



# Spatial variability and environmental drivers of arbuscular mycorrhizal fungal communities associated with *Solanum aethiopicum* (L., 1756) in Côte d'Ivoire

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## ABSTRACT

**Objective:** This study assesses the diversity of spore-based arbuscular mycorrhizal fungal (AMF) communities associated with *Solanum aethiopicum*, as well as the role of the main environmental factors and management practices in shaping their spatial distribution across the agroecological regions of Côte d'Ivoire.

**Methodology and Results:** Rhizospheric soil and fine-root samples were collected in June 2023 from 16 *Solanum aethiopicum* fields across four agroecological regions of Côte d'Ivoire: South, East, Centre, and North. AMF spores were extracted by wet sieving, identified morphologically at the genus level, and analyzed together with root colonization, soil properties, and farming practices using univariate and multivariate statistics in R. Spore density and root colonization varied significantly among regions, with the highest values in the Centre and East and the lowest in the North. AMF communities were dominated by *Glomus*, *Acaulospora*, and *Funneliformis*. While alpha diversity did not differ significantly among regions, community composition was mainly structured by soil properties, with additional effects of phosphorus inputs and fungicide use.

**Conclusions and application of Results:** The results indicate soil fertility acts as the main environmental filter structuring spore-based arbuscular mycorrhizal fungi (AMF) communities in African eggplant systems whereas local farming practices modulate community composition. Organic matter and mulching gradients covaried with multivariate ordination patterns, suggestions that management can influence AMF associated soil biological functioning beyond purely regional effects. The moderate regional effect observed suggests that local edaphic and agronomic conditions are more important than geography alone for explaining AMF community turnover in

the studied systems. These findings support the integration of soil biological indicators and AMF-sensitive management practices into fertility management strategies to improve the sustainability of tropical vegetable production in Côte d'Ivoire and similar agroecosystems.

**Keywords:** African eggplant; interspecific interactions; diversity; distribution; agricultural practices.

## INTRODUCTION

Eggplant (*Solanum* spp.) is an ancient vegetable crop belonging to the family Solanaceae. The earliest domesticated forms of the cultivated Asian species (*Solanum melongena*) originated in the Indo-Burmese region, where domestication is thought to have occurred more than 4,000 years ago (Meyer *et al.*, 2012). From Southeast Asia, eggplant cultivation gradually spread to the Middle East and the Mediterranean through Arab trade routes, before reaching Africa, where it diversified into a wide range of local forms. Among these, *S. aethiopicum*, commonly known as African eggplant, represents a distinct species that arose from an independent domestication of the wild taxon *S. anguivi* (Song *et al.*, 2019). This secondary domestication on the African continent led to pronounced morphological and genetic diversification, shaped by heterogeneous agroecological conditions and locally specific farming practices. In West Africa, *S. aethiopicum* occupies a prominent position within smallholder farming systems. It is cultivated for both its fruits and leaves, providing household income as well as essential nutrients. In Côte d'Ivoire, African eggplant production is distributed across several agroecological zones (Central, North-Eastern and Southern Forest zones). At the global scale, eggplant production reached 59.31 million tonnes in 2022 according to FAOSTAT (FAO, 2024), underscoring the importance of this crop within the horticultural sector. Owing to its high contents of dietary fibre, vitamins and antioxidant compounds, eggplant contributes to the prevention of non-communicable diseases such as diabetes and cardiovascular disorders (Yarmohammadi &

