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Structure, dynamics, and ecological functions of rhizosphere fungal communities associated with maize (*Zea mays* L.) across contrasting rainfed agroecosystems.

Adrien Byamungu Ndeko[1,2,3*], Abdala Gamby Diedhiou[2,3], Papa Mamadou Sitor Ndour[4,5], Saliou Fall[3,5,6], Geant Basimine Chuma[1], Yannick Mugumaarhahama[7], Gustave Nachigera Mushagalusa[1], Aboubacry Kane[2,3]

1. Department of Crop Production, Faculty of Agriculture and Environmental Sciences, Université Evangélique en Afrique (UEA), P.O. Box 3323, Bukavu, Democratic Republic of the Congo (DRC),
2. Département de Biologie Végétale, Université Cheikh Anta Diop of Dakar, P.O. Box 5005, Dakar, Sénégal ;
3. Laboratoire Commun de Microbiologie (LCM: IRD-ISRA-UCAD), P.O. Box 1386, Bel-Air, Dakar, Sénégal
4. Unité de Chimie Environnementale et Interactions sur le Vivant (UCEIV), Université du Littoral Côte d'Opale, UR 4492, 50 Rue Ferdinand Buisson, 62228 Calais cedex, France
5. LMI IESOL, LAPSE, Centre de Recherche, ISRA-IRD de Bel Air, Dakar, Sénégal
6. Institut Sénégalais de Recherches Agricoles, Laboratoire National de Recherches sur les Productions Végétales (ISRA/LNRPV), Dakar, Sénégal
7. Statistics and Biometry Unit, Faculty of Agriculture and Environmental Sciences, Université Evangélique en Afrique (UEA), P.O. Box 3323, Bukavu, Democratic Republic of the Congo (DRC)

***Corresponding author:** ndeko.byam@gmail.com , ndekobyamungu@uea.ac.cd

Abstract

Rhizosphere fungi play a critical role in maintaining soil health and enhancing crop productivity. However, knowledge of their diversity and population structure in maize fields across contrasting territories or agroecological zones (AEZs) remains limited, especially in Africa. This study aimed to characterize the diversity, composition, and distribution of fungal communities in the maize rhizosphere across three territories belonging three territories located in two distinct AEZs in South Kivu (Democratic Republic of the Congo). Maize Rhizosphere soils were collected from 19 sites across the territories (Kabare, Walungu and Uvira) and their associated fungal community was analysed by ITS sequencing using the Illumina MiSeq platform. Fungal richness varied significantly across territories and AEZs (lowland vs highland), with higher richness observed in Walungu (highland-). Fungal communities were dominated by Basidiomycota, accounting for 70.2% of the total relative abundance, followed by Ascomycota (13.4%), and Glomeromycota (7.25%). Together, they represented 90.85% of ASVs, although their distribution varied significantly among territories. Basidiomycota was relatively more abundant in Kabare and Walungu (highland), whereas Ascomycota and Glomeromycota were relatively more abundant in Uvira (lowland). Functional guild analysis indicated a predominance of putative saprotrophs, followed by putative symbiotrophs (including AMF and endophytes) and a smaller proportion of putative pathotrophs, with several guilds showing site-specific patterns. NMDS and RDA analyses showed that edaphic and microclimatic gradients strongly influenced fungal community structure. In Uvira, fungal abundance was positively associated with temperature, wind speed, soil organic matter, phosphorus, and CTI (*Compound Topographic Index*), but negatively correlated with slope and soil nitrogen. In Kabare, cation exchange capacity, potassium, soil moisture, and bulk density were the main drivers of fungal abundance. In Walungu, sodium content and landscape curvature positively shaped fungal communities, whereas soil organic matter negatively affected several taxa. Overall, these findings provide valuable insights into the environmental drivers of fungal communities in maize rhizospheres and may support future strategies to harness beneficial fungi for disease management and biofertilization in South Kivu.

Key words: Fungal communities, *Zea mays L*, Rhizosphere microbiome, Next-generation sequencing, Climate characteristics, Soil properties.

Introduction

The rhizosphere hosts a complex microbial community critical for plant health and crop productivity. In this zone, interactions between plants and microorganisms are particularly intense, leading to the proliferation of many microorganisms due to the organic compounds released by the plant [15]. In agroecosystems, rhizosphere microorganisms play pivotal roles in various ecological functions, ensuring the maintenance of soil fertility and sustainable productivity [20]. Specifically, fungi, as key components of the rhizosphere microbiome, are involved in nutrient cycling, organic matter decomposition, disease suppression, and plant growth promotion [30]. Among the rhizosphere fungal communities, there are beneficial fungi including mycorrhizal fungi and the fungi used as biocontrol agents that contribute both to plant productivity. Conversely, other groups of rhizosphere fungi are known to negatively impact crop productivity by infecting roots and causing various plant diseases [2]. Therefore, understanding the composition of the fungal community in the rhizosphere is necessary to identify major groups of beneficial fungi involved in promoting plant growth (biostimulants) and protecting against diseases (biocontrol agents), making them potential candidates for use as biofertilizers [19].

Furthermore, it has been demonstrated that the diversity and composition of rhizosphere fungal communities can be highly variable from one region to another and are influenced by the plant host, the growth stage, as well as by environmental factors such as climate and soil properties [61]. Several studies have shown that the quality and quantity of root exudates released into the rhizosphere significantly influence the diversity and composition of soil fungal populations [17, 51]. Indeed, plants can release carbohydrates, amino acids, lipids, and vitamins through their roots to stimulate microbial activity, and particularly fungal activity, in the soil [15]. Similarly, Ren et al. [44] showed that soil properties, such as soil mineral content, significantly influence the composition of rhizosphere fungi. Furthermore, Jerbi et al. [22] showed that high concentrations of phosphorus (P) and low soil pH reduce the diversity of arbuscular mycorrhizal fungi (AMF) and mycorrhizal symbiosis in three cereals (*Avena sativa* L., *Hordeum vulgare* L., and *Triticum turgidum* L.). The influence of climate on the distribution and composition of rhizosphere fungal communities has also been elucidated by several researchers, indicating that temperature, rainfall, altitude, and latitude are among the main predictors of soil fungal diversity [54, 13, 35, and 39].

Maize is one of the most important cereal crops in sub-Saharan Africa [58], and particularly in the Democratic Republic of the Congo (DRC), where it ranks second after cassava in terms of

cultivated area [8]. The province of South Kivu is among the major maize production areas, with most production occurring in the territories of Kabare, Walungu, and Uvira. However, maize production remains low in these territories, with a downward trend since the 2019 agricultural season [8]. The poor soil quality coupled with severe degradation [21] and the emergence of fungal maize diseases partly such as Soft rot (*Rhizopus stolonifer*), Blue mold (*Penicillium variabile*), and Ear rot (*Fusarium verticillioides*), explain the decline of maize production in South Kivu [25]. On the other hand, it has been elucidated that soil microorganisms, such as rhizosphere fungi, play a crucial role in improving soil fertility and protecting crops against pathogens [33, 49]. Specifically, maize develops close interactions with beneficial fungi living in its rhizosphere through its high exudation capacity [5]. These beneficial rhizosphere fungi contribute to the health and productivity of maize [38]. Conversely, soil-borne fungi can colonize the rhizosphere, causing diseases in maize [25].

It is therefore imperative to explore and understand the dynamic of fungal populations in the maize rhizosphere to select those that can reduce pathogen pressure and promote the growth and productivity of maize in South Kivu [33]. To our knowledge, no study has yet been conducted to investigate the diversity of fungal communities, with a particular focus on pathogenic and beneficial communities in the maize rhizosphere in South Kivu. Therefore, this study aims to i) assess the fungal diversity and composition in the maize rhizosphere across local farming systems in maize production areas in South Kivu and ii) determine the influence of environmental factors on fungal diversity in the maize rhizosphere across territories and agroecological zones (AEZs). The current study used metabarcoding of fungal ITS region to analyse fungal community in the rhizosphere of maize cultivated in three distinct maize-producing territories in eastern Democratic Republic of Congo.

Materials and Method

Site description and soil sampling

This study was conducted in South Kivu province, in the eastern part of the Democratic Republic of Congo (DRC). Three territories from two distinct agroecological zones (lowland and highland) were chosen based on their suitability for maize cultivation and geographical location (Figure 1). These territories include Kabare and Walungu in highland, and Uvira in lowland. Uvira is located between 29 and 29°30′ E (longitude), and 3°20′ and 4°20′ S (latitude), characterized by a low altitude (600-900 meters above the sea level) and a tropical W4 climate according to the Köppen-Geiger classification, and exhibiting lower annual rainfall (900-1000 mm), compared to Kabare and Walungu. The annual average temperature is notably higher in

Uvira (30.5 to 32.5°C) compared to Kabare and Walungu (19.67 and 18°C, respectively). Predominant soil types in Uvira are humic ferralsols, haplic acrisols, and luvic phaeozems. Kabare features a humid tropical AW3 climate, with high rainfall (1601±150 mm on average), mountainous topography, and soil typology dominated by ferralsols, cambisols, nitisols, and acrisols [9, 38]. Walungu is located between 28˚24.6' and 28˚45.5' East longitude and 2˚41.5' and 3˚ South latitude, with altitudes ranging from 900 meters to 3000 meters above sea level. This region receives an average annual rainfall of 1,600 mm, with the annual average temperature reaching 25˚C. The soil in Walungu consists mainly of ferralsols and nitisols, which are predominantly acidic, rich in kaolinite, and have low fertility [43]. In all three territories, the bimodal rainfall pattern determines two cropping seasons: the rainy season (from September to June) and the dry season (from July to August).

