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Biodiversity of African soil fungi

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, which are referred to in the text by their corresponding Roman numerals.

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II. Kumah, F. J., **Kupagme, J. Y**., Yorou, N. S., & Koné, D. (2025). Fungal diversity and community composition in cocoa agroforestry farms across two West African countries using DNA metabarcoding. *Open Journal of Ecology*, *15*(3), 268–287.

III. Saadi, O., Tadjine, A., Bouam, I., **Kupagme, J. Y**., Alwutayd, K. M., Anslan, S., Põlme, S. (2026). A molecular assessment of ectomycorrhizal fungal communities associated with North African *Alnus glutinosa* forests. *MycoKeys*, *127*, 169.

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Was responsible for ***, contributed substantially **, contributed *

	Study design	Carry out the experiment	Analyzing the data	Manuscript writing
I	***	***	***	***
II	**	***	***	***
III	—	**	*	**

1. INTRODUCTION

Fungi are among the most ecologically important and evolutionarily diverse groups of eukaryotes on Earth. They facilitate nutrient cycling, regulate ecosystem functioning, influence plant productivity, establish mycorrhizal symbioses, and play a key role as decomposers in terrestrial environments (van der Heijden et al., 2015; Peay et al., 2016). Despite their ecological importance, global fungal diversity is poorly documented, with estimates ranging from 2.2 to 3.8 million species (Hawksworth & Lücking, 2017). These estimates leave us with ~ >95% of undescribed fungal taxa globally (Hawksworth & Lücking, 2017). This knowledge gap is particularly significant in tropical and subtropical regions, where fungi are thought to be extremely diverse but remain poorly understood and underdocumented.

With the advent of high-throughput sequencing (HTS) and metabarcoding of environmental DNA (eDNA), our understanding of fungal diversity has expanded significantly, revealing extensive cryptic diversity in soils, plant tissues, and extreme environments that were traditionally studied using morphological methods (Nilsson et al., 2019; Tedersoo & Anslan, 2019). Despite these improvements, global fungal diversity remains concentrated mainly in the temperate regions of Europe and North America (the global north). Large tropical and subtropical areas, particularly in Africa, are still notably underexplored (Tedersoo et al., 2014; Cameron et al., 2018; Větrovský et al, 2020; Makhalanyane et al., 2023). Across Africa, numerous fungal species exist at different taxonomic levels, many of which are poorly documented. Based on the plant-fungus ratios proposed by Hawksworth (2001) and initial metabarcoding studies, it is estimated that the continent likely supports a vast diversity of fungal taxa, though only a small number have been documented so far (Cheek et al., 2020; Tedersoo et al., 2021; Tsakem et al., 2024). Africa, with its diverse range of biomes—including Guineo-Congolian rainforests, Miombo woodlands, Mediterranean forests, and Sahelian drylands—supports distinct fungal communities influenced by climate, soil chemistry, and available hosts (Bâ et al., 2012; Tedersoo et al., 2011, 2014). For instance, ectomycorrhizal fungi (EcMF) are dominant in forests and woodlands in Sub-Saharan Africa and in Mediterranean forests across the continent. These are mainly associated with the families Fabaceae and Dipterocarpaceae, while arbuscular mycorrhizal fungi (AMF) and saprotrophs are more prevalent in savannas and agricultural landscapes (Bâ et al., 2012; Rodríguez-Echeverría et al., 2017). Fungal research in Africa faces limitations that have created a substantial knowledge gap, with limited data available on fungal diversity patterns and their potential drivers.

1.1. Drivers of soil fungal diversity in Africa

Soil-inhabiting fungi constitute a significant part of terrestrial biodiversity and are vital for ecosystem functioning, including decomposition of organic materials, nutrient cycling, soil aggregation, and the development of mutualistic relationships with plants (van der Heijden et al., 2008; Crowther et al., 2019). In African ecosystems, soil fungal communities play a crucial role by supporting productivity and resilience across various climatic zones, soil types, and vegetation. Despite their ecological importance, soil fungal diversity in Africa has historically been underrepresented in global biodiversity assessments, mainly due to limited sampling and methodological limitations (Tedersoo et al., 2014; Tedersoo et al., 2021; Kupagme et al., in press).

Climate is one of the most significant large-scale factors affecting soil fungal diversity across Africa. Mean annual precipitation (MAP) and mean annual temperature (MAT) have been shown to notably influence fungal richness and community composition by regulating soil moisture, plant productivity, and organic matter inputs (Tedersoo et al., 2014; Bahram et al., 2018; Sheng et al., 2019; Zhang et al., 2025). Studies show that increased MAP generally promotes higher fungal diversity by boosting plant biomass and litter production, thereby increasing resource availability for saprotrophic and symbiotic fungi (Tedersoo et al., 2014; Delgado-Baquerizo et al., 2021; Mikryukov et al., 2023). Conversely, arid and semi-arid areas, characterized by high temperatures and low precipitation, often exhibit reduced fungal diversity and different community assemblages adapted to drought stress (Egidi et al., 2019; Cowan et al., 2022).

Other important factors that significantly influence soil fungal communities at local, regional, and continental scales are edaphic factors. Soil pH is often recognized as a key factor affecting fungal diversity, impacting nutrient solubility, enzyme activity, and competitive dynamics among fungal taxa (Rousk et al., 2010; Tedersoo et al., 2014). Global-scale studies, conducted partly in African drylands and savanna ecosystems, indicate that soil organic carbon, nitrogen availability, and cation concentrations (e.g., Ca and Mg) are key predictors of fungal community composition (Tedersoo et al., 2014; Maestre et al., 2021; Mikryukov et al., 2023). African soil fungal communities, especially ectomycorrhizal fungi, are influenced by a combination of host identity, vegetation composition, soil properties, climatic gradients, spatial heterogeneity, and fungal functional traits (Tedersoo et al., 2011, 2014). Mixed forests support more diverse communities than monodominant stands, and root interactions influence host shifts in plantations (Jairus et al., 2011; Tedersoo et al., 2011, 2012; Diedhiou et al., 2014). These studies emphasize that both biotic and abiotic factors jointly shape fungal diversity and community structure across African tropical and savanna ecosystems.

Vegetation composition and plant diversity are key biotic factors influencing soil fungal diversity. The identity and richness of plant species affect fungal communities through root exudation, litter quality, and the availability of host plants for symbiotic fungi such as arbuscular mycorrhizae (Wardle et al., 2004;

van der Heijden et al., 2015). Many studies from Africa have shown strong links between plant community composition and fungal assemblages, especially for mycorrhizal fungi that rely on specific host plants, as demonstrated in *Gnetum* spp. (Bechem & Alexander, 2012). Alterations in vegetation structure, such as forest fragmentation and conversion of forests to agricultural lands, can therefore result in significant shifts in soil fungal diversity and function (Sui et al., 2019; Balami et al., 2020; Zhu et al., 2025).

In addition to natural environmental gradients, human activities are increasingly impacting soil fungal diversity across Africa. Land-use change, agricultural intensification, and deforestation change soil structure, nutrient inputs, and microclimatic conditions, often leading to reduced fungal diversity and simplified community networks (Lauber et al., 2013; Delgado-Baquerizo et al., 2021). In African agroecosystems, management practices such as fertilizer application, tillage, and crop selection have been shown to alter fungal community composition, with potential implications for soil health and crop productivity (Hartmann et al., 2015; Cheeke et al., 2017). In contrast, agroforestry systems frequently sustain higher fungal diversity than monocultures primarily due to increased plant diversity and habitat complexity (Arévalo-Gardini et al., 2020; Kumah et al., 2025).

Finally, biogeographic and historical factors play a key role in shaping soil fungal diversity across continents. Large-scale surveys have identified distinct fungal communities, including novel and rare species at global scales, reflecting variations in climate, soil type, vegetation, and land-use history (Tedersoo et al., 2014; Bahram et al., 2018; Aslani et al., 2024). These patterns emphasize the importance of regional context and dispersal limitation in influencing fungal communities, even among ecosystems with similar environmental conditions (Peay et al., 2016).

1.2. Factors influencing fungal communities in cocoa agroecosystems

Agroforestry is a land-use approach that promotes ecosystem sustainability, supporting both agricultural productivity and environmental health (Nair, 2009; Jose, 2009). Combining woody perennials with crops enhances ecosystem services, including carbon storage, soil fertility, erosion mitigation, water regulation, and biodiversity (Montagnini & Nair, 2004; Bhagwat et al., 2008). These systems are vital in tropical regions facing agricultural expansion, land degradation, and severe climate change (Tscharntke et al., 2011; Schroth et al., 2016). Cocoa (*Theobroma cacao* L.) cultivation is one of the most important tropical agroforestry systems with significant ecological and economic value. As a major global commodity, cocoa supports millions of smallholder farmers in the humid tropics (Daymond et al., 2017; Otekunrin, 2025). Traditionally cultivated under forest canopy shade, cocoa agroforestry combines native forest trees, fruit, and exotic timber species, forming complex landscapes (Ruf & Schroth, 2004; Asare et al., 2014).

West Africa accounts for over 70% of global cocoa production, led by Côte d'Ivoire and Ghana (Daymond et al., 2017). Its diverse cocoa agroforestry farms range from low-shade to complex, forest-like multi-strata farms (Gockowski & Sonwa, 2011; Asare et al., 2014). However, rising cocoa production has led to the removal of shade trees, shorter fallow periods, and increased use of agrochemicals, risking soil health, biodiversity loss, and ecosystem resilience (Ruf & Schroth, 2004; Schroth et al., 2016). Cocoa has numerous benefits; for instance, cocoa beans, the seeds from the cocoa pod, are processed to produce cocoa liquor, cocoa butter, and cocoa powder. Cocoa liquor, obtained by grinding roasted cocoa beans, is essential for chocolate production. Cocoa butter, the fat extracted from cocoa liquor, contributes to the chocolate texture. Cocoa powder, from which most of the fat has been removed, is utilized in beverages, baking, and confectionaries (Konan et al., 2025). In addition to culinary uses, cocoa butter is valued in cosmetics and medicine for its moisturizing and stabilizing properties, commonly found in lotions, creams, soaps, lip balms, and ointments. Furthermore, cocoa compounds such as flavonoids are being researched for their health benefits, including antioxidant and cardiovascular effects. By-products such as cocoa husks and shells serve various purposes, such as organic fertilizers, animal feed, mulch, and bioenergy, highlighting the versatility of cocoa beyond just chocolate (Bahrun et al., 2018; Konan et al., 2025). Beyond its economic importance, cocoa farming has a significant impact on tropical landscapes, biodiversity, and ecosystem health. In recent decades, growing concerns about deforestation, land degradation, and climate change have heightened interest in sustainable cocoa production systems that balance productivity and environmental sustainability (Amponsah-Doku et al., 2022).

Although the importance of fungi cannot be overemphasized, their functional duality poses a significant threat to other organisms. This means they can have both positive and negative effects on crop growth. In cocoa agroforestry systems, fungi are especially important because they enhance nutrient uptake, cause diseases (black pod disease), increase plant stress tolerance, and promote decomposition (Akrofi et al., 2015; Mortimer et al., 2018; Jaimes-Suárez et al., 2022). Understanding the variety and composition of fungi is essential for evaluating the ecological health and strength of cocoa agroforestry systems (Arévalo-Gardini et al., 2020; Armengot et al., 2020).