Hosseinzadeh, 2021). Socio-economically, vegetable value chains can contribute to rural incomes and are strongly intertwined with gender relations, including opportunities and constraints for women producers (Fischer *et al.*, 2025). African eggplant (*S. aethiopicum*) is nutritionally demanding, requiring an optimal balance of major mineral elements such as nitrogen (N), phosphorus (P) and potassium (K), as well as sufficient availability of organic matter and water to sustain vegetative growth, flowering and fruiting (Fondio *et al.*, 2016 ; Mwinuka *et al.*, 2021 ; Nanyanzi *et al.*, 2018). These requirements make the crop particularly sensitive to environmental disturbances. Rising temperatures, prolonged droughts and recurrent flooding - direct consequences of climate change disrupt nutrient availability, reduce soil microbial activity and impair root uptake, thereby compromising productivity (Szejgis *et al.*, 2024). In addition, soil erosion, exacerbated by unsustainable agricultural practices, depletes nutrient-rich topsoil layers and accelerates fertility degradation (Feeney *et al.*, 2023 ; Mandal *et al.*, 2023). These abiotic constraints are further compounded by increasing pressure from phytopathogenic diseases, for which few resistant varieties or effective control measures are available (Mvungi *et al.*, 2025), as well as by technical and economic limitations such as low mechanisation and restricted access to inputs that persistently constrain productivity (Zaato *et al.*, 2025). To address these challenges, the integration of beneficial soil microorganisms, particularly arbuscular mycorrhizal fungi (AMF), has emerged as a promising ecological strategy. These fungi form symbiotic associations with the roots of many cultivated

plants, enhancing phosphorus uptake and the acquisition of other nutrients (Parniske, 2008), while increasing tolerance to water stress and pathogens (Begum *et al.*, 2019). They also contribute to soil structure and long-term fertility (Fall *et al.*, 2022). In tropical environments, mycorrhizal plants often exhibit improved growth and greater nutrient-use efficiency compared with non-mycorrhizal plants (Frosi *et al.*, 2016; Zaman *et al.*, 2024). Inoculation with AMF in eggplant (*Solanum* spp.) grown on nutrient-poor soils has been shown to result in significant gains in yield and resilience (Douds *et al.*, 2017). However, the large-scale adoption of AMF in cropping systems remains limited, partly due to mismatches between introduced isolates and local edaphic conditions, which reduce their effectiveness and persistence (Basiru and Hijri 2022). Moreover, the spatial variability of native AMF communities in eggplant cultivation systems particularly in *S. aethiopicum* remains poorly documented. Understanding how AMF diversity and

abundance vary across regions is therefore essential for assessing their potential for natural inoculation and their role in soil health (Wolfe *et al.*, 2007 ; Cheeke *et al.*, 2015). The overall objective of this study is to analyse spatial variability and to identify the main environmental determinants structuring AMF communities associated with *S. aethiopicum* in Côte d'Ivoire. We hypothesize that the composition of AMF communities varies according to soil conditions and agricultural management practices. To test this hypothesis, the study pursues three specific objectives:

- (i) characterize functional mycorrhizal parameters associated with *S. aethiopicum* across different production zones in Côte d'Ivoire.
- (ii) assess the diversity of AMF communities within these production zones; and
- (iii) evaluate the influence of a set of agroecological variables in Côte d'Ivoire on the characteristics of their associated AMF communities.

## MATERIALS AND METHODS

**Description of the study area:** The study was conducted across four major agroecological regions recognized for the production of *S. aethiopicum* in Côte d'Ivoire: the Southern, Eastern, Central and Northern regions. Each of these regions is characterized by distinct combinations of climatic conditions, edaphic properties and agricultural production systems, reflecting the diversity of their agroecological contexts. Within each region, one to two production zones were selected based on their importance within the value chain and the accessibility of cultivated fields:

