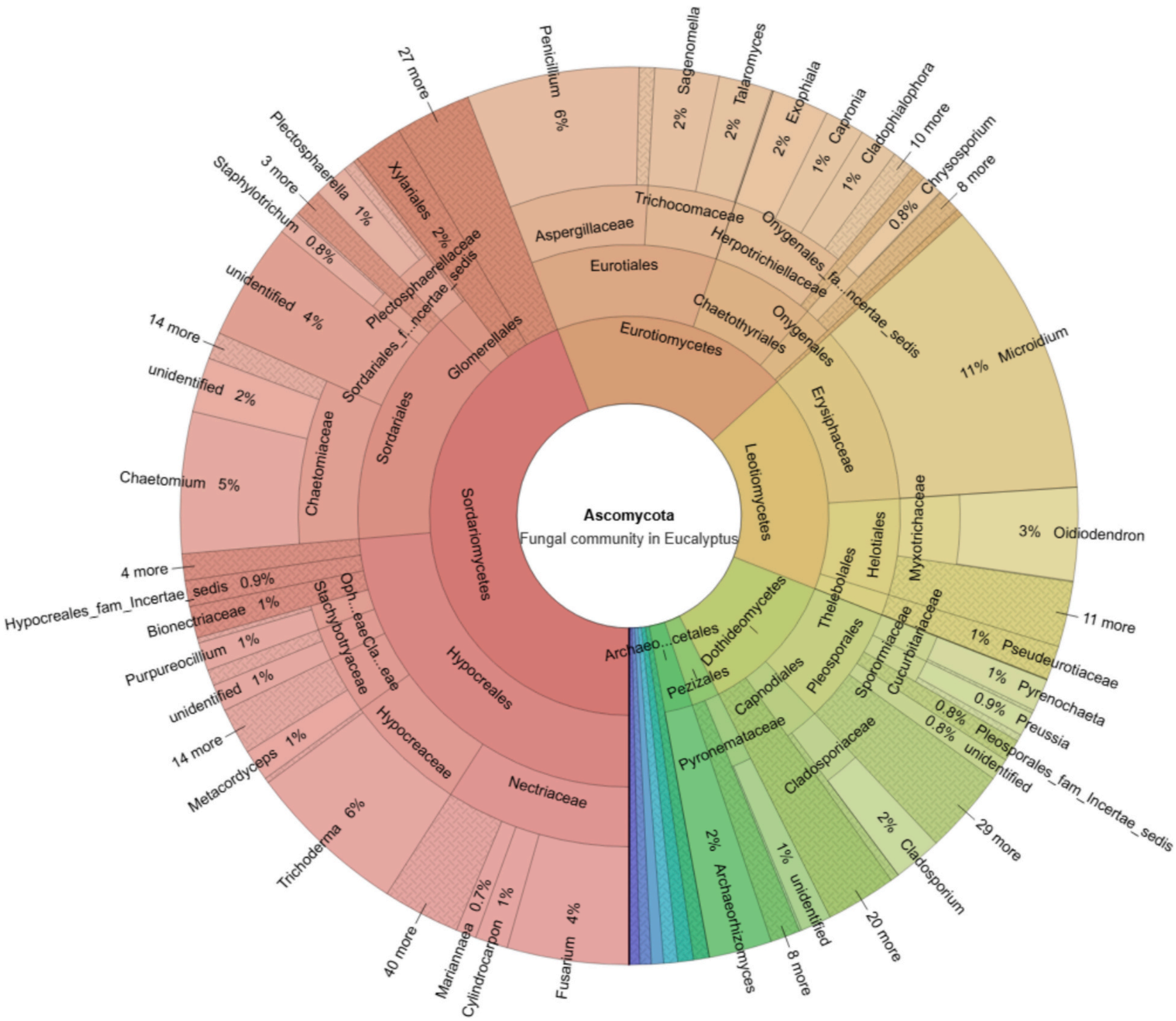

Fig. 3. Taxonomic hierarchy of the soil fungal community belonging to the phylum Ascomycota associated with plantations of *Eucalyptus* species across different landscapes in Ethiopia. The Krona chart represents the Ascomycota fungal community composition grouped up to genus level. The circles and sizes are proportional to the number of fungal species within each order, and colors represent absolute taxon abundance (sum of read number).