Soil samples were collected from maize fields located in the three territories (Kabare, Walungu and Uvira) across the two contrasted agroecological zones (low and high altitude) of South Kivu. Specifically, rhizosphere soil was collected from continuous maize cultivation fields in two consecutive cropping seasons. Thirty two sites were considered. 13 in Kabare, 11 in Uvira, and 8 in Walungu. Nine maize fields distributed across different locations within each site along a transect were sampled, and the samples were mixed to constitute three composite samples per site. The rhizosphere soil of maize was collected at a depth of 0 to 20 cm. Thus, rhizosphere soil from 1440 maize plants (9 fields x 5 plants per field x 32 sites) was collected across the 32 sites. The samples intended for DNA extraction were stored in the laboratory at -20°C until utilization, whereas the samples designated for physicochemical soil analysis were dried and maintained at ambient temperature. Information related to past land use and management at the different sites was also considered. This includes the cultivation system, the variety used in the field, the topography and soil cover.

Prior to the implementation of the study, informed consent was obtained from all participating farmers. The farmers voluntarily agreed to participate in the study and granted access to their fields for soil and plant sampling after being clearly informed about the objectives of the research and the nature of the activities to be carried out. No personal or sensitive data were collected.

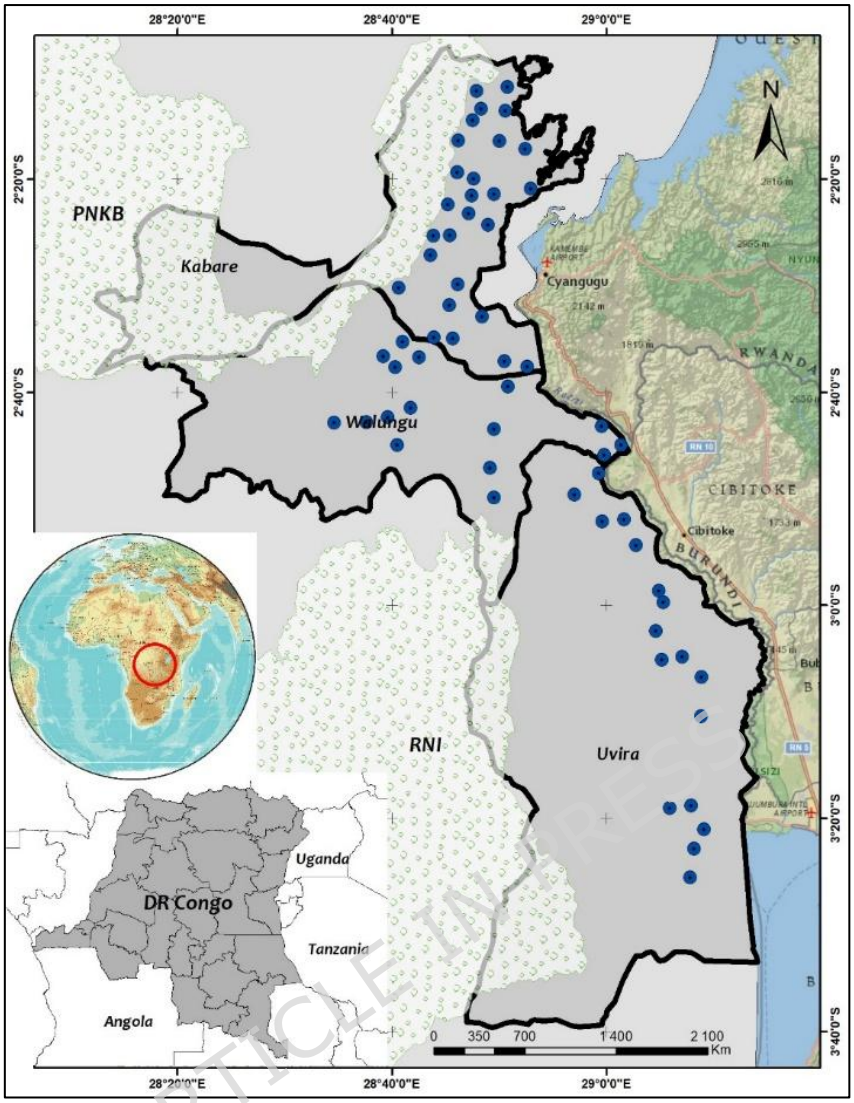

Figure 1. Map of the South Kivu Province showing the distribution of maize rhizosphere soil sample collection points in agricultural fields in the East of the DRC. *The map was generated using ArcGIS Pro version 3.3 (Esri, Redlands, CA, USA; https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview).*

Soil physicochemical analysis

Prior to analysis, soil samples were air-dried and passed through a 2-mm sieve. Soil pH was determined in a 1:1 soil-to-water suspension following standard procedures [38]. Total nitrogen was quantified using the Kjeldahl digestion method with sulfuric acid and selenium, followed by ammonia distillation and titration. Soil organic carbon was determined using the Walkley-Black method, and soil organic matter was estimated as organic carbon × 1.725 [29]. Exchangeable cations were extracted with ammonium acetate and quantified using flame photometry and spectrophotometry [23]. Available phosphorus was measured using the Olsen method based on sodium bicarbonate extraction and molybdenum blue colorimetric detection

[41]. In addition to the laboratory analyses, selected soil properties were retrieved from the ISRIC database (https://www.isric.org/), including bulk density (t m^{-3}), clay, silt and sand contents, cation exchange capacity (CEC), and soil water retention at field capacity.

Total DNA extraction from rhizosphere soil, PCR amplification and sequencing

DNA extraction was performed using 1g of soil with the FastDNA Spin Kit for soil (MP Biomedicals, Cleveland, USA) following the manufacturer's instructions. The quality and concentration of DNA were assessed using the Nanodrop ND-2000 UV–VIS spectrophotometer (NanoDrop Technologies, Wilmington), and DNA samples were stored at -20°C before sequencing. Macrogen Europe Company (Seoul, South Korea) conducted DNA amplification and rDNA sequencing. After DNA extraction, only 19 out of the 32 sampled sites yielded sufficient DNA quantities for successful PCR amplification, even after three repeated extraction attempts. The remaining samples were distributed as follows: 7 in Kabare, 7 in Uvira, and 5 in Walungu. Consequently, all subsequent analyses were conducted using only these 19 samples. The internal transcribed spacers (ITS region including the 5.8S), was amplified with illumina Miseq using ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS4 (TCCTCCGCTTATTGATATGC) primers under the conditions described by Banerjee et al (2024). The reactions were conducted in a final volume of 20 µl, comprising 2 µl of 10× PCR buffer (10 mM Tris–HCl, pH 9.5, 50 mM KCl, 1.5 mM MgCl2, 0.1 % Triton X-100, 0.2 mg/ml bovine serum albumin) (Q-BIOgene, France), 200 mM of dNTPs, 500 nM of each primer, 0.8 U of Taq DNA polymerase (Q-BIOgene), and 5 µl of genomic DNA. Each reaction was carried out in a thermocycler (T3000 thermocycler; Biometra, Germany). Equivalent PCR products from each sample were then delivered to the Illumina MiSeq sequencing platform at Macrogen-Europe (Seoul, South Korea). The sequences generated during sequencing were deposited at the National Center for Biotechnology Information (NCBI) through the Sequence Read Archive (SRA) submission platform, under the BioProject accession number PRJNA1406538 (https://www.ncbi.nlm.nih.gov/sra/?term=PRJNA1406538).

Bioinformatic and statistical analyses, and ecological characterization of fungal communities in maize rhizosphere

For the processing of obtained sequences, we employed Quantitative Insights Into Microbial Ecology (QIIME2, Version 2023.2) [6]. First, the raw FASTQ files from sequencing were demultiplexed using the DADA2 package implemented in QIIME2 and subjected to quality filtering (Version 1.9.0). Raw sequences count varied between 52,945 to 17,5641 per sample.

Forward and reverse sequences with a quality score >25 were paired based on a 20-base pairs overlap. Sequences derived from chloroplasts, mitochondria and singletons were then filtered out. Final ASV count varied between 30 to 7,234 sequences per sample. The final representative sequences (ASV) were compared to those in the UNITE Version 9 database (Abarenkov et al., 2010) [1]. The table of Amplicon Sequence Variants (ASVs) was generated and utilized for (i) calculating alpha diversity indices (Shannon index, number of ASVs) and (ii) computing betadiversity using Principal Coordinates Analysis (PCoA) based on the Bray-Curtis dissimilarity matrix. After taxonomic classification, all taxa were assigned to their putative ecological functions using the FUNGuild tool database (www.stbates.org/funguild_db.php), as described by [47].