Fungal communities in tropical agroecosystems remain poorly characterized, especially in West Africa, where research often focuses on pathogens or culturable taxa such as *Aspergillus* and *Trichoderma* spp. (Schoch et al., 2012; Tedersoo et al., 2014; Hawksworth & Lücking, 2017; Piepenbring et al., 2020). Traditional methods, such as culturing and morphological identification, are limited in capturing full diversity, especially for cryptic or rare fungi (Ekanayaka et al., 2025). Abiotic factors such as shade tree diversity, farm age, soil properties, and geographic selection influence microbial communities (Schmidt et al., 2022; Katrevičs et al., 2025; Kumah et al., 2025; Lin et al., 2025). Soil microorganisms are more abundant in agroforestry systems than in monocultural tree/crop systems (Beule et al., 2022; Huang et al., 2025), supporting beneficial fungi such as mycorrhizal fungi and saprotrophs. Studying these agroforestry systems in cocoa farms across regions provides insights into environmental and management factors that influence belowground biodiversity, which is crucial for cocoa farming sustainability and disease management.

Ultimately, a better understanding of fungal diversity in cocoa agroforestry systems can inform sustainable management practices that enhance ecosystem services while supporting the livelihood of cocoa farmers. As pressures on cocoa-growing landscapes increase, integrating belowground biodiversity into research and policymaking will be essential to the long-term resilience of cocoa production in West Africa and potentially elsewhere in the world.

1.3. Biogeography of *Alnus*-associated ectomycorrhizal fungal communities

Ectomycorrhizal fungi (EcMF) play a crucial role in most terrestrial ecosystems worldwide by establishing a mutualistic relationship with host plant species, thereby enhancing resilience to pathogen attack, improving nutrient and water uptake, and contributing to biodiversity and ecosystem functioning. EcMF typically form symbiotic associations with woody perennials, mostly trees, in temperate regions and some tree families in the tropics (Smith & Read, 2008; Corrales et al., 2022). *Alnus glutinosa* (L.) Gaertn. (black alder) is a riparian tree species native to Europe, which extends its range into western Asia and into the southernmost natural areas of North Africa, where it is found in Morocco, Algeria, and Tunisia (Kajba & Gračan, 2003). In Algeria, the species is geographically restricted to the humid and sub-humid regions of the northeast, particularly in riparian forests, wetlands, and groundwater-fed systems, such as those found in the El Kala Biosphere Reserve and nearby areas (Belouahem-Abed et al., 2011). These Algerian populations are relics, which hold significant conservation value due to their long-term survival under climatically unfavourable conditions (Lepais et al., 2013).

A key ecological feature of *A. glutinosa* is its ability to form a tripartite symbiosis involving nitrogen-fixing actinobacteria (*Frankia* spp.) and mycorrhizal fungi, including both AMF and EcMF (Põlme et al., 2013; Tedersoo & Brundrett, 2017). Among these symbionts, EcMF play a vital role in nutrient acquisition, water uptake, and protection against abiotic stress, particularly in nutrient-poor or hydrologically variable soils (Smith & Read, 2008). This dual mycorrhizal strategy is relatively uncommon among most trees and is believed to enhance the ecological success of *Alnus* species in adverse conditions or early-successional environments (Teste et al., 2020). Due to the reliance of *A. glutinosa* on EcMF symbiosis for nutrient acquisition and host specificity, its distribution is closely connected to that of its associated EcMF communities. Global and regional studies demonstrate that alder-associated EcMF assemblages are moderately diverse but exhibit a higher degree of plant genus-level specialization compared with other trees, with consistent dominance of fungal genera such as *Tomentella*, *Thelephora*, *Alnicola*, and *Cortinarius* across continents (Põlme et al., 2013; Rochet et al., 2011). A large-scale biogeographic analysis revealed that host phylogeny and historical migration routes greatly influence EcMF communities associated with *Alnus* at continental and global scales (Põlme et al., 2013). These patterns suggest long-term co-dispersal and ecological filtering rather than random fungal colonization.

Research on EcMF is generally limited but largely centred on desert truffles, especially the genera *Terfezia*, *Tirmania*, and *Picoa*, found in North African and Mediterranean drylands (Farag et al., 2021; Henkrar et al., 2022). These studies show that desert truffle distribution is heavily influenced by soil texture, pH, rainfall variability, and host plants like *Helianthemum* spp., emphasizing the role of soil and climate factors in arid ecosystems. Meanwhile, the biogeographical position of Algerian alder forests suggests that their EcMF communities may reflect a mix of Mediterranean refugial history and significant environmental filtering caused by climate and hydrology (Belouahem-Abed et al., 2011; Roy et al., 2017). Genetic and cytogeographic studies of *A. glutinosa* show historical connectivity between North African and southern European populations during Quaternary climatic fluctuations, supporting the idea that Algerian populations served as long-term refugia rather than recent colonization frontiers (Havrdová et al., 2015; Lepais et al., 2013; Mandák et al., 2016). Such refugial systems are often linked with unique or highly structured EcMF communities (Roy et al., 2017).

1.4. Hypotheses

The following hypotheses were defined in this thesis:

- At the continental scale, climatic factors are the main determinants of soil fungal diversity, followed by soil chemical properties.
- Soil fungal communities in African forests are shaped by the composition of mycorrhizal plant species, where dense forest zones tend to be more abundant in fungi.
- Fungal diversity is affected by soil depth and soil chemical properties (driven mainly by soil management systems) at the local scale.
- EcMF assemblages exhibit distinct patterns of structure and diversity in Algeria compared to those in other regions.

2. MATERIALS AND METHODS

2.1. Sample collection and study design

Soil samples were collected from various terrestrial biomes across 32 African countries, following the protocol described in Tedersoo et al. (2014) (**I**). We collected soil from cocoa agroforestry farms in plots measuring 35 m × 35 m (Dawoe et al., 2014) with varying ages (5, 15, and 30 years) and soil depths (0–15 cm and 15–30 cm) in Ghana and Côte d'Ivoire (**II**). Soil and root samples were collected in December, March, June, and September, 2023 at three locations (El Mellah, Righia, and Verge) within the El Kala Biosphere Reserve (KBR) and its surroundings in El Tarf Province, northern Algeria (**III**). At each site, we randomly selected five *Alnus glutinosa* trees during each survey, ensuring they were at least 10 m apart to minimize spatial correlation among the samples (Lilleskov et al., 2004). Around each tree, we collected one soil core (5 cm diameter × 25 cm depth) within a one-metre radius of the trunk. Root samples were excavated from the same core. Following collection, the roots were placed in plastic bags and stored at –4 °C for later processing. Sampling was conducted once per season, specifically in December, March, June, and September, yielding a total of 60 root samples (5 trees × 3 sites × 4 seasons). Soil samples were homogenised and pooled by site and season for edaphic physico-chemical analyses, resulting in a total of 12 samples (3 sites × 4 seasons) (**III**). Soil samples were air-dried, sieved through a 2-mm sieve, and the fraction ≤ 2 mm was analysed. Electrical conductivity (EC) and pH were measured for each soil sample in a 1:5 soil-to-water mixture using a conductance meter and a pH meter, respectively. Organic matter (OM) content was determined by the Nelson and Sommers (1996) method. Total lime (TL) was assessed using volumetric calcimetry. Practical salinity (PS) was calculated from EC using the Fofonoff and Millard (1983) method. These edaphic variables have previously been identified as major determinants of EcMF composition, especially in habitats associated with *Alnus* (e.g., Becerra et al. 2005b; Tedersoo et al., 2014; Sun et al., 2016; Kjøller et al., 2017; Thiem et al., 2018) (**III**). Soil samples were treated and processed as described by Tedersoo et al. (2014) for DNA extraction (**I–III**).

2.2. DNA extraction and sequencing

DNA was extracted from soil samples following the method described in Tedersoo et al. (2014) (**I** & **II**). For *Alnus,* root samples were dried at 35 °C for 24 hours, and then DNA was extracted from 0.25 g of roots for each sample using the PowerMax Soil DNA Isolation kit (Qiagen). Before the extraction, roots were pulverized by bead beating, using Retsch MM400 mixer mill (Retsch, Haan, Germany). A 520 µL volume of proteinase K (600 units per mL) was added to the root samples to facilitate protein digestion and aid DNA extraction. The full ITS region (ITS1-5.8S-ITS2) was amplified via PCR using the primer pair

ITS9mun and ITS4ngsuni (Tedersoo & Anslan, 2019) (**I–III**). PCR reactions contained the following components: 5 µL of 5x HOT FIREPol Blend Master Mix, 0.5 µL of each 20 mM primer, 1 µL of DNA extract, and 18 µL of ddH_2O. The cycling conditions were as follows: initial denaturation at 95 °C for 15 min, followed by 30 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min, with a final extension at 72 C for 10 min, and a hold at 4 °C. PCR products from duplicate reactions were pooled and visualized on a 1% agarose gel to ensure appropriate amplicon size (600–800 bp). Negative controls were used to detect potential contamination; the gel electrophoresis image showed no contamination. Pooled amplicons were purified with FavorPrepTM kit (Favorgen) and sent to the Norwegian Sequencing Centre for Pacific Biosciences (PacBio) SMRTbell library preparation and sequencing on a Sequel II instrument.

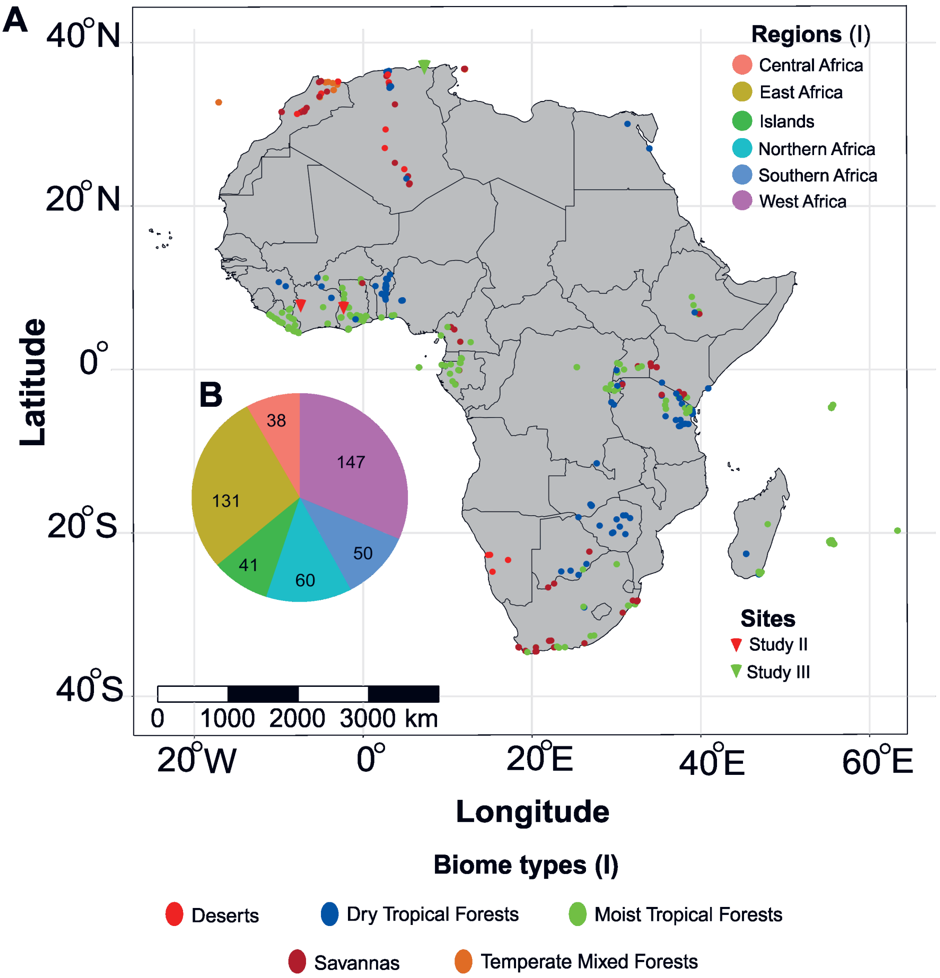

Figure 1 (A) shows the geographic distribution of samples collected for all studies (**I–III**), with different colours indicating the specific biome type associated with each sample and site. (B) shows the number of African regions represented in (**I**) based on the number of samples.