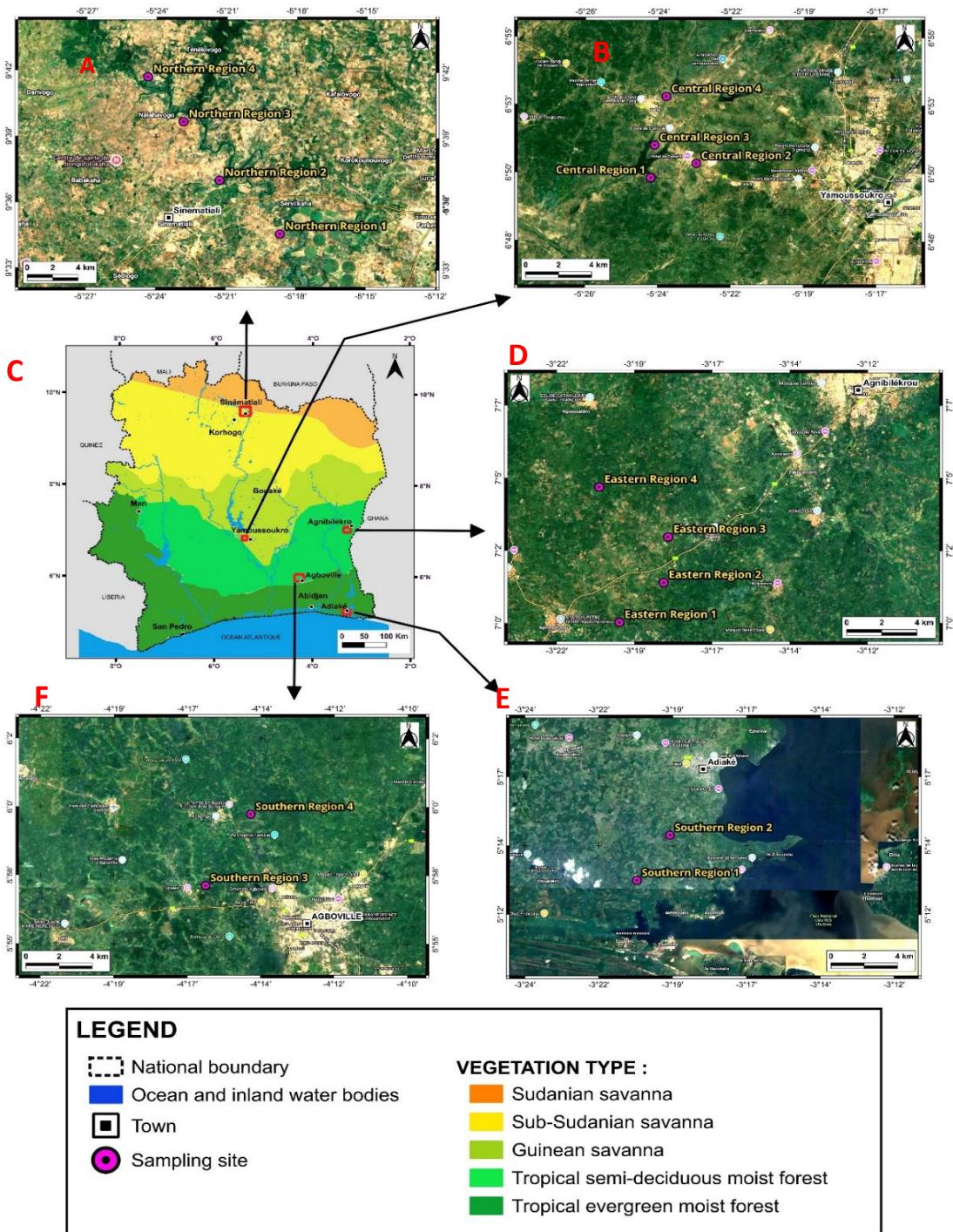
☞ Southern region: Agboville and Adiaké zones;

☞ Eastern region: Agnibilékrou zone;

☞ Central region: Yamoussoukro zone;

☞ Northern region: Sinématiali zone.

In each region, four study plots were selected, resulting in a total of sixteen sampling plots. These sites were randomly chosen within the identified zones following a preliminary exploratory survey aimed at locating fields cultivated with African eggplant. The surveyed eggplant fields were selected such that they were separated by a minimum distance of 10 km from one another, to minimize spatial redundancy and to better capture local variability in soil characteristics and cropping practices (Figure 1).



**Figure 1:** Satellite images showing the location of the study regions, zones, and plots in Côte d'Ivoire. (A) Division of the country according to vegetation types; (B - F) corresponding to the Northern, Central, Eastern, and Southern regions, respectively.