Taxonomic composition of fungal communities was investigated across agroecological zones and agricultural practices using relative abundances of various taxonomic classes. Relative abundance of fungi at the phylum and genus levels were visualized using bar plots to compare the fungal taxonomic composition in the maize rhizosphere across sites. PCA was used to characterize study sites based on environmental variables and relate them to fungal species abundance, following Bartlett's sphericity test and KMO adequacy assessment. Input variables are described in **SMTable 1**. Finally, the relationship between taxonomic composition and environmental parameters was visualized using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances and RDA analysis, using the vegan package [64]. The Variance Inflation Factor (VIF) was applied to reduce multicollinearity, and only variables with VIF values < 10 were retained for the final redundancy analysis (RDA). The environmental parameters considered in this study are those mentioned by [40].

Statistical analyses were performed using R (version 4.3.0). Apha diversity metrics were subjected to ANOVA to assess the effect of different factors (agroecological zone and territories). Post-hoc Tukey pairwise comparison tests ($p < 0.05$) were performed to identify significant differences between treatments. To examine the impact of different soil land on microbial community structure, permutational analysis of variance (PERMANOVA) were employed using the *vegan* R package.

Results

Fungal richness and diversity

The results reveal differences in alpha diversity across territories and agroecological zones (Figure 2 A, B, C and D). The specific richness (Chao1) ranges from 6 to 35 and the diversity (Shannon-Weaver diversity index) from 0.2 to 2, across territories (**Figure 2A**). The one-way

ANOVA results show a significant variation in the Chao1 index according to the territories (p = 0.001) and agroecological zones (p = 0.045). The fungal richness was higher in the Walungu territory (27.75 ± 10.1) than in the Kabare and Uvira territories (12.13 ± 7.84 and 7.85 ± 2.9, respectively). Moreover, by grouping samples according to their agroecological zone (lowland vs highland), we found a greater fungal richness in high altitude (17.3 ± 11.2) compared to low altitude (7.8 ± 2.9) (**Figure 2B)**.

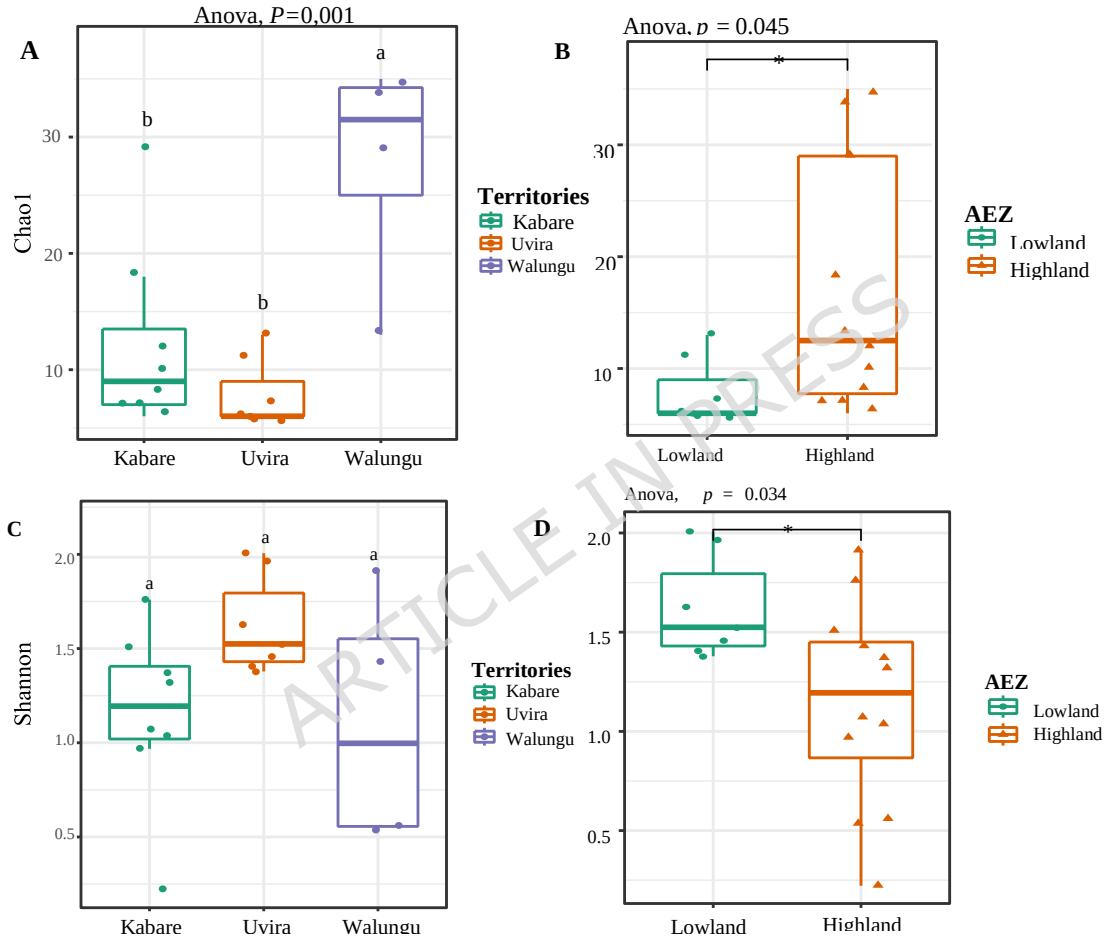

Figure 2. Alpha diversity (Chao1 index and Shannon-Weaver index) of the fungal community in the maize rhizosphere according to territories. Chao1 richness index (A), Shannon diversity index (B), Simpson diversity index (C) and Pielou's diversity index (D). A significance level * (P < 0.05) indicates a statistically significant difference. Boxplots labeled with different letters represent significantly different values

The one-way analysis of variance (ANOVA) conducted on the Shannon-Weaver diversity index with respect to territories showed non-significant difference between territories (p = 0.11). However, the results revealed a significant variation according to agroecological zones (p =

0.034). Indeed, higher Shannon diversity was observed at low altitude (1.62 ± 0.26), as compared to at high altitude (1.14 ± 0.51).

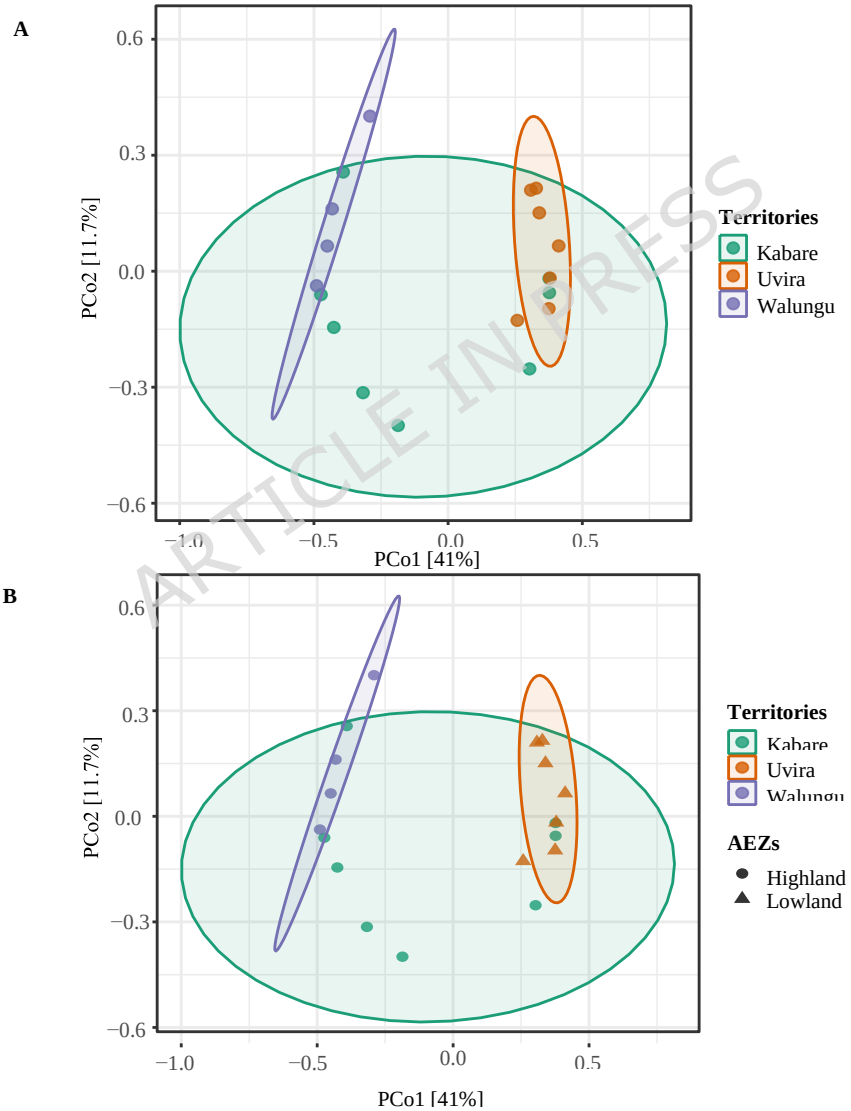

Figure 3. Beta diversity of the fungal community based on Principal coordinates analysis of fungal communities in the rhizospheric soil of maize collected from continuous maize cultivation fields in South Kivu. AEZs "agroecological zones".