2.3. Bioinformatics

We used circular consensus sequences (CCS) generated with SMRT Tools v.9.0.0.92188, using default settings, including a minimum of 3 passes and a minimum accuracy of 0.99 (**I** & **II**). Subsequent bioinformatics analyses were carried out using the NextITS pipeline v.0.5.0 (Mikryukov et al., unpublished, https://github.com/vmikk/NextITS) and the Nextflow workflow manager (Di Tommaso et al., 2017). Firstly, we demultiplexed the multiplexed sequences using dual 12-base primer indices (Tedersoo et al., 2022) in LIMA v.2.9.0 (PacBio, https://lima.how/). Sequences lacking primer sites were removed using cutadapt v.4.6 (Martin, 2011). Full-length internal transcribed spacer (ITS) sequences were extracted using ITSx v.1.1.3 (Bengtsson-Palme et al., 2013). Chimeric sequences were removed using VSEARCH v.2.27.0 (Rognes et al., 2016) through a two-step process: first, de novo detection with the UCHIME algorithm (Edgar et al., 2011) and a maximum chimera score of 0.6 (Nilsson et al., 2015), then reference-based detection with the EUKARYOME database v.1.7 (Tedersoo et al., 2024). For (**III**), raw PacBio sequences were converted into an operational taxonomic unit (OTU) table using PipeCraft2 (v0.1.4; Anslan et al., 2017), a metabarcoding data processing software which incorporates the following tools at each step. Cutadapt v3.5 (Martin, 2011) was employed for demultiplexing (allowing one mismatch and an overlap of 11 bp for tagging sequences) and for primers clipping (allowing two mismatches and an overlap of 18 bp). Quality filtering was performed by allowing a maximum error rate of one per sequence and excluding ambiguous bases, using VSEARCH (version 2.18.0; Rognes et al., 2016), as implemented in PipeCraft2 (v0.1.4; Anslan et al., 2017). Putative chimeric sequences were eliminated using the "uchime_denovo" method in VSEARCH. The sequences were then subjected to ITSx v1.1.3 (Bengtsson-Palme et al., 2013) to extract the full ITS region, excluding conservative gene fragments (using default settings, except $E = 1^{e-2}$). ITS sequences were clustered into OTUs with VSEARCH (--iddeff = 2, similarity threshold of 98%), and subsequently refined with LULU (v.0.1.0; Frøslev et al., 2019) to merge potential "daughter-OTUs" (using default settings except minimum match = 98 and minimum relative co-occurrence = 0.8). The match list for LULU was generated using BLASTn (Camacho et al., 2009). Taxonomic assignment was done using a BLASTn search against the UNITE v9 database (Nilsson et al., 2019; Abarenkov et al., 2022), retaining only matches with a minimum sequence identity of 90% and an alignment coverage greater than 20% (**III**). Fungal functional groups were identified at the genus level using the FungalTraits database (Põlme et al., 2020) (**I** & **II**). Five fungal functional guilds (primary lifestyles)—arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EcMF), saprotrophs, parasites, and pathogens—were selected based on their specialized function and economic importance in ecosystem processes to compare with all fungi across different biome types (**I**). To visualize the hierarchical taxonomic composition and coverage of fungal communities in soil samples across the continent, we generated a Krona chart using KronaTools v 2.8.1 (Ondov et al., 2011) (**I** & **II**).

2.4. Acquisition of environmental and spatial data from public databases

Mean annual precipitation (MAP), mean annual temperature (MAT), and elevation were all obtained at 30 arc-seconds from the CHELSA database (Karger et al., 2017) (**I** & **II**). Elevational and climatic data for the study sites were obtained from WorldClim (version 2.1), offering a spatial resolution of 30 arc-seconds (Fick & Hijmans, 2017) (**III**). The European Space Agency (ESA) Climate Change Initiative (CCI) land cover data (ESA Land Cover CCI project team, 2019) was obtained from https://maps.elie.ucl.ac.be/CCI/viewer/index.php to serve as a proxy for extracting vegetation classes based on our coordinates (**I**). Biome types classified (*sensu* Olson et al., 2001) were consolidated into four main categories: tropical and subtropical moist broadleaf forests as moist tropical forests; tropical and subtropical dry broadleaf forests as dry tropical forests; tropical and subtropical grassland, savanna, and shrubland grouped as savannas; and deserts and xeric shrublands as deserts. Additionally, two biome types, temperate broadleaf and mixed forests, were combined into temperate mixed forests (Fig. 1A). All sample plots were grouped into six regions (Central Africa, East Africa, Northern Africa, Islands, Southern Africa, and West Africa) (Fig. 1B) based on our geocoordinates and national boundaries (Good, 2011), to examine the community composition of fungi at different regional levels (**I**).

2.5. Statistical analyses

All statistical analyses were performed using specific packages (as indicated in each case) within the R statistical computing environment (v.4.2.2) (R Core Team, 2023). To prevent differences in sequencing depth between samples and obtain a reliable alpha diversity metric, we used the residuals from a linear regression of the logarithmically transformed number of fungal OTUs against the logarithm of the sequencing depth (Tedersoo et al., 2022) (**I**). Alpha and beta diversity indices (Shannon index and richness) were measured using the vegan package (Oksanen et al., 2023) (**I–III**). One-way ANOVA and Tukey's Honestly Significant Difference (HSD) test were performed to statistically compare alpha diversity indices with variables at $\alpha = 0.05$ (**I** & **II**). Before model fitting, we checked for multicollinearity among predictors by calculating variance inflation factor (VIF) using the vif() function from the car package (Fox & Weisberg, 2018) (**I–III**). Climatic variables, including the mean temperature of the warmest quarter (BIO10) and annual precipitation (BIO12) from the CHELSA database (Karger et al., 2017), were combined with our fungal richness data to produce a detailed map of fungal diversity using the generalized additive model (GAM) (**I**). We also performed spatial predictions of mycorrhizal fungal richness based on BIO10 and BIO12 using a random forest modelling approach (van den Hoogen et al., 2019), separately for AMF and EcMF (**I**). To examine the influence of tree cover/composition—which in many cases include potential mycorrhizal species—on fungal diversity in Africa, specifically on mycorrhizal fungal (AMF and EcMF) richness, we employed the European Space Agency (ESA) Climate Change Initiative (CCI) land cover data (ESA Land Cover CCI project team, 2019) as a proxy for extracting vegetation class based on our geographic coordinates (**I**). To evaluate spatial autocorrelation in model residuals, we calculated Moran's I statistic (Moran, 1950) using the spdep package in R (Bivand & Wong, 2018) (**I**). To investigate how environmental variables (MAP, MAT, and biome types) and soil factors (pH, soil organic carbon, N, Ca, K, Mg, P, $\delta^{15}N$, and $\delta^{13}C$) affect soil fungal diversity and community structure across Africa, we used permutational multivariate analysis of variance (PERMANOVA) with the help of the adonis2 function in the vegan package, with 999 permutations (**I–III**). To explore the link between soil fungal communities and soil chemical properties, we conducted a distance-based redundancy analysis (dbRDA) with the dbrda function from the vegan package v2.6-4 (Oksanen et al., 2023) (**I & II**). This analysis used the Hellinger transformation, the Bray-Curtis distance, and standardised environmental variables (method="standardize") via the decostand function in vegan (**I & II**). Variable importance was calculated using the random Forest() function (Liaw & Wiener, 2002), indicating the significance of each model's effect on the linear models (**I**). Non-metric multidimensional scaling (NMDS) was employed with Bray-Curtis dissimilarity to visualize community differences based on variables such as biome types and regions, using the metaMDS function in vegan (**I & III**). The beta-diversity distribution was plotted on an NMDS plots, and PERMANOVA with 999 permutations tested the significance of dissimilarity between biome types and regions (**I**).

3. RESULTS

3.1. Taxonomic and functional diversity (I)

Following the demultiplexing of 19 PacBio sequencing libraries, a total of 3,429,761 sequences were assigned to biological samples. These sequences were then clustered into 511,437 OTUs based on 98% similarity threshold. Taxonomic annotation identified fungi as the dominant kingdom, with 3,200,058 sequences and 327,761 OTUs. At the phylum level, Ascomycota (59.4%), Basidiomycota (31.7%), Mortierellomycota (2.66%), Chytridiomycota (1.38%), Mucoromycota (1.37%), Rozellomycota (1.14%), and Glomeromycota (1.08%) were the prevailing groups, collectively accounting for over 90% of the relative abundance (**I**, Fig. 1B). At the order level, Pleosporales (11.4%), Hypocreales (9.97%), Agaricales (9.45%), and Eurotiales (8.11%) were the most prominent, contributing 40% of the relative abundance (**I**, Figs. 2 &3).

At the family level, Aspergillaceae was the most abundant in Ascomycota, accounting for 13.8% of the dataset. Nectriaceae followed as the second most abundant family within the Ascomycota group, constituting 9.77% of the OTUs (**I**, Fig. 2). In Basidiomycota, Russulaceae was the dominant family, accounting for 16.5%, while Thelephoraceae (10.3%) was the second most prevalent (**I**, Fig. 3). Agaricomycetes was the dominant class among the taxa identified at the highest taxonomic resolution, accounting for more than a third of the taxa within this group (Fig. 2A). Two OTUs were the most dominant within this group, representing Chaetomellales (8.2%) belonging to the phylum Ascomycota and Agaricales (7.5%) belonging to the phylum Basidiomycota (Fig. 2B).

Fungal richness exhibited significant variation across the five defined principal African biomes ($F = 2.66$, $df = 4$; $p = 0.022$). Savannas, temperate mixed forests, dry tropical forests, and moist tropical forests demonstrated the highest richness, whereas deserts recorded the lowest levels (**I**, Figs. 4C, 5A). Notably, species composition showed distinct differences between moist and dry tropical forests (**I**, Fig. 5B). Regionally, Central and East Africa harbored the greatest richness, while Northern Africa had the lowest (**I**, Fig. 5C). Furthermore, fungal guilds OTU richness showed variability across ecosystems, with saprotrophs being the dominant group among them (**I**, Fig. 4H).