**Soil sampling and analysis:** Soil sampling was carried out in the agricultural plots surveyed in June 2023, corresponding to the

harvest period of African eggplant (*Solanum aethiopicum*). In each plot, four soil sampling points were established. Each point

corresponded to a square sub-plot measuring 10 m × 10 m, separated from the others by a minimum distance of 50 m (Peyret-Guzzon, 2014). Soil samples were collected using a hand auger by extracting five soil cores to a depth of 20 cm: one at the centre and one at each of the four corners of the sub-plot. The five cores were homogenized to form a representative composite sample. Consequently, four composite soil samples were obtained per plot. Soil analyses focused on pH, phosphorus, organic carbon, nitrogen, and the C/N ratio, as these variables are among the most widely recognized determinants of mycorrhizal functioning and the structuring of arbuscular mycorrhizal fungal (AMF) communities. Soil pH and phosphorus strongly influence nutrient availability and plant investment in symbiosis, potentially altering AMF community composition (Smith and Read, 2010). Carbon, nitrogen, and the C/N ratio characterize soil organic matter status and biogeochemical dynamics, which may modulate the rhizosphere environment and, consequently, AMF colonization and community assembly (Smith & Read, 2010). Soil pH was measured potentiometrically in a soil–water suspension (1:2.5) following Pansu and Gautheyrou (2003). Available phosphorus (Olsen P) was determined using the Olsen *et al.*, (1954) method with 0.5 M NaHCO<sub>3</sub> (pH 8.5). Soil organic matter was quantified according to the Walkley and Black method as described by Mathieu and Pieltain (2003). Organic carbon (C<sub>org</sub>) was determined using the classical Walkley and Black (1934) method, and total nitrogen (N) was measured using the Kjeldahl method (Bremner, 1960). The C/N ratio was subsequently calculated to assess soil nutrient balance.

**Assessment of mycorrhization of fine eggplant roots:** Fine roots collected from eggplant plants were first cleared in a 10% KOH solution for 30 minutes at 90 °C, then thoroughly rinsed with distilled water. The roots were subsequently stained with 0.05%

trypan blue following the method of Phillips and Hayman (1970) and cut into fragments approximately 1 cm in length and less than 1 mm in diameter, corresponding to fine rootlets that are readily observable under a microscope. Root fragments were mounted on microscope slides in a drop of lactoglycerol for observation. The frequency (F%) and intensity (M%) of mycorrhizal colonization were assessed under a light microscope using the method of Trouvelot *et al.*, (1986).

**Extraction and morphological identification of arbuscular mycorrhizal fungal spores:**

For spore extraction, each 50 g subsample of air-dried soil was subjected to wet sieving and decanting according to the method of Gerdemann and Nicolson (1963). Each sample was suspended in 500 mL of tap water and allowed to decant for 10 seconds to separate fine particles. The supernatant was then passed through a series of stacked sieves with mesh sizes of 500, 250, 90, and 45 µm. This procedure was repeated three times for each sample. Coarse debris (>500 µm) was discarded, while the fractions retained on the 250, 90, and 45 µm sieves were collected and centrifuged at 2000 rpm for 5 minutes. The resulting pellet was resuspended in a 50 % sucrose solution and centrifuged again at 2000 rpm for 1 minute. In contrast to the first centrifugation, the supernatant was recovered and filtered through a 45 µm sieve to retain the spores. The spores were carefully rinsed with distilled water to remove residual sucrose and then suspended in 10 mL of distilled water. Spores were counted and pre-classified according to size, colour and morphological condition using a Leica EZ4 W stereomicroscope (40×), following the reference protocol of the International Culture Collection of (Vesicular–) Arbuscular Mycorrhizal Fungi (INVAM). For morphological identification, 90 spores were randomly selected per site from the total spore assemblage in order to minimize selection bias and to cover the observed morphological

diversity. Spores were mounted in polyvinyl alcohol–lactic acid–glycerol (PVLG), with or without Melzer's reagent, and examined using a Leica DM500 light microscope equipped with 10×, 40× and 100× objectives. For morphological identification, 90 spores were randomly selected per site to capture the observed morphological diversity while limiting selection bias. Spores were mounted on slides in polyvinyl alcohol–lactic acid–glycerol (PVLG), with or without Melzer's reagent, and examined under a Leica DM500 light microscope. Identification was performed at the genus level using diagnostic morphological characters, including spore size, colour, wall structure, number and thickness of wall layers, subtending hypha characteristics, and, where present, structures such as germination shields, sporiferous saccules, or suspensor bulbs. Morphological determinations were made by comparison with standard taxonomic keys and INVAM reference descriptions. The number of spores analysed per site was intended to support reliable genus-level identification and not to provide an exhaustive estimate of species richness.