The Figure 3 presents the beta diversity of fungal communities assessed by the Principal Coordinates Analysis (PCoA) based on Bray-Curtis distance. The plot showed structuration of fungal community according to territories and AEZ. The results show that samples from Uvira differ significantly from those of Walungu as clearly separated along the first axe of the PCoA (PERMANOVA, R^2= 0.31, F=3.75, *p*=0.003). Even not clearly clustered or separated with samples of the two other territories, the samples from Kabare, exhibited more similar diversity patterns with those of Walungu to which 5 points out of the 8 are very close (**Figure 3**). Therefore, samples from the high-altitude zone (Kabare and Walungu) were separated from those from the low-altitude zone (Uvira) and then exhibited different beta-diversity.

The composition of fungal communities in rhizosphere soils was analyzed to characterize the fungal population groups associated with maize roots, with particular emphasis on confirming the presence of arbuscular mycorrhizal fungi (AMF) and quantifying their relative abundance within the overall fungal communities. **Figure 4** illustrates the relative abundance of different fungal phyla detected in the maize rhizosphere. The fungal community in the maize rhizosphere soil was predominantly composed of five identified phyla: Basidiomycota, Ascomycota, Glomeromycota, Rozellomycota, and Olpidiomycota. However, a substantial proportion of ASVs belonged to unclassified phyla that were not identified using the available reference database. Among the identified phyla, Basidiomycota was the most dominant (70.2% of the total ASVs), followed by Ascomycota (13.4%), and Glomeromycota (7.25%), together they accounted for 90.85% of the total ASVs (**Figure 4**).

Fungal community composition in the maize rhizosphere

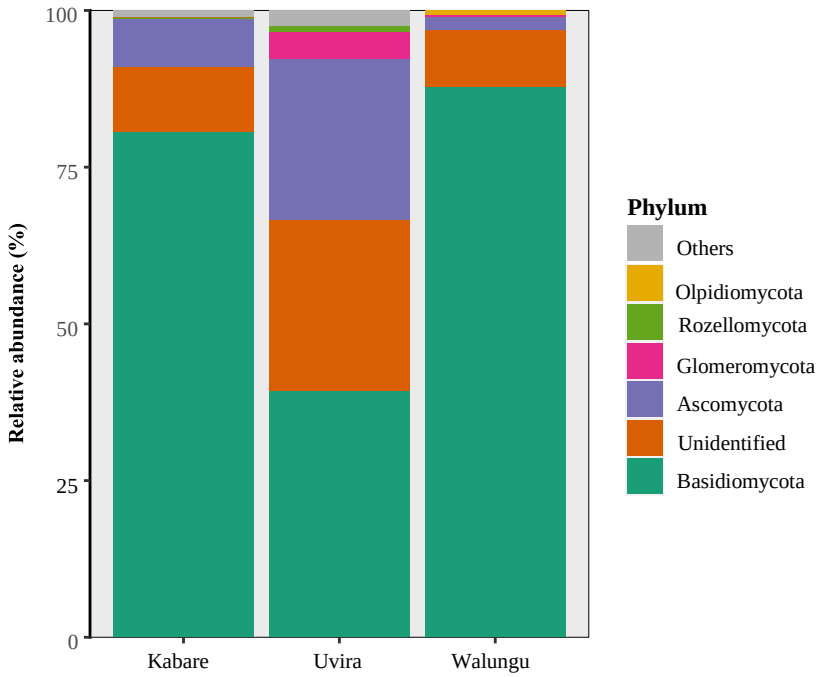

Figure 4. Relative abundance at the phylum level of the fungal community in the maize rhizosphere soil across territories (Kabare, Walungu, and Uvira). "Unidentified" represents the sum of genera with incomplete taxonomy in the database. "Others" represents the sum of phyla with a relative abundance of less than 2%.

The distribution of fungal phyla across territories reveals that soil samples from Walungu and Kabare contained all five identified phyla, whereas samples from Uvira comprised only four: Basidiomycota, Ascomycota, Rozellomycota, and Glomeromycota. Basidiomycota was the dominant phylum in Kabare and Walungu, accounting for 91% and 90.43% of the ASVs, respectively, while its relative abundance was markedly lower in Uvira (28%). In contrast, Ascomycota was more abundant in Uvira, with a relative abundance of 33.04%. Regarding the phylum Glomeromycota, it was detected in all three territories, with varying relative abundances. Its highest relative abundance was recorded in Uvira (20%), while the lowest was observed in Kabare (0.07%). In Walungu, it accounted for 1% of the fungal community. At order taxonomic level (**SM Figure 1**), arbuscular mycorrhizal fungi (AMF) were represented by five orders: Archaeosporales, Diversisporales, Gigasporales, Glomerales, and Paraglomerales.

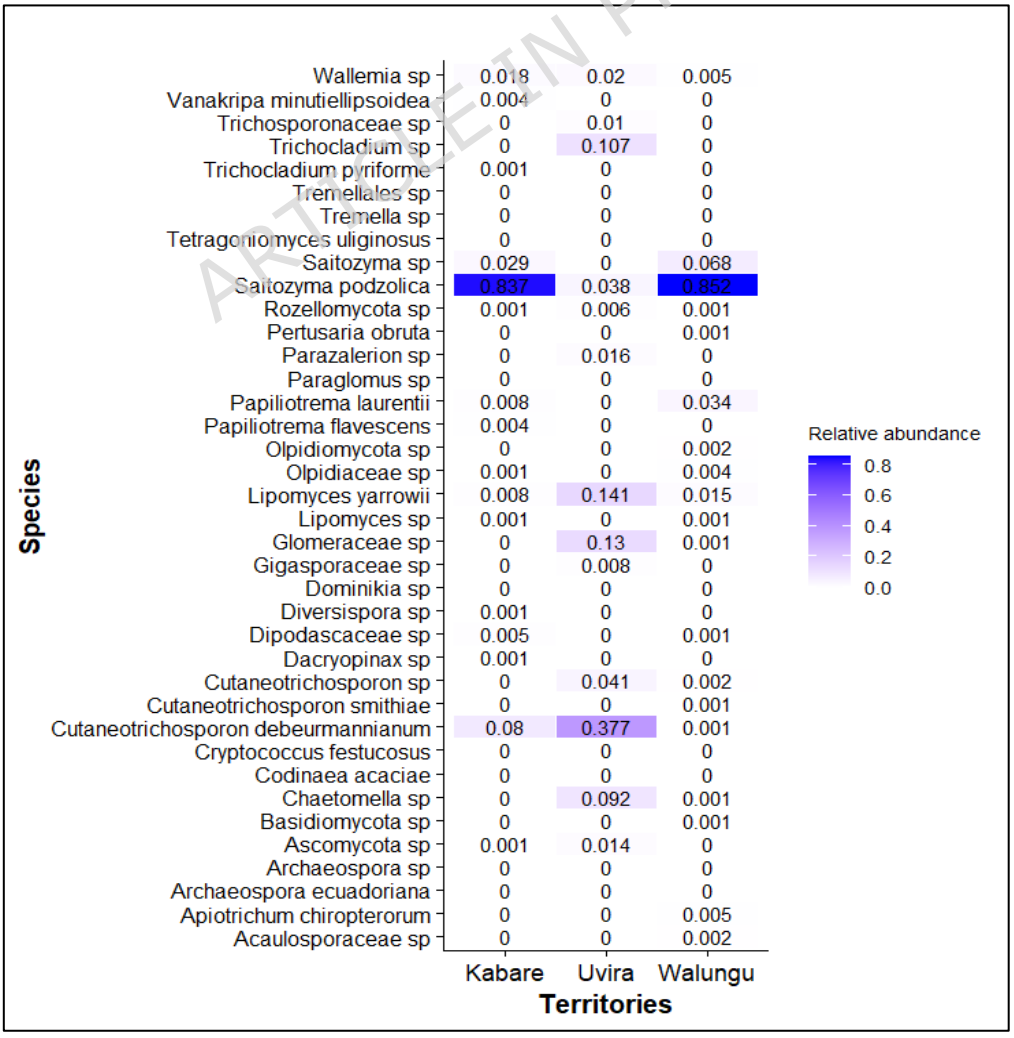

Figure 5. Heatmap illustrating the relative abundance of fungal species identified in the maize rhizosphere across the different territories (Kabare, Uvira, Walungu).

At the family level, the analysis of fungal population composition revealed the presence of 27 families distributed across the five previously mentioned phyla (**SM Table 2**). Two families, Trimorphomycetaceae and Trichosporonaceae, belonging to the phylum Basidiomycota, are the most represented, with relative abundances of 42.16% and 21.27%, respectively. However, their relative abundance varies according to the territories. The family Trimorphomycetaceae is more abundant in Walungu and Kabare (81.89% and 56.12%, respectively) and less abundant in Uvira (3.5%). Conversely, the family Trichosporonaceae which is abundant in Uvira (35.22%) declined in Kabare (19.5%) and particularly in Walungu (0.44%). In addition, the family Lipomycetaceae shows a relatively higher abundance in Uvira (9.42%) compared to Kabare (3.86%) and Walungu (1.77%). Other identified families exhibited low relative abundances, and the sum of their relative abundance is below 5%.