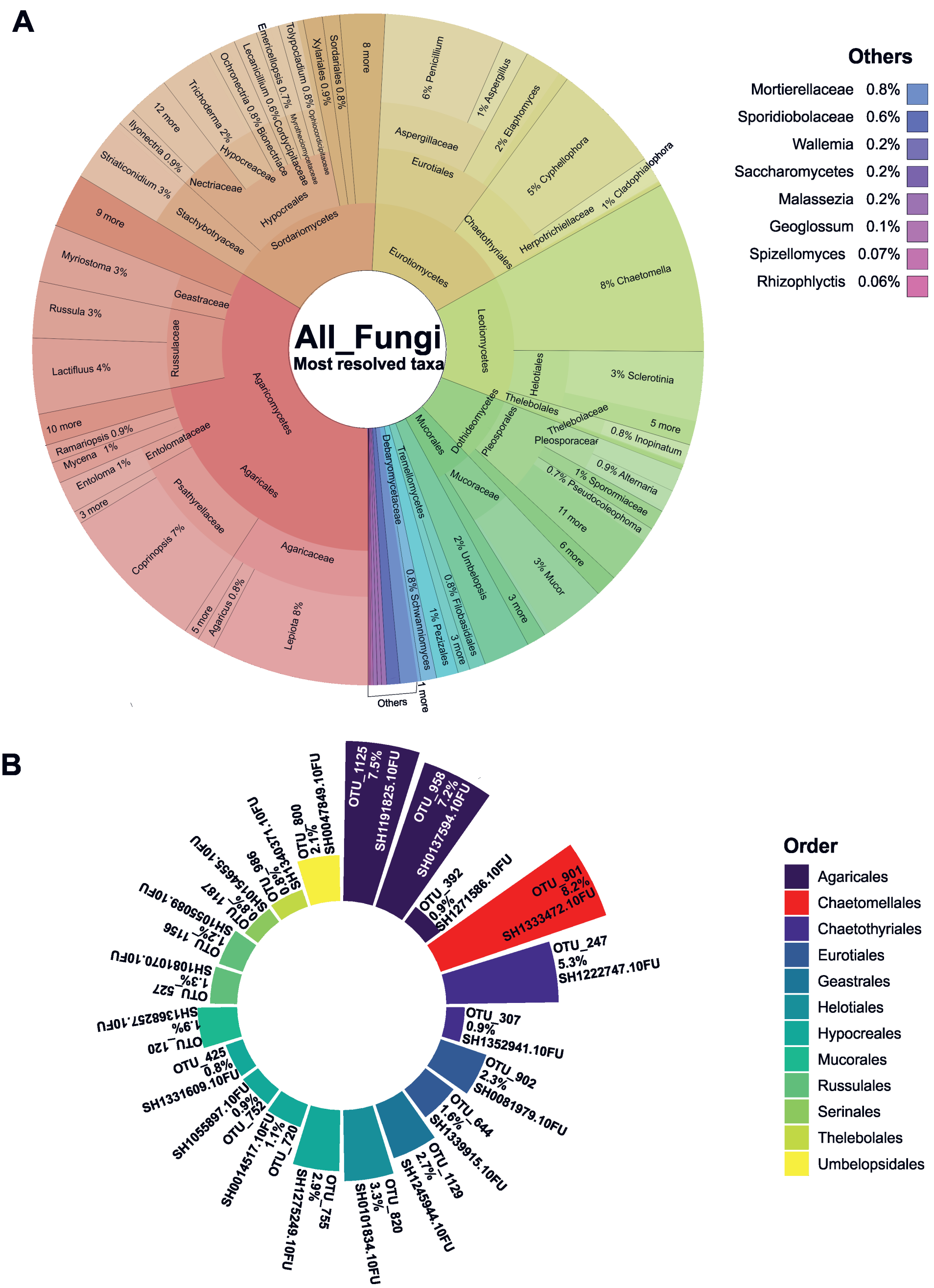

Figure 2. Taxa identified at the highest taxonomic resolution in the dataset. (A) Krona chart showing the taxonomic distribution of the most resolved proportion of the recovered OTUs. (B) Distribution of OTUs belonging to the top twelve taxa identified at the highest taxonomic resolution with SH-code at the order-level.

However, saprotroph diversity was highest in tropical forests and lowest in deserts ($F = 8.89$; $p < 0.001$). EcMF were more abundant in savannas and tropical forests ($F = 4.56$; $p = 0.001$), where host trees are abundant, possibly due to the high abundance of EcMF host plants in these biomes (**I**, Fig. 4I). AMF were prevalent in dry tropical forests; however, there were no significant differences in their richness among biomes ($p > 0.05$), although they were more abundant in West Africa, especially in forest-savanna ecotones (**I**, Fig. 4J). Parasites and pathogens differed significantly across biomes, with the highest diversity observed in savannas ($F = 3.66$; $p = 0.008$; $F = 10.03$; $p < 0.001$) (**I**, Fig. 4G & H).

We produced a high-resolution map of fungal richness across Africa by integrating BIO10 and BIO12 raster data from the CHELSA database with our fungal dataset. This map shows the distribution of fungal richness throughout Africa, emphasizing environmental influences and identifying cold spots in desert regions and hot spots along the West and East African belt, as well as in Central and Southern Africa (**I**, Fig. 5E). Our random forest models effectively predicted the spatial patterns of fungal richness for both mycorrhizal types (AMF and EcMF). The models accounted for a substantial proportion of the variance in observed richness, showing higher predictive accuracy for AMF ($R^2 = 0.857$, $RMSE = 0.907$) than for EcMF ($R^2 = 0.569$, $RMSE = 0.743$). The spatial prediction maps revealed distribution patterns of AMF and EcMF across Africa, with EcMF showing higher richness in forested and tree-dominated areas, while AMF richness was distributed in open habitats and savannas (**I**, Fig. 6). Areas with dense tree cover and high moisture environments—particularly along the West and East African belt—showed the greatest AMF richness (**I**, Fig. 6A). Conversely, EcMF showed higher richness around the Congo Basin and Central Africa, where there is a dense concentration of forest trees (**I**, Fig. 6B). Including vegetation class in the spatial analysis revealed notable clustering of both tree distribution and fungal richness, indicating that vegetation structure influences the geographic patterns of soil fungal diversity.

The Moran's I test indicated significant spatial autocorrelation in the model residuals ($I = 0.23$, $p = 0.04$). Moran's I scatter plots also showed clusters of different degrees of richness across the continent, signifying local deviations from regional trends (**I**, Fig. 6C). MAP, K, elevation, C, N, P, Ca, and Mg positively influenced fungal richness (**I**, Fig. S1). Carbon and nitrogen emerged as the main soil chemical factors driving soil fungal richness in our dataset, accounting for 23% and 24% of the variation, respectively, in our model (**I**, Fig. S1). Conversely, latitude, soil pH, MAT, and C:N ratio (**I**, Fig. S1) negatively affected fungal richness.

3.2. Drivers of fungal community structure (I)

PERMANOVA analysis revealed that the climatic variables MAT and MAP, along with soil pH, were the primary factors affecting fungal community structure (MAT: $R^2 = 0.022$, $F = 9.38$, $p < 0.001$; MAP: $R^2 = 0.018$, $F = 7.96$, $p < 0.001$; soil pH: $R^2 = 0.02$, $F = 8.71$, $p < 0.001$) (**I**, Table S1). Distance-based RDA also indicated that MAT, MAP, and soil pH significantly shape fungal community structure (**I**, Fig. S2). Our variable importance analysis, performed with the random forest algorithm, showed that climate and other factors influence the soil fungal community, with total nitrogen identified as the most important variable (**I**, Fig. S2).

African fungal communities were mainly influenced by the contrasting climatic regimes and biomes across the continent. Clustering of samples by regions ($p < 0.001$, $R^2 = 0.056$) and biome types ($p < 0.001$, $R^2 = 0.046$) significantly explained variation in fungal community structure. Our NMDS plot also revealed greater diversity in moist and dry tropical biomes than in other biome types, with notable differences in species composition. Although Northern Africa had the lowest fungal richness, all regions showed significant variation in species composition (**I**, Fig. 5C & D). The fungal prediction map from our study also shows the distribution of fungal richness across Africa, emphasising environmental dependencies while identifying cold spots in deserts and hot spots in the West and East African belt, as well as in Central and Southern Africa (**I**, Fig. 5E).

We employed a partial Mantel test to further analyse the impact of individual edaphic and climatic factors on fungal beta diversity. The correlations between edaphic and climatic factors and soil fungal beta diversity were mainly significant. In all our dataset, MAP and pH were the factors most influencing total and abundant fungal beta diversity, while MAP had the most influence on rare fungal OTUs (Fig. 4A). At the functional guild level, MAT, pH, and Ca had the strongest influence on saprotrophic fungi, while P had no significant interaction with the three functional guilds (Fig. 4B). Soil pH notably influenced fungal richness in West, North, and Southern Africa ($p < 0.05$), but not in East Africa, Central Africa, or island regions ($p > 0.05$) (Fig. 4C–D).

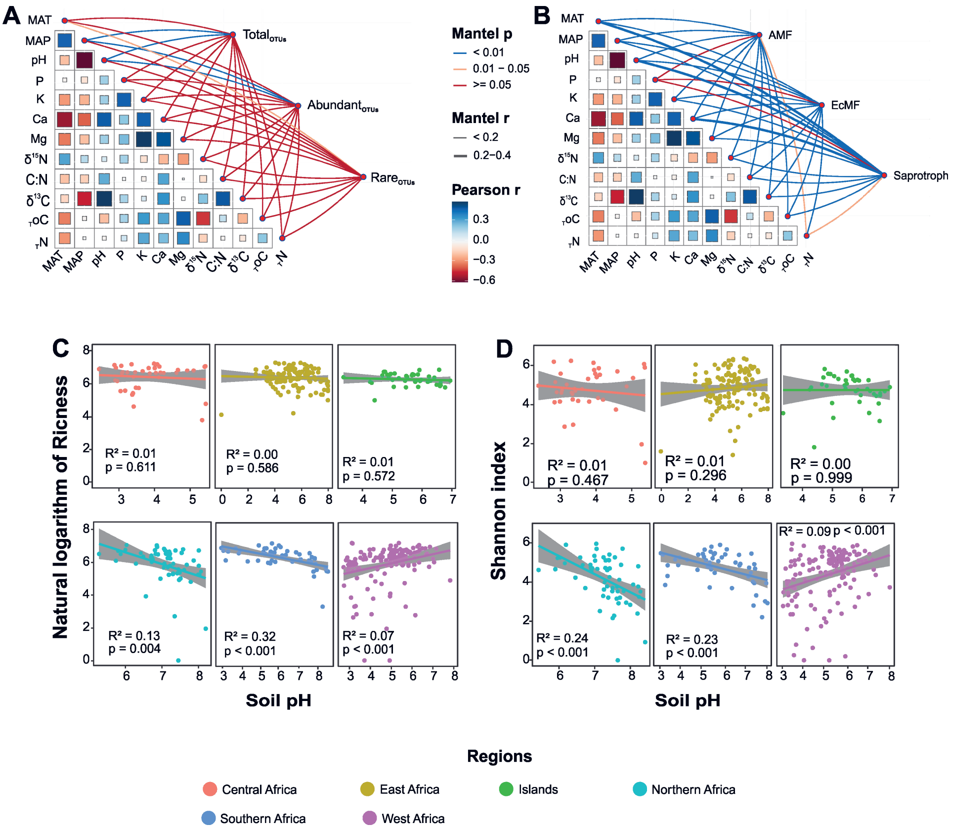

Figure 3: Effects of edaphic and climatic variables on fungal richness. (A) Pairwise comparisons between edaphic and climatic factors, and partial Mantel tests for total, most abundant, and rare OTUs with each individual environmental factor. (B) Pair-wise correlations between edaphic and climatic, and partial Mantel tests for AMF, EcMF and saprotrophs with each individual environmental factor. (C). Effect of soil pH on fungal richness across regions. (D). Effect of soil pH on Shannon index across regions. Colour gradient denotes the Spearman correlation coefficients. Curve width represents the significant correlation coefficients ($p < 0.05$) of the partial Mantel tests.