**Characterization of cropping practices and plot management context:** To complement field observations and interpret ecological data within their socio-agronomic context, a semi-structured survey was conducted among the farmers responsible for the plots used for soil and root sampling. A standardized questionnaire was administered to a sample of sixteen farmers (four per study zone), purposively selected based on their direct involvement in the management, maintenance, and agronomic operation of the sampled sites. The survey aimed to collect detailed information on cropping practices likely to influence soil ecological and biological dynamics, particularly AMF communities. The main topics investigated included the frequency and methods of weeding, the use of mulching, the type and application rates of

organic amendments, the possible use of fungicide treatments, and mineral fertilizer inputs, with particular emphasis on phosphorus fertilizers expressed as P<sub>2</sub>O<sub>5</sub> equivalents.

**Statistical analysis:** Data were first subjected to exploratory analyses to verify the assumptions of parametric tests, notably the normality of residuals (Shapiro–Wilk test) and homogeneity of variances (Levene's test). When these conditions were met, mean comparisons among zones were performed using one-way analysis of variance (ANOVA), followed by Tukey's post hoc test ( $p < 0.05$ ). In cases of non-normality, non-parametric Kruskal–Wallis and Mann–Whitney tests were applied, with Benjamini–Hochberg correction for multiple comparisons. The relationship between AMF colonization frequency (%) and intensity (%) was tested using a two-tailed Spearman correlation, with a 95% confidence interval obtained by bootstrap resampling (5000 iterations). To control for the effect of “region”, an intra-regional correlation was calculated using residuals after removing the regional effect, and a fitted linear model (intensity ~ frequency + region) was used to estimate the effect of frequency at constant region. Results were visualized using a scatter plot colored by region with a LOESS trend and 95% confidence interval. Alpha diversity was estimated from genus-level abundance matrices, as AMF were identified based on spore morphological criteria. Given the well-known limitations of species-level morphological identification and the variability in sporulation, genus richness was used here as an operational proxy for taxonomic diversity (Landis *et al.*, 2004; Redecker *et al.*, 2003; Sanders, 2004; INVAM, n.d.). Shannon–Wiener and Simpson indices, as well as taxonomic richness, were calculated using the *vegan* package following standard recommendations (Magurran, 2004). Inventory completeness was further assessed using genus accumulation curves by region, converting abundances to incidence

(presence/absence) data and comparing observed richness ( $S_{obs}$ ) with the first-order jackknife estimator ( $\hat{S}_{jack1} = S_{obs} + (R - 1)/R \times Q_1$ ), where  $R$  is the cumulative number of sites and  $Q_1$  the number of genera observed in only one site. Curves of  $S_{obs}$  versus  $\hat{S}_{jack1}$  and the ratio  $S_{obs}/\hat{S}_{jack1}$  were used as indicators of relative sampling effort (Heltshe & Forrester, 1983; Gotelli & Colwell, 2001). Relative abundances (%) were calculated by regional pooling: genus counts were summed across the four sites within each region and divided by the total AMF counts for that region; absent genera were coded as 0%. Beta diversity of communities (genus-level abundance matrix,  $n = 16$  sites) was quantified using Bray–Curtis dissimilarity (and, in sensitivity analyses, Jaccard dissimilarity based on presence/absence). A two-dimensional non-metric multidimensional scaling (NMDS) ordination was performed on the Bray–Curtis matrix using *metaMDS* (*vegan* package; random seed fixed for reproducibility), and ordination quality was assessed using the stress value (Kruskal, 1964; Oksanen *et al.*, 2024). Differences in community composition among regions (agroecological zones) were tested using PERMANOVA (*adonis2*, 999 permutations) (Anderson, 2001). The assumption of homogeneity of multivariate dispersions, which is critical for PERMANOVA