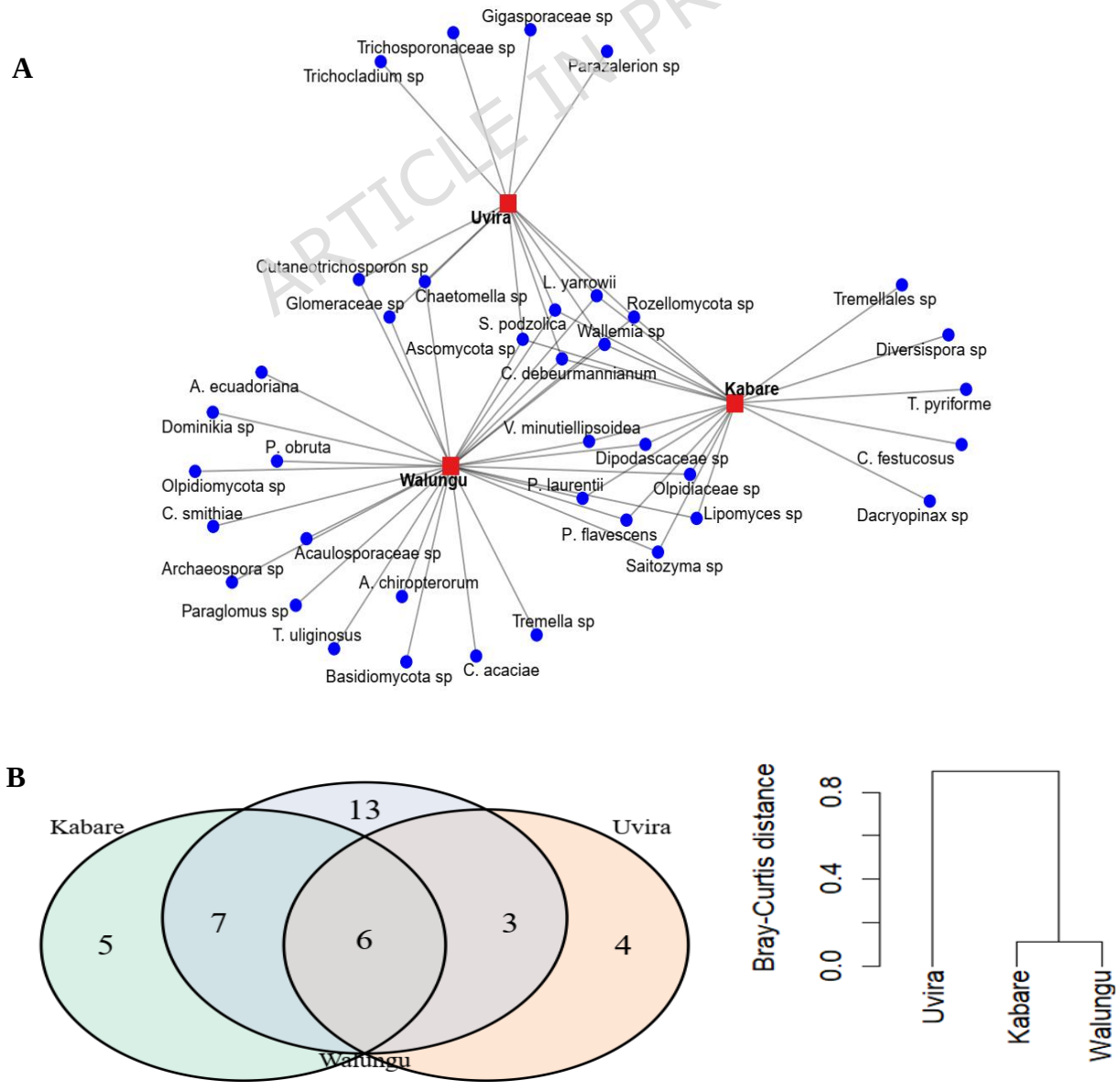

Figure 6. Distribution and association network of fungal species (A) and Venn diagram showing the number of species across different territories (B).

Six families of arbuscular mycorrhizal fungi were distinguished in the study, including Acaulosporaceae, Archaeosporaceae, Diversisporaceae, Gigasporaceae, Glomeraceae, and Paraglomeraceae. However, their relative abundance remains modest compared to that of non-AM fungal sequences. The analysis of the distribution of AMF families according to territories shows that among the six identified AMF families, three (Acaulosporaceae, Archaeosporaceae, and Paraglomeraceae) were found more abundant in Walungu than in other territories. Two families were found exclusively in Kabare (Diversisporaceae) and in Uvira (Gigasporaceae). The remaining family, Glomeraceae, was found in both Uvira and Walungu, with a higher relative abundance in Uvira (3.43%) compared to Walungu (0.13%). At the species level, the analyses did not allow identification of all species present in the maize rhizosphere (**Figure 5**). The majority of taxa were only identified at the genus level. Eighteen species were observed in Kabare, twenty-nine in Walungu (high altitude), and thirteen in Uvira (low altitude). The distribution network of fungal species is presented in Figures 6A and 6B. The results indicate the presence of species shared among the different territories, as well as species that are specific to each site (**Figure 6B and SM Figure 2**).

Functional diversity of fungal communities in the maize rhizosphere

The **Table 1** presents the fungal genera identified in the maize rhizosphere according to their frequency of occurrence, putative trophic mode, ecological guild, and ecological roles. Several putative symbiotrophic genera are recorded, mainly associated with arbuscular mycorrhizal fungi (AMF), such as Acaulospora (4.29%), Archaeospora (2.86%), Diversispora, Dominikia, Gigasporale, Glomerale (4.29%), and Paraglomus. These genera belong to the guild of fungi forming symbiotic associations with plant roots. Putative saprotrophs are also well represented. Notable genera include Saitozyma (14.29%), Lipomyces (10.00%), Cutaneotrichosporon (7.14%), Trichocladium (4.29%), Wallemia (4.29%), as well as Papiliotrema and Parazalerion. These genera are associated with the decomposition of organic matter, wood, or plant litter.

Putative pathotrophs include Chaetomella, Olpidiaceae, and Rozellomycota, were identified. While Cryptococcus and Tremella are identified as putative opportunistic yeasts. Some are

classified as plant pathogens, others as mycoparasites or parasites of various organisms. Their individual occurrence ranges from 1.43% to 4.29%. Some unassigned or poorly known genera, such as Fungi (7.14%), GS18 (2.86%), and Vanakripa (1.43%), whose ecological roles are not clearly defined at this stage were also reported. Finally, some genera such as Pertusaria (2.86%) represent symbiotic lichens, while other genera such as Papiliotrema show mixed or ambiguous trophic modes (e.g., saprotrophic and symbiotrophic).

Table 1. Identified fungal genus with their putative trophic mode, guild and ecological role

Genus	Occurence	Trophic mode	Guild	Ecological roles
Acaulosporaceae	4.29%	Symbiotroph	Arbuscular Mycorrhizal Fungi	Establishing a symbiotic relationship with plant roots
Apiotrichum	1.43%	Saprotroph	Undefined saprotroph	Decomposition of organic debris in the soil
Archaeospora	2.86%	Symbiotroph	Arbuscular Mycorrhizal Fungi	Establishing a symbiotic relationship with plant roots
Chaetomella	1.43%	Pathotroph	Undefined plant pathogen	Often associated with plants as an opportunistic pathogen
Codinaea	1.43%	Saprotroph	Wood Saprotroph	Decomposers of wood and lignous (woody) material
Cryptococcus	1.43%	Pathotroph	Animal Pathogen	Animal pathogen, sometimes opportunistic in humans
Cutaneotrichosporon	7.14%	Saprotroph/Pathotroph	Undefined saprotroph	Organic matter decomposer
Dacryopinax	1.43%	Saprotroph	Wood Saprotroph	Primarily decomposes dead wood
Dipodascaceae sp	2.86%	Saprotroph	Undefined saprotroph	Sometimes found in sugary substrates
Diversispora	1.43%	Symbiotroph	Arbuscular Mycorrhizal	Establishing a symbiotic relationship with plant roots
Dominikia	1.43%	Symbiotroph	Arbuscular Mycorrhizal Fungi	Establishing a symbiotic relationship with plant roots
Fungi	7.14%	Unassigned	Unassigned	Unclassified and poorly known fungal group
Gigasporaceae sp	1.43%	Symbiotroph	Arbuscular Mycorrhizal	Establishing a symbiotic relationship with plant roots
Glomeraceae	4.29%	Symbiotroph	Arbuscular mycorrhizal	Establishing a symbiotic relationship with plant roots
GS18	2.86%	Unassigned	Unassigned	Unclassified and poorly known fungal group
Lipomyces	10.00%	Saprotroph	Undefined Saprotroph	Organic matter decomposition
Olpidiaceae	4.29%	Pathotroph	Obligate Biotroph Parasite	Obligate parasites, pathogens of algae or plants
Papiliotrema	2.86%	Saprotroph/Symbiotroph	Endophyte/undefined saprotroph	Basidiomycete, sometimes endophytic or soil-associated
Paraglomus	1.43%	Symbiotroph	Arbuscular Mycorrhizal	Establishing a symbiotic relationship with plant roots
Parazalerion	2.86%	Saprotroph	Saprotroph wood decay fungi	Degrading lignin and cellulose in dead wood
Pertusaria	2.86%	Symbiotroph	Symbiotroph (lichenized fungus)	Lichens, symbiosis between fungi and algae
Rozellomycota	2.86%	parasites ou parasitoïdes	Pathotroph (parasite or pathogen)	Parasite of other microorganisms
Saitozyma	14.29%	Saprotroph	Saprotroph - Undefined saprotroph	In forest soils, involved in decomposition and soil health
Tetragoniomyces	1.43%	Saprotroph	Saprotroph - Undefined saprotroph	Organic matter decomposition
Tremella	4.29%	Pathotroph	Mycoparasite	Fungal parasite, organic matter decomposition, opportunistic
Trichocladium	4.29%	Saprotroph	Undefined Saprotroph	Decomposition of dead organic matter in the soil
Vanakripa	1.43%	Unassigned	Unassigned	Very poorly documented genus, recently discovered
Wallemia	4.29%	Saprotroph	Undefined saprotroph	In extreme environments, ecological role poorly understood