3.3. Taxonomic resolution of soil fungi in agroforestry systems (II)

A total of 10,067 full-length ITS reads were classified into 4,025 fungal OTUs. Ascomycota was the dominant phylum, accounting for 73.6% of the total, followed by Basidiomycota (23.8%), while other phyla, including Rozellomycota, Chytridiomycota, Mortierellomycota, and Glomeromycota, collectively contributed less than 3% of the total relative abundance (**II**, Fig.2). Eurotiales and Dothideales were the dominant orders in our dataset, accounting for 30% and 27% of abundance, respectively (Fig. 2A). Alpha-diversity analyses revealed notable geographic differences in fungal diversity. Shannon diversity showed significant variation between countries (one-way ANOVA: $F = 5.56$, $p = 0.04$), but there were no significant differences across soil depth classes or farm ages ($F = 0.82$, $p > 0.05$) (**II** Fig.3A). Functional guild classification showed that fungal communities were mainly composed of saprotrophic taxa, with undefined saprotrophs and litter saprotrophs representing the largest functional groups across all sites and soil depths (**II**, Fig. 4B). Ectomycorrhizal fungi (EcMF) were consistently found in both shallow and deep soils, but they accounted for only a small proportion of the total community. Arbuscular mycorrhizal fungi (AMF) were rare, accounting for about 0.02% of all sequences, and were only found in shallow soil samples. Plant pathogenic fungi were present at nearly all sites and soil depths, with higher relative abundance in 5-year-old cocoa farms than in older farms (**II**, Fig.4B).

At the genus level, fungal communities exhibited a high dominance by the genera *Phialophora* and *Penicillium*. These two genera together accounted for a significant proportion of the total OTUs observed in our dataset. This dominance emphasises the ecological importance of these fungi, indicating their possible roles in nutrient cycling and interactions within the broader microbial community. The widespread presence of *Phialophora* and *Penicillium* may also reflect specific environmental conditions or substrate availability that favour their growth, establishing them as key players in the ecosystem dynamics of the sampled areas.

Other frequently detected genera included *Rhodotorula*, which was more abundant in soils from Côte d'Ivoire; and *Agaricus* and *Lepiota*, which were prevalent in Ghana soils. Several genera, including *Ganoderma* and *Inocybe*, showed site-specific distributions, suggesting that local environmental or management factors influence the composition of fungal communities (**II**, Fig. 5B).

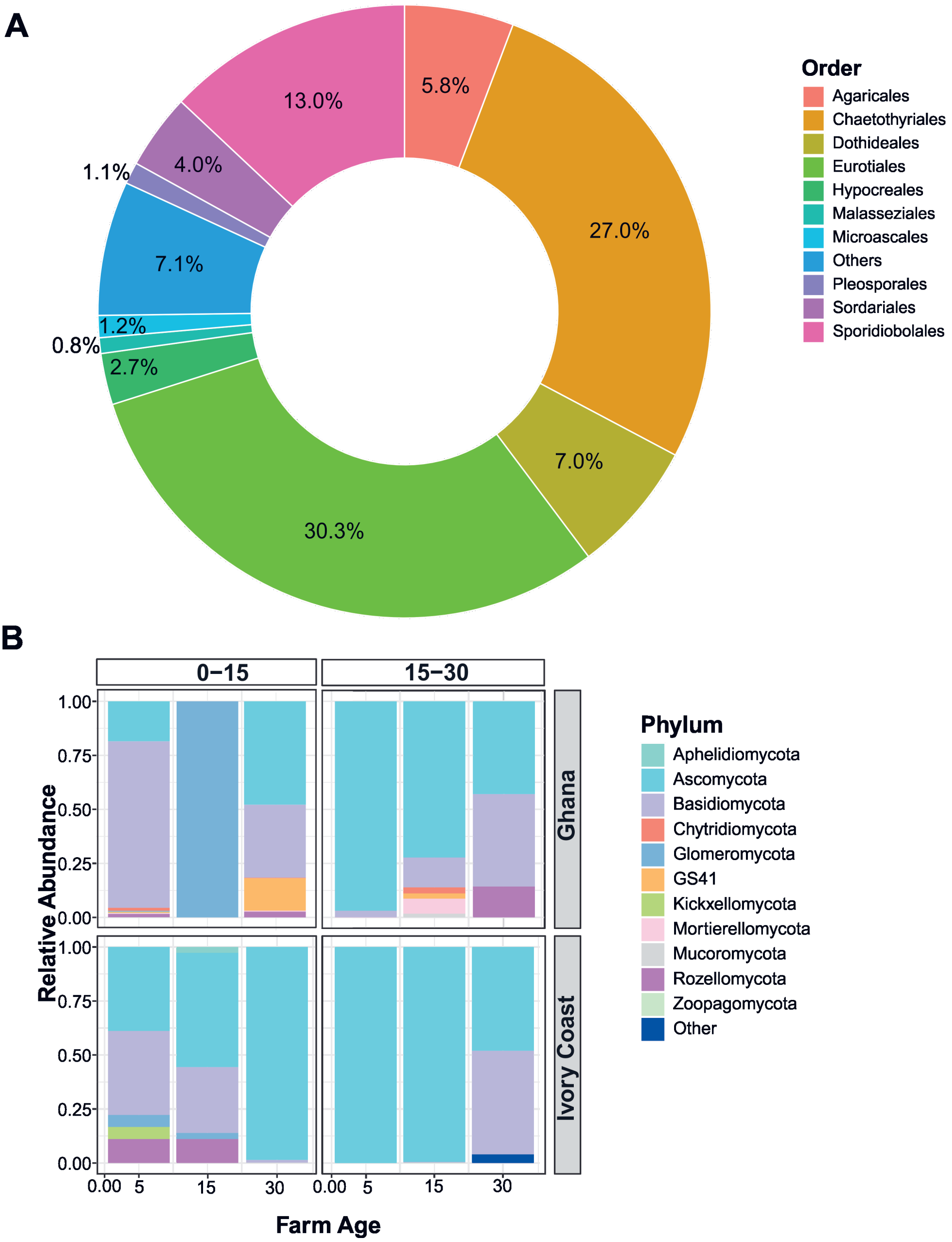

Figure 4: Taxonomic coverage of fungal communities across countries. (A) Relative abundance of fungal orders. (B) Relative abundance of fungal phyla based on farm age, country, and soil depth.

3.4. Community variations of fungi within agroforestry systems (II)

Multivariate analysis of fungal community structure showed that soil pH was the main environmental factor significantly explaining variation in community composition (PERMANOVA, $p < 0.05$). This indicates that pH variation between sites significantly influenced differences in fungal community composition. Other factors, including latitude, longitude, MAT, MAP, available phosphorus, soil organic carbon, and total nitrogen, did not exhibit significant independent effects ($p > 0.05$) (**II**, Table 1). To visualize these relationships, a distance-based redundancy analysis (dbRDA) was conducted, which demonstrated that soil chemical properties collectively explained 20.1% of the variation in fungal community structure, with soil pH, soil organic carbon, total nitrogen, calcium, magnesium, and C:N ratio identified as the most influential explanatory variables (**II**, Fig. 6A). The dbRDA ordination showed distinct clustering patterns of fungal communities, with samples from 5-year-old and 30-year-old cocoa farms in Ghana forming partially overlapping but distinguishable groups. These clusters indicate differences in community composition that may be related to farm age, although the clustering was not absolute, suggesting some shared OTUs between farms of different ages. Variation partitioning analysis showed that soil pH had the greatest impact on fungal community structure, accounting for 8.7% of the variation. This was followed by country (8.1%), farm age (7.6%), and soil depth (2.8%) (**II**, Fig. 3B).

Overall, the combined results of PERMANOVA, dbRDA and variation partitioning analyses demonstrate that soil chemical properties, particularly pH, nitrogen, and organic carbon, are crucial in shaping fungal community composition in cocoa agroforestry farms in West Africa. The grouping of samples by farm age and the relationships among soil variables underscore the complex nature of fungal community structure, emphasizing that no single factor operates independently. The patterns observed in (**II**, Fig. 6A & B, Fig. 3B) provide a detailed view of how environmental gradients and soil chemistry jointly influence the diversity and composition of soil fungal communities. These findings establish a foundation for understanding fungal community dynamics across farms of different ages and soil conditions within West African cocoa agroforestry systems.

3.5. Taxonomic composition and biogeographic patterns of *Alnus*-associated EcMF (III)

Overall, the EcMF community associated with *Alnus glutinosa* roots in KBR consisted of 101 OTUs across two phyla, two classes, seven orders, 15 families, and 18 genera (**III**, Table S1). Most of these OTUs (99) were from the phylum Basidiomycota, representing 98.59% of the sequences, while the remaining OTUs belonged to the phylum Ascomycota. The most abundant OTUs (>10% of sequences) came from the genera *Lactarius*, *Tomentella*, and *Inocybe*, collectively accounting for over 71% of the sequence abundance (**III**, Fig. 1). The sequencing depth averaged 13,682 reads per sample after demultiplexing. Sample completeness values were 0.87 for El Mellah, 0.79 for Righia, and 0.89 for Verges, indicating satisfactory coverage and sufficient sequencing depth (**III**, Fig. S3). Comparing our sequences with global datasets revealed 94 EcMF OTUs unique to Algeria. Sharing of OTUs with other regions was limited, encompassing only four genera: *Cortinarius*, *Inocybe*, *Lactarius*, and *Tomentella*. Notably, one OTU was shared with the Northeast USA, two with Ecuador, three with Northern Europe (Finland, Lithuania), four with Southern Europe (Austria, Italy, Slovenia), one with Eastern Europe (Romania), and two each with Northeast China and Japan (**III**, Fig. 2). In terms of sequence count, the shared OTUs accounted for 67.5%, while unique OTUs encompassed 32.5% of the sequences in this study. Limiting the analysis to the dominant ectomycorrhizal genera by sequence abundance—*Lactarius*, *Tomentella*, and *Inocybe*— increased the proportion of shared OTUs to 83.6%. This refinement emphasizes the strong ecological links and common evolutionary features among these main groups. As a result, 16.4% of the OTUs are unique to specific genera, suggesting possible niche differentiation and adaptation strategies that warrant further studies. Verges recorded the highest diversity of unique EcMF OTUs, with 23 distinct categories identified. Following closely was Righia, which hosted 22 unique OTUs, while El Mellah had a comparatively lower count of 8 unique OTUs (**III**, Fig. S4). Notably, 15 OTUs were common across all three sampling sites, indicating some shared ecological characteristics. Furthermore, pairwise comparisons revealed significant overlaps in OTU diversity: there were 14 OTUs shared between El Mellah and Verges, 10 OTUs shared between Righia and Verges, and 9 OTUs shared between El Mellah and Righia (**III**, Fig. S4). This data highlights not only the richness of fungal diversity in these distinct environments but also the complex interrelationships among the sites.

Results from the Linear Mixed-Models (LMMs) analysis indicated that Verges exhibited the highest average OTU richness and diversity among the studied sites. Statistical analyses revealed significant differences in both OTU richness and diversity when comparing Verges with the other two sites, El Mellah and Righia, highlighting the ecological distinctiveness of Verges in this context (**III**, Fig. 3). This suggests that Verges may provide a more favourable habitat or show unique environmental conditions that support a greater variety of species compared to the other locations.

3.6. Environmental factors influencing EcMF community structure (III)

Soil properties across all three sites and the results of the Kruskal-Wallis test are summarised in Table S2 (**III**). Most edaphic variables exhibited minimal spatial or temporal variation; Kruskal-Wallis tests showed no significant differences among sites or between seasons for pH, electrical conductivity, total lime, or salinity. A notable difference was observed in organic matter content, with Righia exhibiting significantly higher values than both El Mellah and Verges. However, the Dunn's test revealed significant differences only between Righia and Verges (**III**, Table S3). No significant differences in soil properties were observed between seasons.

The NMDS ordination plot (**III**, Fig. 4) showed a low stress score of 0.10, indicating clear separation among the three sites and suggesting site-specific differences in the EcMF community structure. A significant correlation was also found between organic matter content and the ordination (**III,** Fig. 4; **III**, Table S4). The PERMANOVA results (**III**, Table 1) confirmed these findings, demonstrating that both site and organic matter content significantly affected the EcMF community structure, with the impact of organic matter being weaker. The site explained 43.3% of the variation, while organic matter content accounted for 19.0%. Other factors tested, including season, electrical conductivity, pH, total lime, and practical salinity, did not significantly influence the EcMF community structure. The analysis of homogeneity of dispersion across groups showed no significant differences.