significantly from that in *E. camaldulensis* plantations ($R^2 = 0.0349$, $F = 0.7959$, $p = 0.528$). The low-stress value obtained in the NMDS analysis indicated a good fit of guild data (Fig. 7B), with stress type 1 and β dispersion ($F = 0.000$, $p = 0.977$). K and CEC were found to be significantly correlated with fungal guilds in *E. globulus* and *E. camaldulensis* plantations (Table 1). Geographic and environmental variables, such as latitude, longitude, and elevation, emerged as dominant drivers of fungal community composition, explaining nearly half (49.4 %) of the variation in fungal community structure. Moreover, climatic factors, including MAP and MAT, also contributed (26.3 %) to fungal community composition,

3.4. Indicator fungal species and guilds

In total, 3003 OTUs were associated with *E. globulus* plantations, of which 40 showed significant associations with this plantation type. By contrast, among the 2656 indicator fungal taxa linked to *E. camaldulensis* plantations, 147 were significantly associated with this plantation type (Table S1). The ten most contributing taxa for each type of *Eucalyptus* plantation are shown in Fig. 8. However, none of the guilds were significantly associated with either *E. globulus* or *E. camaldulensis* plantations. Although *Archaeorhizomyces finlayi* and species of Hydnangiaceae, Sordariales, and Chaetomiaceae were present in both plantation types, their relative abundances differed significantly between the two species.

4. Discussion

Sequencing analysis revealed a high diversity of fungal species in soil samples collected from plantations of *Eucalyptus* tree species. Furthermore, the estimated range of high-quality reads suggests variability in fungal abundance, which could be influenced by both soil conditions and the *Eucalyptus* tree species in the study areas. This finding in general aligns with studies performed by Dejene et al. (2017a) and Castaño et al. (2019), who reported that Ethiopian *Eucalyptus grandis* plantations support a diverse range of fungal species, based on their analyses of sporocarp diversity and soil fungal profiles, respectively. Our findings further highlight the role of *Eucalyptus* plantations in fostering fungal biodiversity, challenging the traditional perspective that *Eucalyptus* has a negative ecological impact on these ecosystems (FAO, 2011; Jaleta et al., 2016; Teketay, 2000). Although concerns about *Eucalyptus* plantations remain, there is a growing body of evidence indicating that they may have some unexpected ecological benefits. For example, *Eucalyptus* plantations have been reported to support diverse herbaceous species