## RESULTS

**Taxonomic composition of mycorrhizal communities:** A contrasting structuring of arbuscular mycorrhizal fungi (AMF) communities was observed across the studied regions (Table 1). The family Glomeraceae, dominated by the genus *Glomus*, was overwhelmingly predominant in all regions, with relatively homogeneous proportions, suggesting a broad ecological adaptability of this genus. The genus *Acaulospora* (family Acaulosporaceae) represented the second most abundant group, particularly in the Eastern and

interpretation, was tested using PERMDISP (*betadisper*), with permutation tests (*permutest*, 999 permutations) (Anderson, 2006; Oksanen *et al.*, 2024). To relate community composition to environmental variables, the abundance matrix was Hellinger-transformed and analysed using redundancy analysis (RDA) (Legendre & Gallagher, 2001; Oksanen *et al.*, 2024). Given the limited sample size ( $n = 16$  sites) and the number of candidate variables ( $n = 10$ ), a parsimonious approach was adopted by constraining the RDA to four biologically justified active variables (pH, phosphorus,  $P_2O_5$ , fungicide use) in order to limit overfitting and collinearity. The significance of the global model and individual variable effects was assessed using permutation tests (999 permutations), including marginal (type III) tests for partial effects (Blanchet *et al.*, 2008; Oksanen *et al.*, 2024). Finally, the relative contribution of chemistry (pH, phosphorus), management practices ( $P_2O_5$ , fungicide), and region (factor) was quantified using variance partitioning (*varpart*) based on adjusted  $R^2$ , and partial RDAs were used to test the “pure” fractions (region, chemistry, practices) while controlling for the other blocks (Peres-Neto *et al.*, 2006). All analyses were performed in R (version 4.3.0) using the packages *vegan*, *ggplot2*, *agricolae*, *dplyr*, and *car*.

Northern regions, indicating a good tolerance to local edaphic and climatic conditions. Other genera (*Gigaspora*, *Scutellospora*, *Paraglomus*, *Sacculospora*, and *Claroideoglomus*) were less abundant and exhibited a heterogeneous distribution, likely reflecting more specific ecological requirements. This regional diversity highlights the influence of environmental conditions and agricultural practices on the composition of AMF communities.