4. DISCUSSION

4.1. Patterns of fungal diversity in African soils

We utilised metabarcoding of the ITS marker to assess soil mycobiome diversity across 32 African countries, spanning all biomes and nearly two-thirds of the nations on the continent. Our results showed higher fungal richness in savanna biomes than in moist tropical forests, contradicting our hypothesis. The similarity between savannas and temperate forests suggests that other factors influence fungal richness, possibly including fire, habitat heterogeneity, and environmental factors (Maquia et al., 2020; Poswa et al., 2024). A recent study identifies AMF hotspots in the Brazilian Cerrado, Southeast Asian tropical forests, and West African Guinean forests (Van Nuland et al, 2025). Soil fungal richness peaks in Central and East Africa, but deserts such as the Sahara and Namib have lower diversity, mainly comprising xerotolerant taxa (Makhalanyane et al., 2015; Johnson et al., 2017; Egidi et al., 2019). Fungal biodiversity is highest in African savannas, temperate forests, and Congo Basin rainforests, with Afrotropical regions supporting high fungal diversity due to rainfall, stable temperatures, and structurally complex vegetation cover (Tedersoo et al., 2014; Corrales et al., 2022; Mikryukov et al., 2023). The Congo Basin and Guinean forests are biodiversity hotspots with diverse EcMF and saprotrophic fungi that are vital to ecosystems (White, 1983; Resende & Meikengang, 2023; Tondeleir et al., 2025). Aspergillaceae, including *Aspergillus*, dominate our dataset, as reported by Kachapulula et al (2017). The abundance of Russulaceae and Thelephoraceae aligns with a recent global study (Tedersoo et al., 2021). This study highlights the ecological significance and distribution patterns of these fungal families, emphasizing their role in various ecosystems and their interactions with plant species. Such alignment with global research underscores the importance of understanding these fungi in the context of biodiversity and environmental health. Russulales was more prevalent in East and Central Africa, likely due to EcMF relationships with dominant host trees (Tondeleir et al., 2025). Fungal diversity is influenced by soil chemistry, climate, and geography. Soil pH, nutrients, and organic matter affect fungal communities. Climate factors such as MAT and MAP shape their distribution and life cycles. Elevation and distance from the equator create microenvironments that support or limit fungal diversity, shaping ecosystem diversity. MAP positively influences fungal richness, highlighting the role of moisture in fungal diversity. Richness peaks in weakly acidic soils, aligning with global patterns, but climate change may disrupt pH and vegetation, impacting fungal diversity at various levels (Tedersoo et al., 2014, 2021; Mikryukov et al., 2023). Soil chemical properties also influence fungal abundance and soil health, affecting nutrient cycling, plant growth, and soil structure (Powell & Rillig, 2018). Soil saprotrophs are most diverse in tropical forests and savannas, while EcMF are prevalent in Moroccan and Pantellerian forests. Animal parasites and mycoparasites exhibit taxonomic diversity in savannas, occupying various niches, while pathogenic fungi are more prevalent in arid deserts, likely due to limited organic material and host availability, which influence microbial interactions.

African soil fungal communities are mainly influenced by climatic factors such as MAP and MAT, as well as soil variables including pH, N, P, and C:N ratio, consistent with studies across various regions (Sarkodee-Addo et al., 2020; Tedersoo et al., 2014, 2022). Most African soils are dominated by saprotrophic fungi. Tropical forests, especially in the Congo Basin, host high fungal diversity, primarily of EcMF and saprotrophs, which are crucial for decomposition and plant symbiosis. AMF are more prevalent, especially in semi-dry woodlands and savannas, aiding plants in water-stressed conditions by improving nutrient uptake and stress resilience (Yan et al., 2022; Zhang et al., 2019). Our NMDS plots reveal unique clusters for savannas, dry tropical forests, and moist tropical forests at the biome level. Tondeleir et al. (2025) identified distinct biome-driven communities, with rainforests, gallery forests, and woodlands forming separate clusters. The regional clustering in West, East, and Central Africa aligns with previous findings attributed to shared climate, vegetation, evolutionary history, and EcMF dominance (Alem et al., 2022; Tondeleir et al., 2025). Notably, much of the fungal community structure remains unexplained by the environmental factors we examined, suggesting that other influences, such as landscape-scale niche differentiation or stochastic dispersal, also shape these communities.

The biogeography of fungi in Africa is shaped by complex interactions among climate, soil properties, vegetation types, and plate tectonics. African biomes, ranging from arid deserts to lush tropical rainforests, host various mycorrhizal types, especially AMF and EcMF. The distribution of these mycorrhizal types is usually influenced by climatic gradients, soil chemical properties, and vegetation types (Soudzilovskaia et al., 2019), all of which affect the functioning of plant communities across the continent (Rodríguez-Echeverría et al., 2017). Here, we observed that biome types significantly influence the distribution of mycorrhizal types. This is mainly attributable to climate and the availability of host plants. Arbuscular mycorrhizae are the most widespread type of mycorrhizae in Africa that primarily associate with grasses, shrubs, and various crop species (Mukhongo et al., 2016). AMF thrive in arid and semi-arid regions due to their drought tolerance and the absence of ectomycorrhizal tree vegetation in these areas. However, we observed a relatively high abundance of AMF in Guinean forests of West Africa and in dry tropical forests with little or no ectomycorrhizal tree vegetation. A previous study also showed that West African savannas harbour a rich diversity of AMF (Tchan et al., 2022), reflecting the high diversity of savanna biomes in our study. The genus *Rhizoglomus* is the most prevalent AMF taxon in our dataset, particularly in Benin and Tanzania, which aligns with the findings of Sarkodee-Addo et al. (2020) and Tchabi et al. (2008).

Our results also revealed that tree presence and vegetation type significantly influence mycorrhizal fungal richness in African ecosystems (**I**, Fig.6A & B). Including land cover as a proxy for tree presence and potential mycorrhizal hosts (e.g., EcMF) significantly improved the accuracy of our model, supporting the hypothesis that fungal richness is associated with tree presence and the availability of potential mycorrhizal hosts. We found that MAT and MAP are the primary predictors of both AMF and EcMF in the random forest models, with AMF showing more pronounced richness hotspots than EcMF, emphasizing the dominance of AMF in tropical climates. This supports recent research (Rodríguez-Echeverría et al., 2017; Van Nuland et al., 2025), which found AMF to be prevalent in these tropical areas. Significant spatial autocorrelation (as indicated by a positive Moran's I statistic) further suggests that vegetation clustering plays a crucial role in determining fungal richness and community patterns (Tedersoo et al., 2011; Meidl et al., 2021).

Conversely, we found EcMF to be more abundant in humid, nutrient-poor forest ecosystems, supporting previously known Africa-wide patterns of mycorrhizal type distribution in plants (Soudzilovskaia et al., 2019). The relative abundance of EcMF peaks in temperate mixed forests found in Morocco and Pantelleria. Central and East Africa also exhibit a relatively higher abundance of EcMF, particularly associated with hosts from the plant families Fabaceae, Phyllanthaceae, and Dipterocarpaceae, compared to other regions. Conversely, EcMF are absent from deserts, forests in the Drakensberg mountains, and the Ethiopian highlands, and are rare in Réunion. Our continent-wide prediction map of all fungi and mycorrhizal fungi can serve as a reference for environmental monitoring and policy development at national and continental levels, as it is the first to reveal soil fungal richness across nearly two-thirds of African countries using eDNA.

4.2. Soil fungal community composition, diversity and distribution in cocoa agroforestry systems

Soil fungal communities in the rhizosphere of cocoa trees in agroforestry farms responded to soil chemical properties, farm age, and soil depth. The soil fungal communities mainly consisted of two dominant phyla, Ascomycota and Basidiomycota, consistent with previous research in cocoa plantations and in managed and natural forest systems (Nilsson et al., 2019; Tedersoo et al., 2021; Nahon et al., 2024). At the genus level, the most common taxa were *Phialophora*, *Rhodotorula*, *Trichoderma*, and *Penicillium*. *Phialophora*, which thrives in soil and decaying material, plays various ecological roles, including as root endophytes (dark septate), often associated with stressed or nutrient-poor soils (Li et al., 2015). *Rhodotorula* is a pigmented yeast that can survive in various environments, including plant surfaces and fruits (Kwodaga et al., 2017). *Trichoderma* plays an important role in agriculture, promoting plant growth and controlling pathogens. *Penicillium*, recognized for its antibiotic production and food spoilage, has industrial and ecological significance, including promoting plant growth through traits such as indole-3-acetic acid production, siderophore production, and phosphorus solubilisation (Radhakrishnan et al., 2015). In this context, a previous study (Arévalo-Gardini et al., 2020) identified *Penicillium* as a prominent potential biocontrol fungus following the transformation of secondary forests into cocoa agroforestry plantations. An earlier study (Kwodaga et al., 2017) also showed that *Rhodotorula* was dominant at all soil depths, whereas *Trichoderma* was less prevalent throughout the soil profile.

Soil depth significantly affected fungal diversity, with higher Shannon diversity indices in the 0–15 cm layer than in the 15–30 cm layer. This pattern aligns with previous studies indicating that soil organic matter and root traits are key factors shaping fungal community composition in cocoa farms in Ghana (Schmidt et al., 2024). The lower diversity in deeper soil layers probably reflects reduced availability and diversity of organic substrates. Our findings revealed variation in fungal diversity across cocoa farms of different ages. Specifically, mid-aged cocoa farms supported greater fungal species diversity, suggesting that farm age affects fungal communities. This diversity is likely due to well-established microhabitats and nutrient-rich organic matter that accumulate over time, thereby fostering interactions among various fungal species and their ecosystems.

Although arbuscular mycorrhizal fungi (AMF) are known to be important throughout cocoa development, they were poorly represented in the soils of both countries. This could be attributed to the widespread use of agrochemicals in cocoa cultivation, as prior research has indicated that AMF are particularly vulnerable to such inputs, leading to reduced abundance (van der Heijden et al., 2015; Helander et al., 2018; Hage-Ahmed et al., 2019). We observed strong correlations between fungal diversity and the environmental variables examined, supporting previous findings that mean annual precipitation (MAP) and mean annual temperature (MAT) influence soil fungal diversity on both regional and global levels (Tedersoo et al., 2014, 2022). Soil pH ranged from 4.04 to 5.39, similar to values reported for arbuscular mycorrhizal fungi in rice fields in Ghana (Sarkodee-Addo et al., 2020). Soil chemical properties also significantly impacted fungal community composition across sites. Consistent with earlier research, soil pH was identified as a crucial factor shaping fungal community structure, exerting a stronger influence than other soil chemical properties such as potassium and soil organic carbon (Kawahara et al., 2016; Lauber et al., 2013; Xiong et al., 2024). This is supported by PERMANOVA (**II**, Table 1) and dbRDA analyses (**II**, Figure 6A). The weak relationship between fungal diversity and other chemical variables is likely due to the dominant influence of pH over the others. For instance, the chemical properties of pesticides are significantly affected by soil acidity, particularly soil pH. As soil pH decreases, indicating increased acidity, the binding affinity of pesticides to soil particles, particularly clay, tends to increase. This stronger adsorption to clay particles reduces the likelihood that pesticides will leach through the soil profile and contaminate groundwater reserves. Consequently, maintaining optimal soil pH levels is crucial not only for the effectiveness of pesticides and other agrochemical applications but also for minimizing environmental risks associated with groundwater pollution (Mishra et al., 2023). Understanding this relationship is essential for developing more sustainable agricultural practices that protect both crop yields, water quality and the environment. For instance, a recent study showed that biochar application positively affects microbial activity, crop productivity, and soil chemical properties (Singh et al., 2022). Overall, these findings establish a foundation for future microbiome research in cocoa agroforestry systems in Ghana and Côte d'Ivoire and offer valuable insights for developing sustainable cocoa production strategies. They also serve as a baseline for policymakers and extension services to support farmers in closing yield gaps and sustainably enhancing cocoa production.