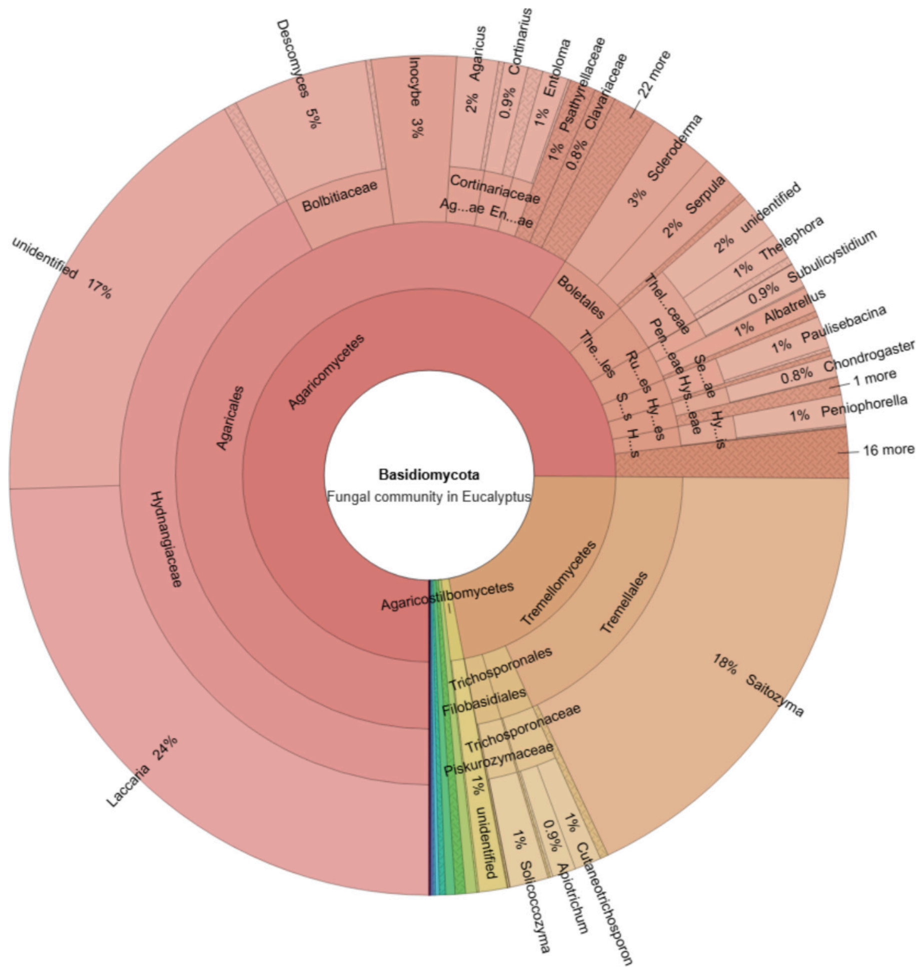

Fig. 4. Taxonomic hierarchy of the soil fungal composition associated with *Eucalyptus* plantations belonging to the phylum Basidiomycota across different landscapes in Ethiopia. The Krona chart represents the Basidiomycota community composition grouped up to genus level. The circles and sizes are proportional to the number of fungal species within each order, and colors represent absolute taxon abundance (sum of read number).

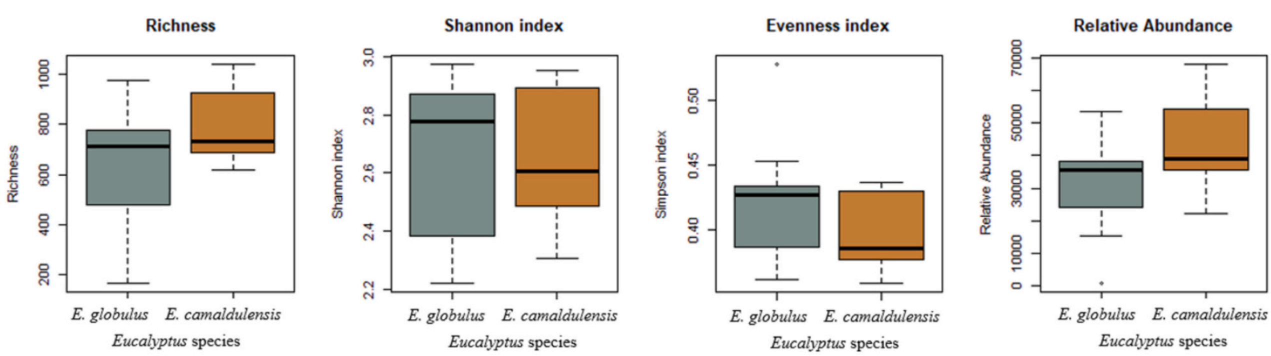

Fig. 5. Total abundance and diversity of the total fungal community detected in *Eucalyptus globulus* and *Eucalyptus camaldulensis* plantations. Box-and-whisker plots indicate the data range; horizontal lines indicate the median.

(Moges et al., 2010), facilitate native flora regeneration (Lemenih and Teketay, 2005; Yirdaw and Luukkanen, 2003), and harbor a rich diversity of fungal species, including economically valuable mushroom species (Castaño et al., 2019; Dejene et al., 2017b). Such findings call for a reconsideration of the role of *Eucalyptus* in Ethiopia's forestry landscape, revealing its potential as a multifunctional resource. Thus, by integrating mycosilvicultural practices into the forest management of *Eucalyptus* plantations, *Eucalyptus* species could be used as multifunctional landscape species that simultaneously support timber production, biodiversity conservation, and the sustainable cultivation of valuable edible mushrooms (Castaño et al., 2019; Dejene et al., 2017b). This approach would not only address environmental concerns but also create economic opportunities for local communities, promoting more balanced and sustainable forestry management strategies (Castellano and Molina, 1989; Trappe, 1977).