Correlation between fungal community composition and environmental factors

The PCA biplot (**Figure 7**) shows that the first two axes together explain 61.6% of the total variance. Dimension 1 accounts for 32.3% of the variance and primarily separates the sites according to soil physico-chemical properties such as pH, clay content, potassium, and cation exchange capacity. Dimension 2 explains 29.3% of the variance and highlights bioclimatic differences among the territories, including temperature, solar radiation, wind speed, and carbon and phosphorus contents. The three territories (Kabare, Uvira, and Walungu) are clearly distinguished on the biplot, each exhibiting a distinct environmental profile. The vector representing species abundance points toward Walungu, indicating that abundance is highest in this territory and is correlated with mineral-rich, alkaline soils. Overall, the PCA reveals a clear structuring of sites and demonstrates that the measured variables significantly explain the total variation among territories. Species abundance is statistically associated with the most fertile soils of Walungu, highlighting the relationships between environmental characteristics and species distribution

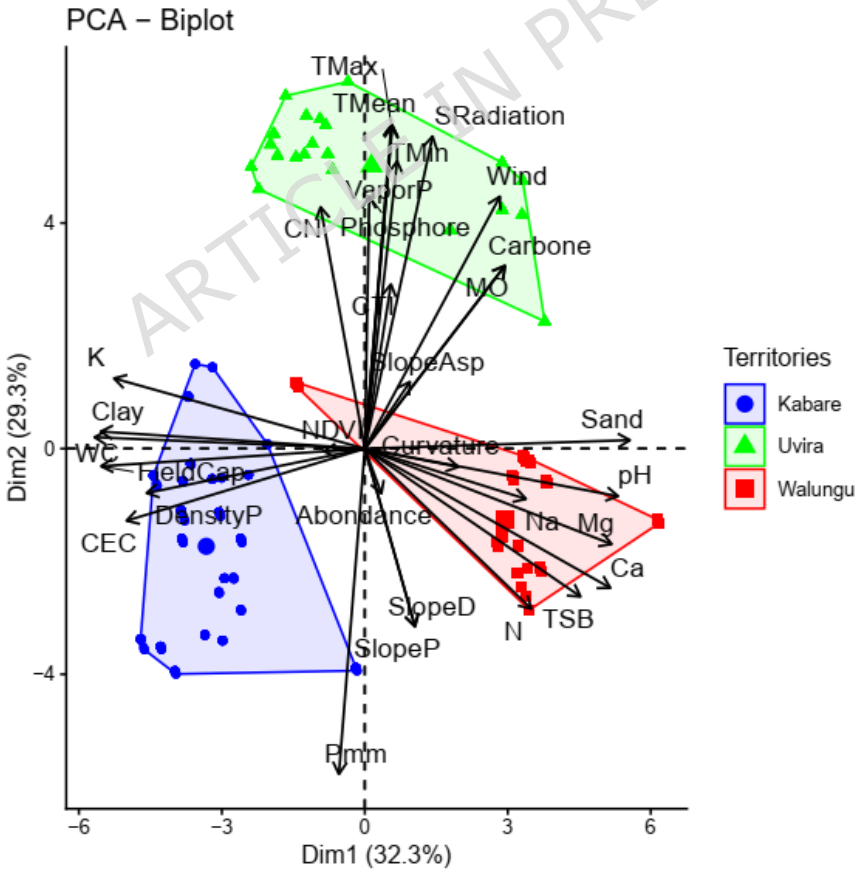

Figure **7.** Principal component analysis (PCA) of territories based on environmental characteristics and species abundance.

Correlation between species abundances and environment parameters is presented in **Figure 8**. and NMDS analysis was employed to depict species composition across the different study sites based on Bray-Curtis dissimilarities. The results indicated a stress value of 0.036, allowing a clear separation of the sites into distinct groups according to species distribution. Redundancy analysis (RDA) was performed to examine the relationships between species abundances and environmental parameters. Species distribution was observed to vary across trerritories (**Figure 9**). Species such as *Glomeraceae sp.*, *Dipodascaceae sp.*, *Schaetomella sp.*, *Trichocladium sp*., and *Gigasporaceae sp.* were more prevalent in the Walungu sites, whereas species including *Trichosporonaceae sp.*, *Parazelerion sp.*, *Cutaneotrichosporon sp.*, *Olpidiomycota sp*., and *Acaulosporaceae sp.* were more abundant in Kabare compared to the other sites. Finally, other identified species such as *Cryptococcus festucosus, Dacrypira sp., Trichocladium pyriforme, Lipomyces yarrowii, Lipomyces sp., Wallemia sp., Rozellomycota sp., Vanakripa munutilipsoidea, Papiliotrema flavescens, Papiliotrema laurentii, Tremella sp., Basidiomycota sp., Saitozyma sp., Saitozyma pdzo, Tetragoniomyces uliginosus, Diminikia sp., Acaulosporaceae sp*., and *Olpidiomycota sp*. were primarily distributed in Uvira, where species richness was higher.

The RDA plot highlights a clear differentiation of soil fungal communities according to the measured environmental gradients across the different study sites. The relative abundance of various identified fungal species displayed distinct patterns depending on the study site. The relative abundance of species such as *Glomeraceae sp*., *Trichocladium sp.*, and *Schaetomella sp*. was significantly and positively correlated with wind speed, temperature, and the CTI, and they were evenly distributed in Uvira. In the same area, the abundance of specific species such as *Parazalerion sp.*, *Trichosporonaceae sp*., and *Rozellomycota sp*. was positively and significantly influenced by soil organic matter and phosphorus content, and inversely correlated with slope and soil nitrogen content. In Kabare, the relative abundance of species such as *Dipodascaceae sp.* and *Gigasporaceae sp.* was significantly and positively correlated with cation exchange capacity, potassium content, soil water content (field capacity), and soil bulk density. In Walungu, the relative abundance of species such as *Papiliotrema laurentii, Saitozyma sp., Ascomycota sp., Cutaneotrichosporon sp.,* and *Lipomyces yarrowii* was positively correlated with sodium content and curvature, and inversely correlated with organic matter content. At the phylum level, RDA analysis showed that the relative abundance of Basidiomycota was significantly and positively correlated with slope and cation exchange capacity, whereas the relative abundance of Glomeromycota and Rozellomycota was

influenced by organic matter content, slope aspect, and the CTI index. Finally, trends indicate that the abundance of Olpidiomycota was more strongly correlated with soil nitrogen and sodium content.