4.3. Patterns and drivers of *Alnus*-associated EcMF diversity in North Africa

This study offers the first characterisation of ectomycorrhizal fungal (EcMF) communities associated with *Alnus glutinosa* populations in North Africa, substantially expanding our understanding of the biogeography of *Alnus*-related EcMF. While previous research has examined the structure and composition of these communities in European and Asian populations of *A. glutinosa* (Tedersoo et al., 2009; Põlme et al., 2013; Roy et al., 2013; Thiem et al., 2018), our work investigates an uncharted region, adding valuable data to the broader biogeographic context of these fungi. We identified 101 OTUs of EcMF linked to *A. glutinosa* root tips in Algeria, representing one of the highest regional diversities reported for *Alnus*-associated EcMF. This level of richness greatly surpasses that of comparable studies: five times higher than *A. glutinosa* in Estonia (18 OTUs; Tedersoo et al., 2009), four times greater than *A. rubra* in the USA (22 OTUs; McBurney et al., 2017), and 15% more than the combined diversity across five *Alnus* species in France (86 OTUs; Roy et al., 2013). Nevertheless, it remains below the 146 OTUs reported globally across 22 *Alnus* species (Põlme et al., 2013), the 175 OTUs found in *A. rubra* in the USA (Kennedy et al., 2014), and the 275 OTUs documented in *A. glutinosa* in Belgium (Boeraeve et al., 2019). These differences may partly arise from methodological variations across studies, such as Sanger sequencing from individual root tips used in earlier research, differences in bioinformatics processing of high-throughput sequencing data, and sampling strategies (Janowski & Leski, 2023). Rarefaction based on sample size indicates that our sampling captured between 79% and 89% of the estimated OTU diversity, with only nine OTUs being singletons belonging to the genera—*Alnicola*, *Cortinarius*, *Inocybe*, *Lactarius*, and *Tomentella*—are traditionally associated with *Alnus* (Rochet et al. 2011), suggesting minimal under-sampling of dominant taxa. Overall, these results imply that the sampled diversity accurately reflects the true EcMF richness in Algerian *A. glutinosa* forests. Consistent with global patterns observed in *Alnus*-associated EcMF communities (e.g., Rochet et al. 2011; Thiem et al. 2018), Basidiomycota was the dominant phylum in our study. The three most common genera—*Lactarius*, *Tomentella*, and *Inocybe*—mirrored the dominance patterns documented by Rochet et al. (2011), with

Lactarius and *Tomentella* consistently ranking among the most frequent taxa across *Alnus* woodlands. While *Inocybe* was relatively abundant at our sites, it has been reported only sporadically in other *Alnus*-associated communities (Rochet et al., 2011). Different regions have displayed varying dominance patterns; for example, Kennedy et al. (2011) observed unusually high levels of *Clavulina* in *Alnus* stands in Mexico, while Iranian *Alnus* forests showed high proportions of ascomycetes (Põlme et al. 2013). This variability indicates that, although a limited set of EcMF genera tend to dominate *Alnus* ecosystems worldwide (Roy et al., 2013), regional shifts in dominant taxa do occur. The ecological drivers behind these patterns remain unclear, though founder effects might be involved (Douhan et al., 2011). Furthermore, three EcMF genera identified in our study—*Amphinema*, *Melanogaster*, and *Rhizopogon*—are typically associated with *Quercus* spp. and *Pinus* spp. hosts (Sulzbacher et al., 2016; Mandolini et al., 2024; Yuan et al., 2024). In the KBR region, *Quercus canariensis* is characteristic of riparian forests, while *Q. suber* and *Pinus pinaster* dominate drier environments (Kahli et al., 2018). The detection of these genera may reflect spore dispersal or propagule input from nearby oak and pine stands, rather than active ectomycorrhizal associations with *A. glutinosa*, which aligns with their occasional presence outside primary host areas (Taylor & Bruns, 1999; Nara, 2009; Peay et al., 2016).

A striking 93% of the 101 OTUs (94 OTUs) identified in this study were specific to Algeria, with only four shared genera and minimal overlap with other regions. Unique OTUs in this context refer to their uniqueness relative to comparison datasets, not necessarily biological endemism, which needs more sampling and phylogenetic analysis (Tedersoo et al., 2022). While most OTUs were unique, community composition was dominated by globally distributed taxa, including species of *Lactarius*, *Tomentella*, and *Inocybe*. A higher abundance of these taxa indicates that Algerian *Alnus*-associated EcMF communities are unique yet influenced by common taxa, reflecting a conserved yet partially shared community structure (Roy et al., 2013). The biogeographic status of these OTUs—whether endemic or globally rare—is uncertain. This may be due to factors such as drier conditions, which support more unique taxa (Tedersoo et al., 2009), and widespread fungal endemism (Tedersoo et al., 2022).

Our study, at the driest margin of *A. glutinosa* range (Kajba & Gračan, 2003), found high diversity and potentially unique taxa, indicating that aridity may promote EcMF richness and uniqueness. Geographic isolation also matters; North African *A. glutinosa* are genetically distinct relicts from the Last Glacial Maximum, diverging from European populations (Lepais et al., 2013). Phylogenetic and biogeographic factors, along with local soil, habitat, and seasonal influences, likely shape these unique fungal communities. The relationships between the plants and their locations likely affect the EcMF communities as well (Põlme et al., 2013). Other local factors, such as soil characteristics and habitat structure, also influence where these fungi grow (Becerra et al., 2005b; Kennedy & Hill, 2010; Põlme et al., 2013) and help shape the unique EcMF communities found in North African *A. glutinosa* stands.

Significant differences in OTU richness and diversity were observed among the three study sites, with notably higher mean values at Verges compared to the other locations. Despite this variation, all sites were consistently dominated by fungal genera commonly associated with *Alnus* species worldwide, including *Alnicola*, *Alpova*, *Cortinarius*, *Lactarius*, *Inocybe*, and *Tomentella* (Rochet et al., 2011). Among the measured soil variables, only organic matter content significantly influenced EcMF community structure, while soil pH, electrical conductivity, total lime, and practical salinity showed no noticeable effects. This lack of influence is expected, as these parameters exhibited minimal spatial variation across the sites. Additionally, no significant seasonal effects on community composition were detected, indicating temporal stability in *Alnus*-associated EcMF assemblages during the sampling period. Nevertheless, a clear site effect was observed, and given the limited number of sites, environmental influences cannot be fully distinguished from site-specific factors. The link between EcMF community structure and organic matter content aligns with patterns reported in other *Alnus*–EcMF systems. For example, Becerra et al. (2005a, 2005b) reported similar relationships in *A. acuminata* forests in Argentina, and Tedersoo et al. (2009) found that organic matter affected EcMF colonisation in *A. glutinosa* and *A. incana* in Estonia. Even after accounting for environmental variables such as pH, N, and SOC, site differences remained significant, suggesting that other spatial or unmeasured factors may also influence the results. Importantly, Tedersoo et al. (2009) also emphasized that site effects strongly influence the EcMF community structure, consistent with our findings. Despite the prominent site effect, the combination of high organic matter at Righia and lower OTU richness matches findings from other *Alnus* systems, where EcMF colonization and richness decline under high organic matter conditions (Harvey et al., 1981). This decline may reflect selective environmental filtering processes, as the organic matter in *Alnus* stands is typically nitrogen-rich, creating an environment that favours the growth and dominance of certain EcMF taxa. This relationship highlights the complex interactions between plant species and their associated fungal communities, where habitat nutrient conditions strongly influence community composition and diversity (Becerra et al., 2005a). Recent studies further demonstrate that the relationship between EcMF communities and soil organic matter is complex and context-dependent, involving multiple ecological processes and feedbacks (Lindahl & Tunlid, 2015; Wang et al., 2025).

5. CONCLUSIONS

- African soil fungal diversity is shaped by strong environmental and climatic gradients, with soil chemical properties—particularly pH and nutrient availability—and climatic factors such as MAP and MAT acting as consistent abiotic factors that affect fungal richness, diversity, and community structure (I).
- The different biomes across Africa influence fungal diversity, with deserts, rainforests, and savannas offering unique niches for distinct communities. Richness peaks in savannas and dry and moist tropical forests, especially around the Congo Basin, and declines in arid zones such as the Sahara and Kalahari. This pattern reflects the influence of edaphic and climatic factors that create microhabitats affecting fungal distribution (I).
- Despite other unsampled areas in Africa, this study offers a continental-scale baseline of fungal distribution and how they respond to environmental factors. It highlights the urgent need to conserve fungal diversity to maintain ecosystem resilience, promote sustainable land use, and enhance climate adaptation strategies across Africa (I).
- Cocoa agroforestry farms in Ghana and Côte d'Ivoire host soil fungal communities that could support cocoa growth and health, while also showing a notable difference in fungal diversity between these two countries. This study provides one of the first baselines on soil mycobiota in these cocoa-producing systems. However, younger cocoa farms and shallow soils tend to harbour higher fungal diversity than older and deeper soils (II).
- North African *Alnus glutinosa* forests host a highly diverse and potentially unique ectomycorrhizal fungal (EcMF) community, emphasizing the distinctiveness of EcMF assemblages in these areas (III).

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SUMMARY IN ENGLISH

Fungi are a diverse and ecologically vital group of eukaryotic organisms crucial for ecosystem functions. They facilitate nutrient cycling by breaking down complex organic materials, returning essential nutrients to the soil, supporting plant growth and ecosystem health. Fungi form intricate mycorrhizal relationships with plant roots, enhancing nutrient uptake—especially phosphorus—and water access. This mutualism promotes plant vigor and resilience to stressors like drought and soil degradation. They also decompose organic matter, recycling nutrients and improving soil structure. Despite their ecological and economic importance in agriculture and pharmaceuticals, global fungal diversity is underdocumented. Estimates suggest that 2.2 to 3.8 million species exist, but fewer than 95% have been scientifically described, especially in tropical regions, which are hotspots of fungal diversity. Many species remain understudied, limiting our understanding of their roles and potential in biotechnology, medicine, and conservation. Urgent research and documentation are essential for conservation and harnessing their benefits.

Recent advancements in high-throughput sequencing techniques have unveiled a wealth of cryptic microorganisms residing in soils, plant tissues, and extreme habitats, prompting a paradigm shift in research methodologies from traditional morphology-based surveys to genetic analyses. Nevertheless, the bulk of diversity research has predominantly focused on Europe and North America, leaving tropical regions, especially those in Africa, vastly overlooked. Africa is home to an array of unique fungal communities present in its varied ecosystems, including rainforests, woodlands, and arid drylands, all of which are shaped by intricate interactions among climate, soil types, and plant communities. Diverse fungal types can be found across these landscapes, including ectomycorrhizal fungi in woodlands, as well as arbuscular mycorrhizal and saprotrophic fungi prevalent in savanna ecosystems and agricultural lands.