Laccaria was the most abundant ectomycorrhizal species detected in this study. The dominance of *Laccaria* in our study forests is particularly advantageous because *Laccaria* enhances plant survival and growth on

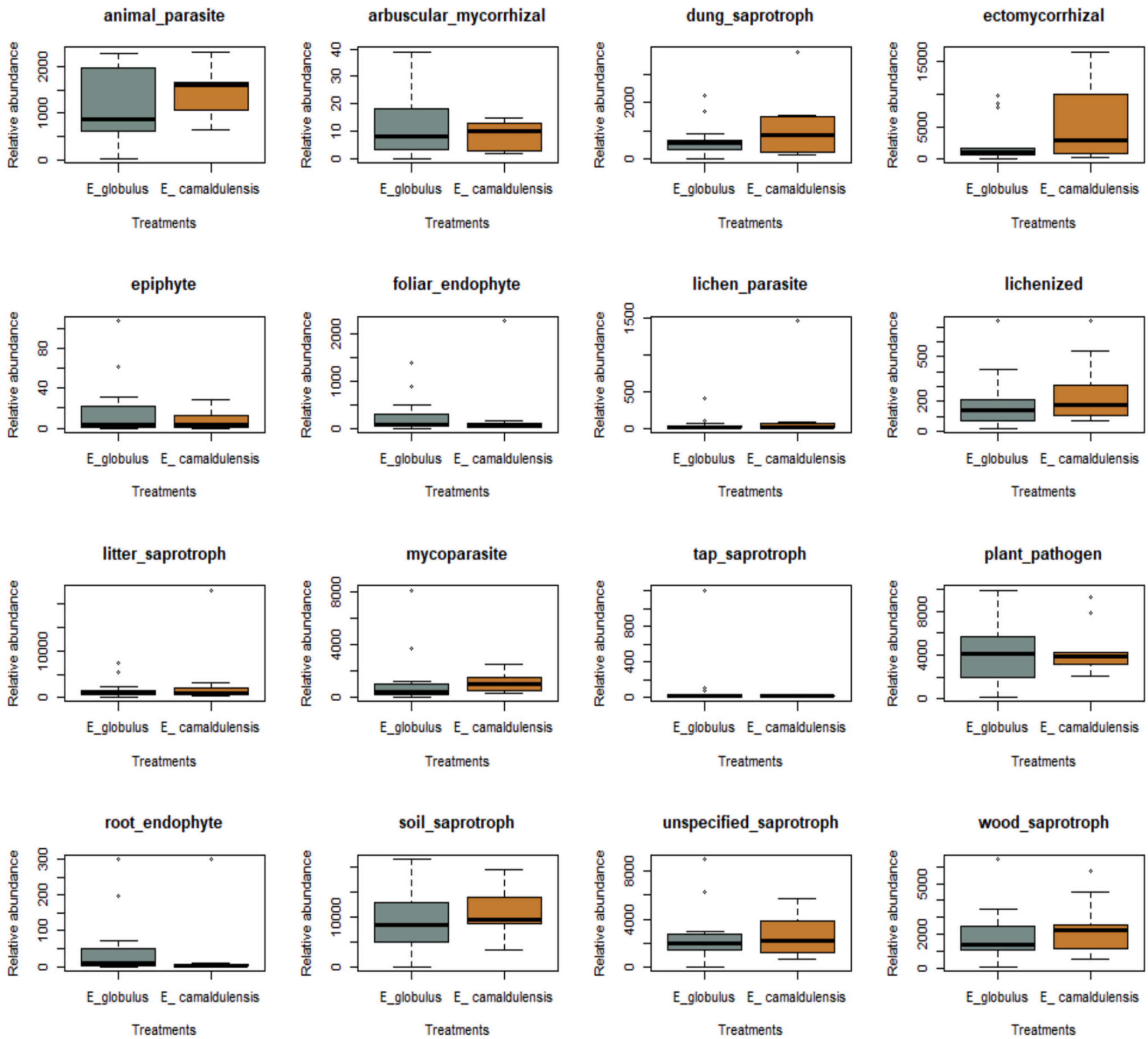

Fig. 6. The relative abundance of the total fungal guilds detected in *Eucalyptus globulus* and *Eucalyptus camaldulensis* plantations. Box-and-whisker plots indicate the range of the data; horizontal lines indicate the median; and dots indicate outliers.