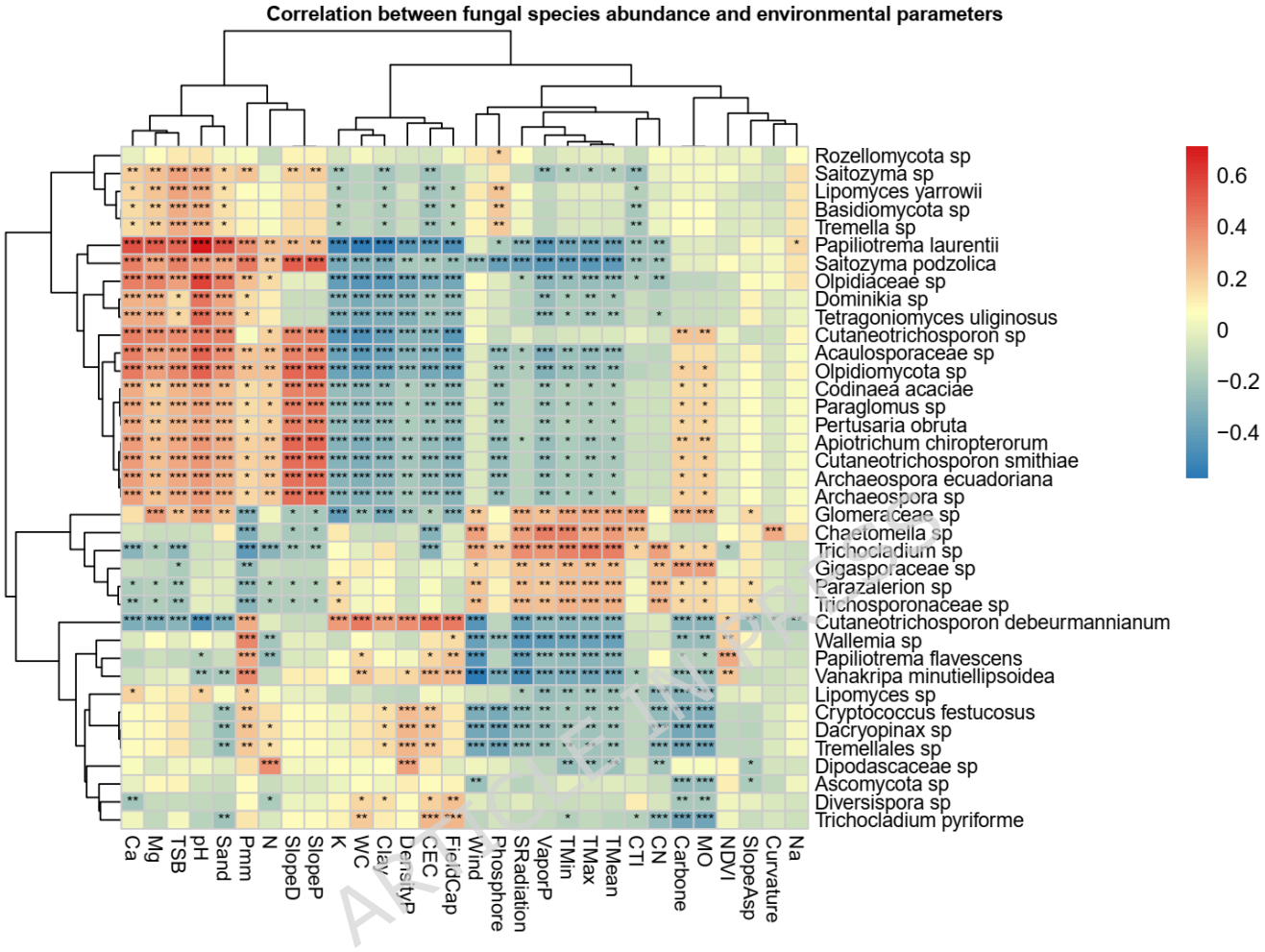

Figure 8. Heat map of the correlation between soil physicochemical properties and maize rhizosphere fungi.

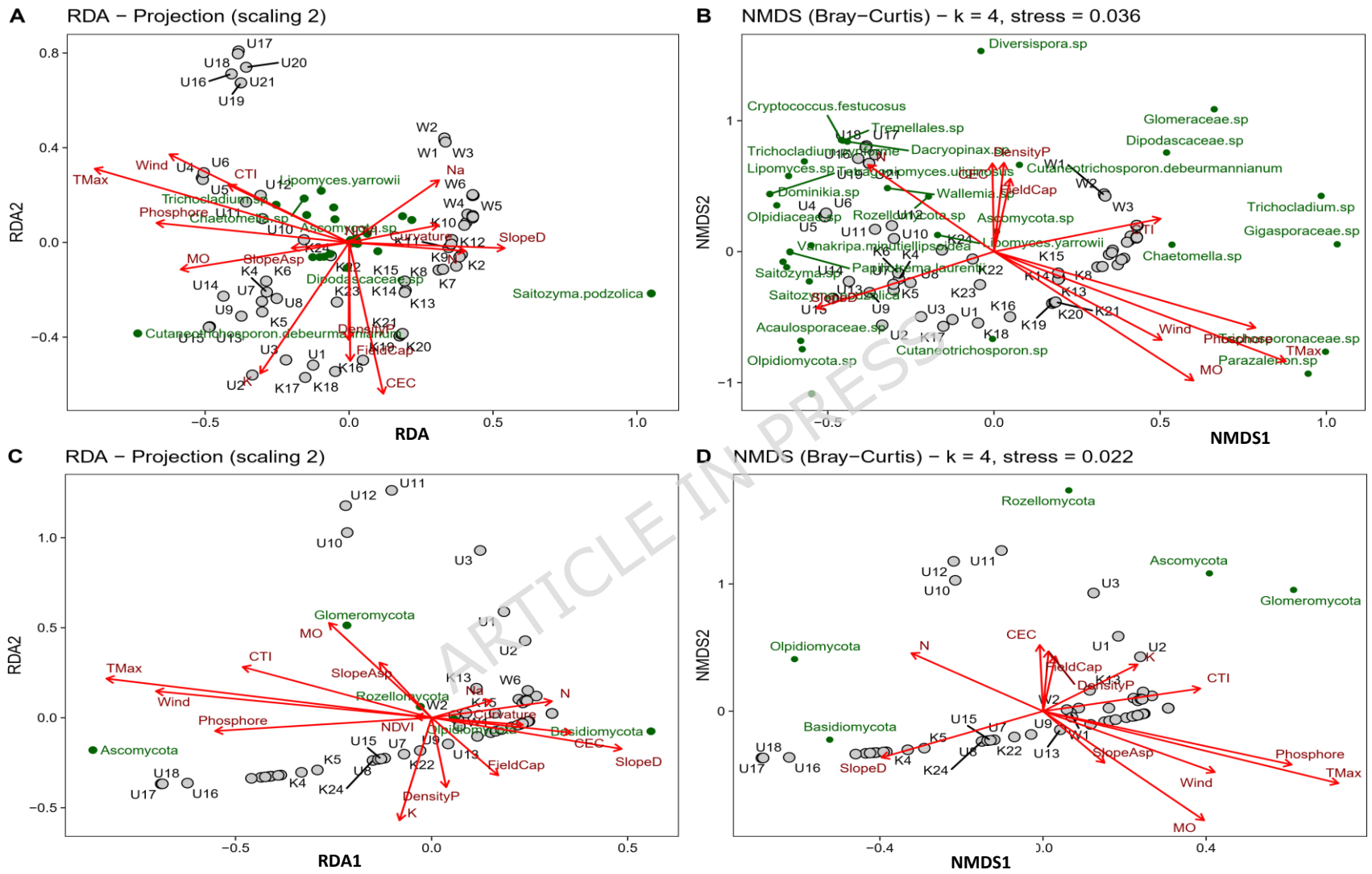

Figure 9. Redundancy analysis (RDA) of fungal community (A-C) and Non-metric multidimensional scaling (NMDS) ordinations of the taxonomy-based dissimilarities (B-D) in maize rhizosphere soil.

Discussion

Fungal community structure

Maize maintains a close interaction with soil microorganisms through its rhizosphere due to its high root exudation capacity [24]. This interaction can promote the development of a large number of microorganisms, whether beneficial to the plant or pathogenic. In this study, we used high-throughput sequencing (Illumina MiSeq) to characterize the fungal populations present in the maize rhizosphere, targeting the Internal Transcribed Spacer (ITS) region of the 18S, 5.8S, and 28S ribosomal RNA genes. This region is one of the best DNA barcodes for fungal species identification and has been successfully used in metagenomic studies [46].

The structure of fungal communities in the maize rhizosphere in South Kivu is characterized bya dominance of Basidiomycota and Ascomycota. Basidiomycota was the most abundant phylum (70.2% of total relative abundance), while Ascomycota showed a moderately high relative abundance (13.4%). They were followed by the phylum Glomeromycota (7.25%), whose contribution was low but not negligible. Glomeromycota were likely underestimated in this study, partly due to the limitations of the ITS primers, which do not cover the full diversity of arbuscular mycorrhizal fungi [50, 55], and because DNA isolated from soil, ungal spores and/or hyphae contains a significant number of amplification inhibitors [45, 16], which could reduce amplification efficiency. However, Mofini et al. [34] noted that Glomeromycota were less represented in the core mycobiome of cereals such as cultivated and wild pearl millet. Furthermore, we observed a large proportion of unclassified fungi in all samples. These findings are consistent with those of Gqozo et al. [19] and Kong et al. [24], who also reported high proportions of Ascomycota and Basidiomycota in the maize rhizosphere. However, unlike our results, their studies showed a predominance of Ascomycota over Basidiomycota. Basidiomycota were more abundant across all study sites compared to the other phyla. This wide distribution in South Kivu is likely associated with their strong adaptive capacity to diverse environments, combined with efficient spore-dispersal mechanisms and versatile nutritional strategies, as this group includes saprotrophs, symbiotrophs, and pathogens [28]. The dominance of Ascomycota at low altitude (Uvira) may be explained by their high tolerance and adaptive ability to arid and water-limited conditions [57].

The fungal distribution patterns observed in this study are typical of degraded tropical soils [59]. The low diversity detected can be attributed to continuous soil disturbance driven by intensive agricultural practices such as frequent tillage and limited crop rotation, as well as to the low soil organic matter content, particularly in the Walungu territory [27]. The territorial variation, characterized by higher fungal richness at high altitudes (Kabare, Walungu) and

lower richness at low altitude (Uvira), likely reflects local climatic and edaphic differences. High-altitude zones benefit from more moderate temperatures and higher relative humidity, conditions that favor the establishment of more diverse fungal communities [39, 40]. The clear separation of fungal communities between lowland and the highland sites, as revealed by the PCoA analysis, highlights the structuring role of local climate and soil characteristics in shaping microbial assemblages. This pattern is consistent with observations reported from other tropical systems [14, 35].