In this thesis, I utilized the eDNA metabarcoding approach to meticulously investigate the composition and diversity of fungal communities residing in soil and root systems across various locations in Africa. Further, I broadened my assessment to include soil fungal diversity across 32 African countries, uncovering marked variations in species composition between moist and dry tropical forest environments. Central and East Africa exhibited the highest fungal species richness, whereas Northern Africa displayed the lowest levels of diversity. Throughout my research, it became evident that fungal operational taxonomic unit (OTU) richness fluctuated, with saprotrophic fungi dominating and exhibiting the greatest diversity in tropical forest ecosystems, contrasting with arid desert environments where diversity was minimal. Ectomycorrhizal fungi (EcMF) were prevalent in savanna and tropical forest habitats, particularly in rich African forests marked by abundant host trees. Conversely, arbuscular mycorrhizal fungi (AMF) were more commonly found in dry tropical forests and showed greater abundance in West African landscapes, especially within forest-savanna

ecotones. Parasitic and pathogenic fungal species were notably more abundant in savanna regions.

Additionally, I discovered that climatic variables, specifically mean annual temperature (MAT) and mean annual precipitation (MAP), along with soil pH, were the primary factors shaping the structure of fungal communities across the investigated landscapes. In collaboration with my research team, we developed a high-resolution map illustrating fungal and mycorrhizal fungal diversity across Africa. This map serves as an essential reference tool for policymakers and researchers, clearly depicting patterns of fungal richness, highlighting the influence of environmental factors, and identifying regions of low (desert cold spots) and high (hot spots along the West-East African belt and in Central and Southern Africa) fungal diversity.

In my thesis, I utilized the eDNA metabarcoding approach to meticulously investigate the composition and diversity of fungal communities residing in soil and root systems across various locations in Africa. Through a series of targeted research studies, I aimed to elucidate how land-use practices, spatial variations, climatic conditions, and edaphic factors influence fungal community dynamics, species diversity, and the ecological parameters driving differences in these microbial communities. I focused my investigation on cocoa agroforestry systems across two West African nations, analyzing the predominant fungal groups present in the soils and exploring the factors affecting their distribution and abundance. Notably, the two countries showcased significant disparities in fungal diversity metrics. While the age of the farms appeared to influence fungal relative abundance, the impact was not statistically significant. In contrast, climatic parameters and edaphic variables emerged as critical determinants significantly impacting fungal diversity.

In a complementary study, we performed a molecular assessment of EcMF communities associated with the tree species *Alnus glutinosa*, revealing that approximately 93% of observed OTUs were unique to Algeria. This finding contrasts with previous studies, in which edaphic factors were significant influencers of EcMF diversity. Instead, differences between sampling sites emerged as the more critical variable shaping these fungal communities.

Overall, my thesis underscores the multifaceted roles of biotic, abiotic, and spatial influences in shaping soil fungal communities. Different fungal groups, such as ectomycorrhizal and saprotrophic fungi, are integral to maintaining ecological balance and functioning within their environments. The findings highlight the urgent need to conserve diverse African soils to support biodiversity and ecosystem health, particularly amid ongoing environmental changes. These results further emphasize the crucial role of land cover and plant diversity in shaping the abundance and diversity of mycorrhizal associations across African biomes.

This work ultimately underscores the complex interplay of biotic, abiotic, and spatial factors in influencing the composition and diversity of soil fungal communities. Various fungal groups, including ectomycorrhizal and saprotrophic fungi, play essential roles in maintaining ecological balance and facilitating energy flow within their respective environments. The implications of our findings are profound, emphasizing the urgent need to prioritize the conservation of diverse African soils, which are vital for supporting biodiversity and ensuring the health of ecosystems, particularly in light of the ongoing environmental changes such as climate change and land-use transformations.

Moreover, our results underscore the critical influence of land cover and plant diversity on the abundance and diversity of mycorrhizal associations across African biomes. By understanding these intricate relationships, we are better equipped to devise strategies that promote ecosystem resilience and sustainability amid increasing anthropogenic pressures.

SUMMARY IN ESTONIAN

Aafrika mullaseente bioloogiline mitmekesisus

Seened on mitmekesised ja ökoloogiliselt väga olulised eukarüootsed organismid, mis on ökosüsteemide toimimiseks hädavajalikud. Nad hõlbustavad toitainete ringlust, lagundades keerulisi orgaanilisi aineid ning tagastades olulised toitained mulda, toetades seeläbi taimede kasvu ja ökosüsteemi tervist. Seened moodustavad taimejuurtega keerukaid mükoriisseid suhteid, mis parandavad toitainete – eriti fosfori – ja vee omastamist. See vastastikune kasu soodustab taimede elujõulisust ja vastupidavust stressiteguritele nagu põud ja pinnase degradeerumine. Seened lagundavad orgaanilist ainet, taaskasutades toitaineid ja parandades mulla struktuuri. Vaatamata nende ökoloogilisele ja majanduslikule tähtsusele põllumajanduses ning farmaatsias on ülemaailmne seente mitmekesisus halvasti dokumenteeritud. Hinnangute kohaselt eksisteerib 2,2–3,8 miljonit liiki, kuid kirjeldatud on vähem kui 95%, eriti troopilistes piirkondades, mis on seente mitmekesisuse tulipunktid. Paljud liigid on uurimata, mis piirab meie arusaama nende rollidest ning potentsiaalist biotehnoloogias, meditsiinis ja looduskaitses. Kiireloomuline uurimistöö ja dokumenteerimine on hädavajalikud nende kaitseks ning kasulike omaduste kasutamiseks.

Viimased edusammud kõrge läbilaskevõimega sekveneerimistehnoloogiates on paljastanud hulgaliselt krüptilisi mikroorganisme mullas, taimekudedes ja ekstreemsetes elupaikades, põhjustades paradigmanihet uurimismetoodikates – üleminekut traditsioonilistelt morfoloogilistelt uuringutelt geneetilistele analüüsidele. Sellegipoolest on enamik mitmekesisusuuringuid keskendunud Euroopale ja Põhja-Ameerikale, jättes troopilised piirkonnad – eriti Aafrika – suuresti tähelepanuta. Aafrika on koduks ainulaadsetele seenekooslustele, mis esinevad selle mitmekesistes ökosüsteemides, sealhulgas vihmametsades savannides ja kuivadel aladel, mida kujundavad keerukad koosmõjud kliima, mullatüüpide ja taimekoosluste vahel. Erinevates ökosüsteemides leidub mitmesuguseid seenerühmi, sealhulgas ektomükoriissed seened savannides ning arbuskulaarse mükoriisa moodustajad ja saprotroofsed seened, mis on levinud savanniökosüsteemides ja põllumajandusmaadel.

Käesolevas doktoritöös kasutasin eDNA metatriipkoodistamise lähenemist, et põhjalikult uurida seente koosluste koosseisu ja bioloogilist mitmekesisust erinevate Aafrika piirkondade mullas ning juurtes. Kontinentaal-skaalal uuringus 32 Aafrika riigis leidsin märkimisväärsed erinevused liigilises koosseisus niiskete ja kuivade troopiliste metsade vahel. Seente liigirikkus oli kõrgeim Kesk- ja Ida-Aafrikas, samas kui Põhja-Aafrika oli madalaima bioloogilise mitmekesisusega. Uuringu käigus selgus, et saprotroofsed seened domineerisid troopilistes metsades ning nende liigirikkus oli seal suurim, võrreldes kuivade kõrbealadega, kus mitmekesisus oli minimaalne. Ektomükoriissed seened olid enam levinud savannides ja troopilistes metsades, eriti niisketes Aafrika metsades, kus on palju peremeespuid. Seevastu arbuskulaarse mükoriisa seened esinesid rohkem kuivades troopilistes metsades ning olid arvukamad Lääne-Aafrika maastikes, eriti metsa-savanni ökotoonides. Parasiit- ja patogeensed seened olid märkimisväärselt arvukamad savannipiirkondades.

Lisaks avastasin, et kliimamuutmujad – eriti keskmine aastane temperatuur (MAT) ja keskmine aastane sademete hulk (MAP) – samuti mulla pH olid peamised tegurid, mis kujundasid uuritud maastike seente koosluse struktuuri. Koostöös uurimisrühmaga lõime kõrge eraldusvõimega kaardi, mis illustreerib seente ja mükoriissete seente mitmekesisust kogu Aafrikas. See kaart on oluline referentsvahend poliitikakujundajatele ja teadlastele, näidates selgelt seente bioloogilise mitmekesisuse mustreid, keskkonnategurite mõju ning madala (kõrbed) ja kõrge (tulipunktid Lääne-Ida-Aafrika savannivööndis ning Kesk- ja Lõuna-Aafrikas) seente mitmekesisusega piirkondi. Doktoritöös kasutasin eDNA metatriipkoodistamist, et põhjalikult uurida seente kooslusi ja bioloogilist mitmekesisust mullas erinevates Aafrika paikades. Seejuures püüdsin selgitada, kuidas maakasutus, ruumiline muutlikkus, kliimatingimused ja mullategurid mõjutavad seente koosluste dünaamikat ja liigirikkust.

Keskendusin ka kakao agrometsamajandussüsteemidele kahes Lääne-Aafrika riigis, analüüsides muldade domineerivaid seenerühmi ning uurides tegureid, mis mõjutavad nende levikut ja arvukust. Riigiti esines seente mitmekesisuse näitajates märgatavaid erinevusi. Kuigi farmide vanus mõjutas seente suhtelist arvukust, ei olnud see statistiliselt oluline. Seevastu kliimaparameetrid ja mullategurid mõjutasid seente mitmekesisust.

Täiendavas uuringus viisime läbi molekulaarse hinnangu puuliigiga *Alnus glutinosa* seotud ektomükoriissete seente koosluste kohta. Tuvastasime, et ligikaudu 93% täheldatud liikidest olid Alžeerias unikaalsed. Proovialade mõju oli tugevam kui mullateguritel seenekoosluste kujundajana, mis erineb varasematest uuringutest leppadel

Kokkuvõttes rõhutab minu doktoritöö bioloogiliste, abiootiliste ja ruumiliste tegurite mitmekülgset rolli mulla seente koosluste kujundamisel. Erinevad seenerühmad, nagu ektomükoriissed ja saprotroofsed seened, on olulised ökosüsteemi tasakaalu ja toimimise säilitamisel. Tulemused rõhutavad tungivat vajadust kaitsta Aafrika mitmekesiseid muldi, et toetada bioloogilist mitmekesisust ja ökosüsteemi tervist, eriti keskkonnamuutuste jätkudes. Need leiud rõhutavad veelgi taimkatte ja taimede mitmekesisuse kriitilist mõju mükoriissete seente arvukusele ja mitmekesisusele Aafrika bioomides.

Doktoritöö rõhutab lõppkokkuvõttes bioloogiliste, abiootiliste ja ruumiliste tegurite keerukat koosmõju mulla seente kogukondade koostise ja mitmekesisuse kujundamisel. Erinevad seenerühmad, sealhulgas ektomükoriissed ja saprotroofsed seened, täidavad olulisi funktsioone ökosüsteemi tasakaalu säilitamisel ja energiavoo tagamisel. Meie uurimustöö rõhutab tungivat vajadust seada prioriteediks Aafrika mitmekesiste muldade kaitse, mis on eluliselt oluline bioloogilise mitmekesisuse toetamiseks ja ökosüsteemide tervise tagamiseks, eriti kliimamuutuste ja maakasutuse muutuste valguses. Tulemused rõhutavad ka taimkatte ja taimede mitmekesisuse kriitilist mõju mükoriisa assotsiatsioonide arvukusele ja mitmekesisusele Aafrika bioomides. Neid keerukaid suhteid mõistes oleme paremini valmistunud strateegiate väljatöötamiseks, mis edendavad ökosüsteemi vastupidavust ja jätkusuutlikkust kasvava inimmõju tingimustes.

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