nutrient-poor and degraded soils, which are common in Ethiopia and, therefore, could promote the rehabilitation and restoration of degraded forest lands. Furthermore, as edible fungi, *Laccaria* species have significant economic potential, thereby increasing the value of *Eucalyptus* plantations, and are becoming an important source of rural income (Abate, 2008; Boa, 2004).

The soil fungal communities detected in *E. globulus* plantations did not differ significantly from those detected in *E. camaldulensis* plantations in terms of fungal abundance, diversity, richness, or evenness when analyzing the total community or when grouping by fungal guilds. However, the dominance of some fungal species in the soil of both types of plantations could also contribute to the lack of significant variation in their diversity indices (Dahlberg, 2002, Kipfer et al., 2010). In addition, factors other than *Eucalyptus* species, such as soil conditions, environmental variables, or forest management practices might have a greater effect on the richness and diversity of soil fungal communities (Drenovsky et al., 2004, Lauber et al., 2009). Therefore, further research is needed to better understand the dynamics and characteristics of these soil fungal communities.

However, as expected, the overall soil fungal community composition of *E. globulus* plantations did differ significantly from that of *E. camaldulensis* plantations. This difference could be due to differences in environmental variables and landscape heterogeneity (Bahram et al., 2015; Ferrari et al., 2016; Peay et al., 2010; Tedersoo et al., 2014). The ordination analysis showed that spatial factors such as elevation and longitude, as well as climate and edaphic variables, highly influenced the soil fungal assembly in *Eucalyptus* plantations. This may be an indication that the combined effects of these variables (Li et al., 2020) affected the spatial variation of the fungal community (Chen et al., 2015) in our study areas. Climate conditions and edaphic variables, such as temperature, rainfall, humidity, and elevation, influence fungal distribution because different fungi have specific environmental preferences and some species may not exist in certain plantations (Li et al., 2020). In addition, the physiology of *Eucalyptus* species, including root exudates and leaf chemistry, affects fungal associations, with some fungi exhibiting host specificity. Different species, in our case *Eucalyptus*, secrete distinct profiles of root exudates, including sugars, which selectively attract or inhibit specific fungal taxa (Sasse et al., 2018;