Based on the RDA results, we observed that the distribution of fungal populations is closely associated with environmental parameters. Wind speed, temperature, and the Compound Topographic Index (CTI) were the main drivers of species distribution in Uvira (low altitude), whereas CEC, potassium content (K), field capacity, and soil organic matter (OM) were the factors that favored species distribution in Kabare. In addition nitrogen content and topographic curvature contributed to improving fungal diversity. These parameters were important determinants of fungal diversity across the three study sites. In contrast, in Walungu, slope, soil nitrogen and phosphorus contents, as well as organic matter levels, negatively influenced fungal diversity, especially abundance of Ascomycota. Several studies have demonstrated that environmental factors strongly shape the structure of soil microbial communities [3, 11, 39, and 40]. In addition, it has been reported that the abundance of Ascomycota is mainly regulated by soil nitrogen content. Our findings showed that high N levels decreased Ascomycota abundance, which is consistent with the results of Paungfoo-Lonhienne et al. [42]. However, Zhang et al. [62] reported an increase in soil Ascomycota abundance under nitrogen application treatments.

Low-altitude conditions, characterized by higher temperatures, generally promote the development of fungal mycelia [23, 39, and 40]. Wind speed exerts an indirect effect on fungal abundance: an increase in wind speed induces water stress in maize by stimulating evapotranspiration [63], which often leads to an increase in root exudation [56, 36]. Enhanced exudation provides more carbon substrates and organic compounds, thereby promoting the development of soil fungal communities [17]. The positive effect of soil organic matter on fungal distribution is attributable to the fact that OM serves as a substrate for saprotrophic species, which are actively involved in its decomposition [52]. Soil phosphorus (P) and nitrogen (N) have been identified as major determinants of fungal diversity [26]. This is particularly true for the phylum Glomeromycota, whose diversity and functioning are markedly reduced under high soil P levels [40].

Functional diversity of fungal taxa

The analysis of functional groups within the fungal communities revealed a dominance of putative saprotrophs, along with a notable presence of putative symbiotrophs, particularly arbuscular mycorrhizal fungi (AMF). In the context of South Kivu, where soils are often nutrient-poor and degraded [21], saprotrophs play a crucial role in the breakdown of organic matter and the release of mineral nutrients available to maize [19, 47]. The high abundance of genera such as Saitozyma, Lipomyces, and Cutaneotrichosporon reflects the importance of maize root exudates as a readily available carbon source [10]. These fungal groups are actively involved in organic matter decomposition and contribute to improving soil nutrient levels for maize nutrition [7], which is consistent with the higher soil organic matter contents observed in Kabare.

The presence of opportunistic pathotrophs such as members of the Olpidiaceae indicates a certain level of pathogenic pressure on maize cultivation in the agroecosystems of South Kivu, likely exacerbated by environmental stress and local agricultural practices [49]. Disease pressure, particularly from fungal pathogens, has been reported as a major constraint on maize production in South Kivu, both during the growing season and in the post-harvest stage (Kulimushi et al., 2018; Ndeko et al., 2025) [25, 37]. This situation is further intensified by the temperature and humidity conditions characteristic of Kabare and Walungu [25, 39, 40]. Moreover, we noted that the relative abundance of putative pathotrophic species was negatively affected by soil organic matter content, temperature, and soil phosphorus levels. This allowed us to infer that improving soil organic matter and adjusting soil P concentrations could help prevent fungal diseases in maize [31].

The presence of symbiotrophs, such as Glomeromycota encompassing arbuscular mycorrhizal fungi (AMF) and endophytes in the maize rhizosphere, demonstrates the ability of maize to recruit beneficial microorganisms that help it overcome both biotic and abiotic stresses [4, 60]. AMF have a very low endemism [13] and maize has been established as a highly mycotrophic crop, associating with a wide diversity of AMF species in South Kivu [38, 40]. This group plays a critical role in enhancing water and mineral nutrition [48, 60], protecting against pathogens [32], and improving maize yield [48]. Furthermore, studies indicate that maize also establishes relationships with fungal endophytes to perform various functions [4, 18, and 27]. AMF and endophytes thus play a strategic role in maize production systems in South Kivu. The presence of families such as Glomeraceae, Gigasporaceae, and Diversisporaceae aligns with their major role in phosphorus acquisition, a nutrient often limiting in tropical soils.

These results are consistent with those of DaSilva et al. [12], who reported the dominance of Glomeraceae and Gigasporaceae in tropical maize agroecosystems. In Uvira, the high

representation of these families reflects adaptation to water stress and low soil fertility, as also observed by Sun et al. [51]. In Walungu, the presence of Acaulosporaceae and Paraglomeraceae indicates the adaptation of AMF to acidic and degraded soils, confirming their resilience under stressed environmental conditions [11, 20, 33]. Finally, fungal endophytes enhance tolerance to biotic stress and protect crops against opportunistic pathogens, a role widely reported in tropical agroecosystems [49]. The coexistence of saprotrophs, symbiotrophs, and pathotrophs underscores the functional complexity of fungal communities and highlights the strong dependence of their composition on local soil physicochemical properties and the intensity of agricultural management [44].

Maize root exudates in South Kivu appear to favor fungi capable of supporting plant nutrition and tolerating environmental stress [17]. In Uvira, fungal communities are strongly correlated with high temperatures, water stress, and wind speed, suggesting a selection for fungi resistant to heat and desiccation, conditions typical of low-altitude environments. In Kabare, the predominance of edaphic factors such as soil organic matter, cation exchange capacity (CEC), and soil moisture promotes saprotrophs as well as some symbiotrophs, although AMF abundance remains limited due to lower temperatures and higher humidity, which may inhibit mycorrhizal activity [61]. In Walungu, the correlation of fungal communities with sodium content and topography indicates adaptation to acidic and eroded soils, a common feature of this area. These observations confirm that the rhizosphere functions as an ecological filter, modulating fungal composition according to local environmental constraints. Furthermore, FUNGuild-based functional assignments should be interpreted with caution because they are putative, taxonomy-derived predictions that may not fully reflect fungal ecological roles, especially in understudied groups such as soil yeasts, and fungal functional plasticity with overlapping trophic modes further reduces the precision of purely database-based annotations [53].

Conclusion

The study highlights the complex structuring of fungal communities in the maize rhizosphere across the territories of Walungu, Kabare, and Uvira, shaped by environmental and edaphic gradients. Alpha diversity analyses indicated an overall low fungal diversity in the maize rhizosphere. Fungal richness was higher in Walungu and at higher elevations, whereas Shannon diversity was greater at lower elevations, suggesting that species diversity is not uniformly distributed across territories and agroecological zones. Beta diversity further revealed pronounced differences among sites, with Uvira exhibiting a fungal composition distinct from that of Kabare and Walungu. The fungal community was dominated by the phyla Basidiomycota, Ascomycota, and Glomeromycota, although several phyla and

families remained partially unidentified. Arbuscular mycorrhizal fungi (AMF) were represented by six major families, each showing territory-specific patterns of distribution.

Functional analysis revealed the simultaneous presence of symbiotrophs, saprotrophs, endophytes, and pathotrophs, reflecting the multifunctional roles of fungi in the maize rhizosphere and the potential of maize to recruit beneficial taxa that may enhance productivity and contribute to disease suppression. NMDS and RDA analyses showed that environmental factors strongly influenced species distribution. In Uvira, fungal abundance was positively associated with temperature, wind speed, soil organic matter, phosphorus, and the CTI index, whereas slope and soil nitrogen exerted negative effects. In Kabare, fungal abundance increased primarily with cation exchange capacity, potassium, soil moisture, and bulk density. In Walungu, sodium and topographic curvature favored several species, while high organic matter content reduced their abundance. Major fungal groups, including Basidiomycota, Glomeromycota, and Rozellomycota, also exhibited distinct responses to soil and topographic gradients. Overall, each territory presented unique environmental conditions that shaped fungal community composition, underscoring the central role of local environmental drivers.

The diversity, composition, and functional attributes of maize rhizosphere fungal communities are thus strongly regulated by local conditions and environmental gradients. Understanding these relationships is essential for developing sustainable soil management strategies and agricultural practices that enhance microbial diversity, improve crop health, and optimize maize productivity in the region.

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Author Contributions

Conceptualization: Adrien Byamungu Ndeko, Abdala Gamby Diedhiou, Saliou Fall, and Aboubacry Kane.
Data curation Formal analysis: Adrien Byamungu Ndeko and Papa Mamadou Sitor Ndour
Investigation and Methodology: Adrien Byamungu Ndeko.
Resources: Adrien Byamungu Ndeko, Gustave Nachigera Mushagalusa, Aboubacry Kane.
Software: Adrien Byamungu Ndeko. Papa Mamadou Sitor Ndour
Supervision: Abdala Gamby Diedhiou, Saliou Fall, Gustave Nachigera Mushagalusa, Aboubacry Kane.
Validation: Adrien Byamungu Ndeko, Abdala Gamby Diedhiou, Saliou Fall,
Gustave Nachigera Mushagalusa, Aboubacry Kane.
Visualization: Adrien Byamungu Ndeko.
Writing – original draft: Adrien Byamungu Ndeko.
Writing – review & editing: Adrien Byamungu Ndeko, Abdala Gamby Diedhiou, Papa Mamadou Sitor Ndour, Géant Basimine Chuma, Diegane Diouf, Saliou Fall, Gustave Nachigera Mushagalusa, Aboubacry Kane

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