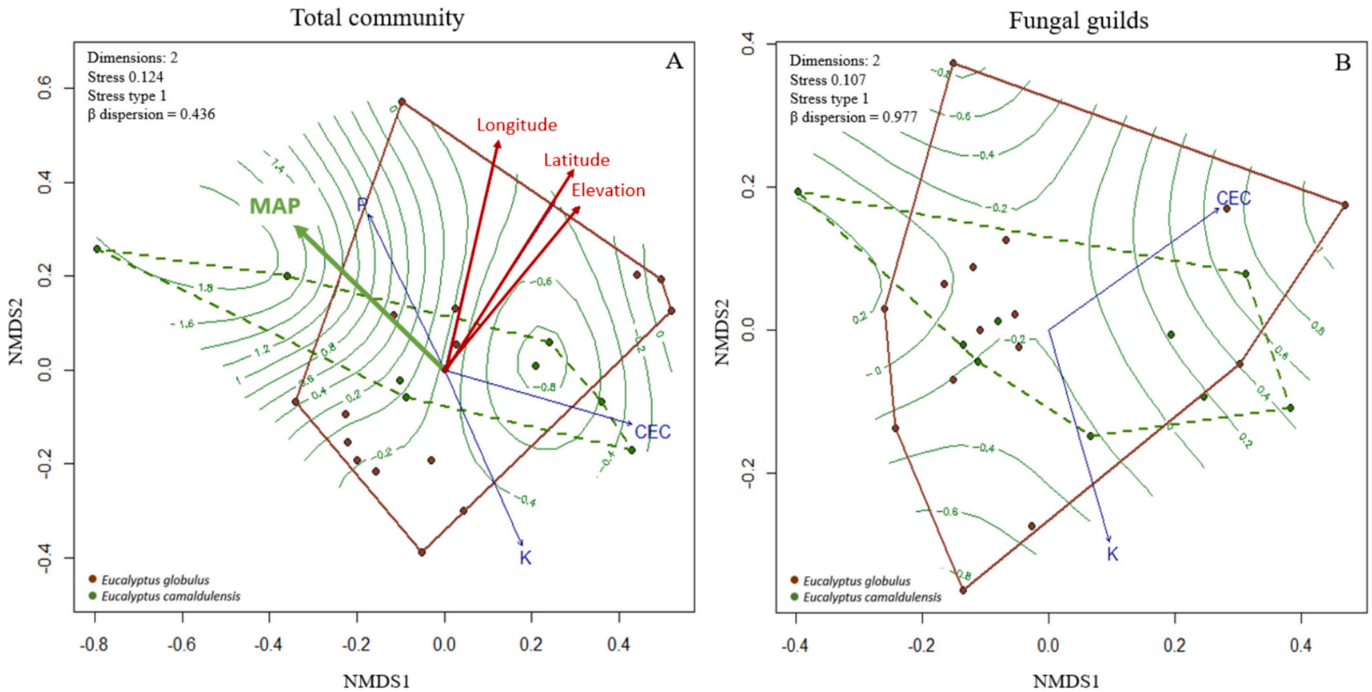

Fig. 7. The relationship between the distribution of the total fungal community (A) and fungal guilds (B) and correlated environmental factors in plantations of *Eucalyptus globulus* or *Eucalyptus camaldulensis*. Visualization is based on nonmetric multidimensional scaling (NMDS) using Euclidean distance. The polygon represents the 95 % confidence intervals surrounding each group. Vector names represent significantly correlated environmental factors. Green lines represent a Generalized Additive Model with a Gaussian error family for the most statistically correlated variables. Mean annual precipitation (MAP) for the total community in A, and elevation for fungal guilds in B. CEC, cation exchange capacity.

Table 2
Variables significantly correlated with the soil fungal community composition.

Community	Study site variables	NMDS1	NMDS2	r^2	*p*-Value
Total fungi	Elevation	0.6635	0.7482	0.3437	**0.015**
	Latitude	0.5760	0.8175	0.4249	**0.006**
	Longitude	0.2476	0.9689	0.3963	**0.006**
	MAP	−0.7410	0.6715	0.2696	**0.011**
	K	0.4236	−0.9035	0.0268	**0.047**
	CEC	0.9659	−0.2586	0.3122	**0.027**
	P	−0.4652	0.8852	0.2219	**0.067**
Guilds	Elevation	0.8527	0.5224	0.2258	**0.063**
	K	0.3107	−0.9505	0.2327	**0.061**
	CEC	0.8449	0.5350	0.2453	**0.061**

Abbreviations: MAP, mean annual precipitation; CEC, cation exchange capacity; K, potassium; P, phosphorus; NMDS, non-metric multidimensional scaling. Bold: significant correlation.

Walker et al., 2003). These chemical differences might be leading to the difference in fungal community composition even if overall diversity metrics are similar. Furthermore, given that the study sites were in different regions, geographic isolation and dispersal limitations would likely further influence fungal composition given that spore movement and colonization potential varies across landscapes (Tedersoo et al., 2014).

More than three times the number of fungal species were significantly correlated with *E. camaldulensis* plantations than with *E. globulus* plantations. On the one hand, this could reflect the distinct ecological niches created by each of the *Eucalyptus* species. On the other hand, many fungal taxa were detected in both *E. camaldulensis* and *E. globulus* plantations. Thus, given the importance of *Eucalyptus* species for fungal diversity promotion, planting different *Eucalyptus* species at separate sites and then combining them at the landscape level would enhance fungal richness and biodiversity.

In this study, the edaphic element of the Potassium (K) was found to correlate with the overall soil fungal community, suggesting that soil cation concentrations may influence fungal community development. Because cations, including the cation exchange capacity (CEC), are involved in various physicochemical processes such as photosynthesis (Shi et al., 2014), which can impact plant photosynthesis and,

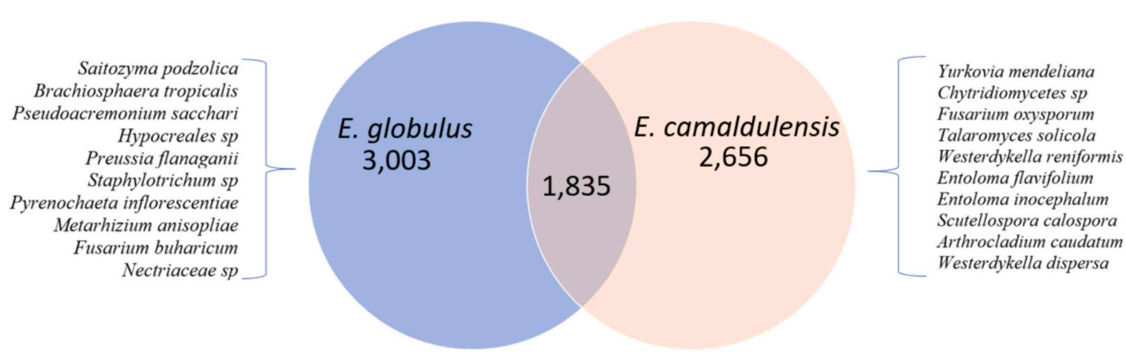

Fig. 8. The number of total soil fungal taxa and the ten most contributing taxa associated with plantations of *Eucalyptus globulus* and *Eucalyptus camaldulensis*.

consequently, the carbon available to soil fungi (Shi et al., 2014). Also, the correlation between phosphorus (P) and fungal taxa aligns with previous studies by Kranabetter et al. (2009); Reverchon et al. (2010), which highlighted the influence of P on fungal distribution patterns. In this study also observed that fungal communities often specialized based on guilds in soils with higher potassium (K) levels. This could be because K-rich environments offer more favorable conditions for certain fungal species that thrive in nutrient-rich soils, allowing them to dominate or establish stable communities (Trudell and Edmonds, 2004). Furthermore, potassium's presence may affect soil pH and other factors that contribute to the specialization of fungal communities in such areas (Li et al., 2020).

5. Conclusions

In this study we have found that *Eucalyptus globulus* and *Eucalyptus camaldulensis* plantations support high and comparable levels of soil fungal diversity in Ethiopia. However, despite similarities in overall abundance, richness, and evenness, the composition of fungal communities differed significantly between the two species. These differences are likely influenced by species-specific factors such as variation in root exudate chemistry, in addition to the environmental variables such as the elevation, temperature, and precipitation. *E. globulus* stands were dominated by distinct fungal taxa compared to *E. camaldulensis* stands, indicating that each tree stands fosters a unique fungal assemblage in the rhizosphere. At the landscape level, managing both species can enhance overall fungal diversity, contributing to soil health, ecosystem resilience, and sustainable plantation management.

While the conservation of native forests remains a priority, *Eucalyptus* plantations, when strategically managed, can contribute to fungal biodiversity and ecosystem health. To maximize biodiversity benefits while reducing pressure on native forests, a mosaic landscape approach should be used, where different *Eucalyptus* species are planted at separate sites and integrated at the landscape level. Moreover, given the importance of soil fungi in maintaining soil fertility and forest productivity, sustainable plantation management should consider fungal dynamics when planning afforestation and reforestation programs. To ensure the long-term productivity of *Eucalyptus* plantations, further research is needed to explore their ecological impacts over extended periods. Understanding these dynamics will provide crucial insights into optimizing plantation forestry for both economic and ecological sustainability, ultimately contributing to resilient forest ecosystems in Ethiopia and beyond.

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CRediT authorship contribution statement

Gonfa Kewessa: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Tatek Dejene:** Writing – review & editing, Project administration, Conceptualization. **Pablo Martín-Pinto:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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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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Data availability

Data will be made available on request.

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