**Table 1:** Composition and relative abundance (%) of arbuscular mycorrhizal fungal genera by region

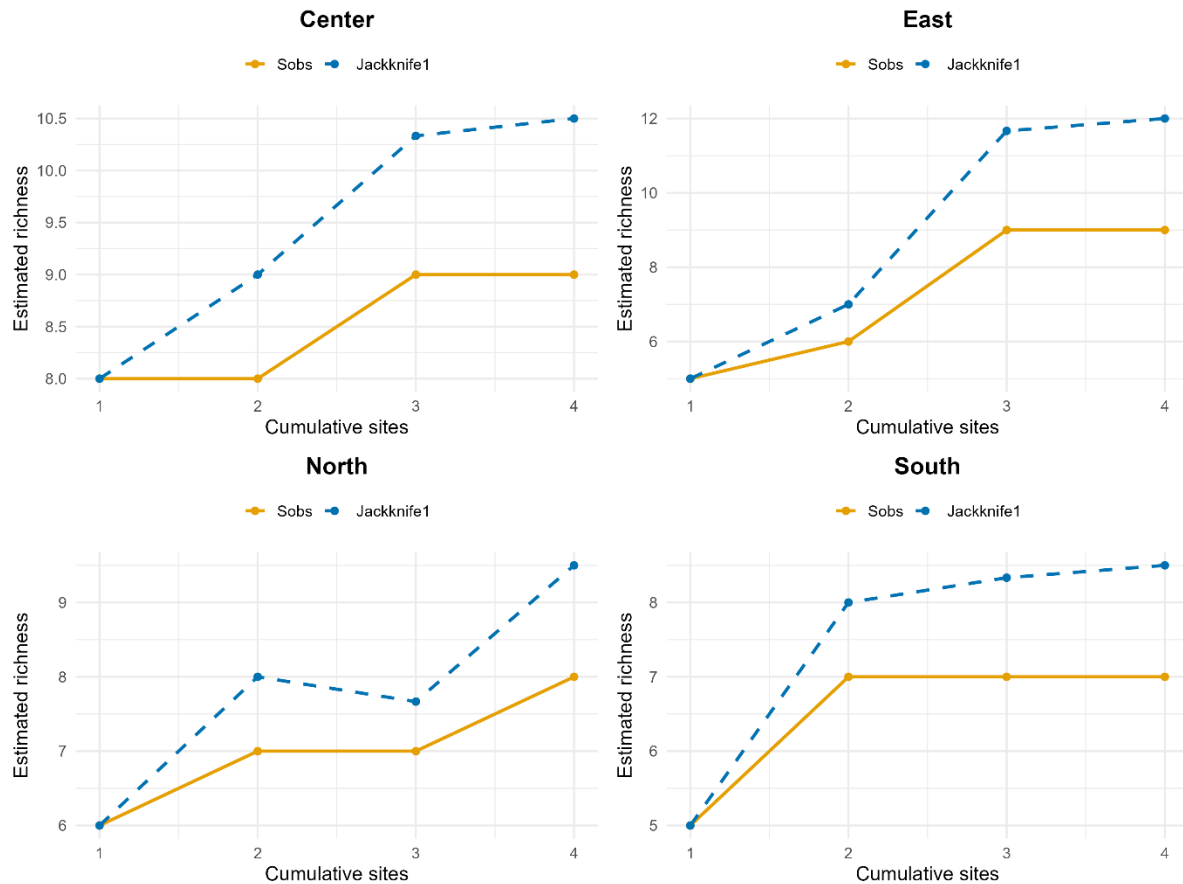
Family	Genus	Center (%)	East (%)	North (%)	South (%)
Glomeraceae	<i>Glomus</i>	45.83	47.50	45.83	48.06
Glomeraceae	<i>Funneliformis</i>	2.50	2.78	0.56	6.39
Glomeraceae	<i>Septoglomus</i>	0.56	0.00	0.00	0.00
Glomeraceae	<i>Rhizophagus</i>	2.22	0.00	0.00	7.78
Acaulosporaceae	<i>Acaulospora</i>	29.44	36.39	34.72	30.56
Gigasporaceae	<i>Gigaspora</i>	6.39	2.50	4.44	1.39
Gigasporaceae	<i>Scutellospora</i>	5.00	0.56	3.06	0.00
Gigasporaceae	<i>Racocetra</i>	0.00	0.83	0.00	0.00
Paraglomeraceae	<i>Paraglomus</i>	6.39	0.56	5.56	3.89
Claroideoglomeraceae	<i>Claroideoglomus</i>	0.00	4.44	2.22	0.00
Sacculosporaceae	<i>Sacculospora</i>	1.67	4.44	2.22	0.00

The values represent relative abundances (%), calculated as the sum of the abundances of each genus across all sites within a region (n = 4 sites per region), divided by the total abundance of AMF in that region; absent genera were assigned a value of 0%.

### Diversity of Arbuscular Mycorrhizal Fungal Communities

**Cumulative richness and sampling completeness:** Across all surveyed regions, the cumulative species richness estimated using the Jackknife 1 estimator was consistently higher than the observed richness ( $S_{obs}$ ) (Figure 5), indicating an under-detection of species given the sampling effort undertaken. The relative convergence of the

observed and estimated curves in the North and East regions suggests a more comprehensive representation of diversity, likely linked to the structural complexity and heterogeneity of the agroforestry systems. However, the absence of an asymptote for all curves indicates that the inventory effort remains insufficient, and further surveys would likely reveal additional species richness, particularly in the Central and Eastern regions.

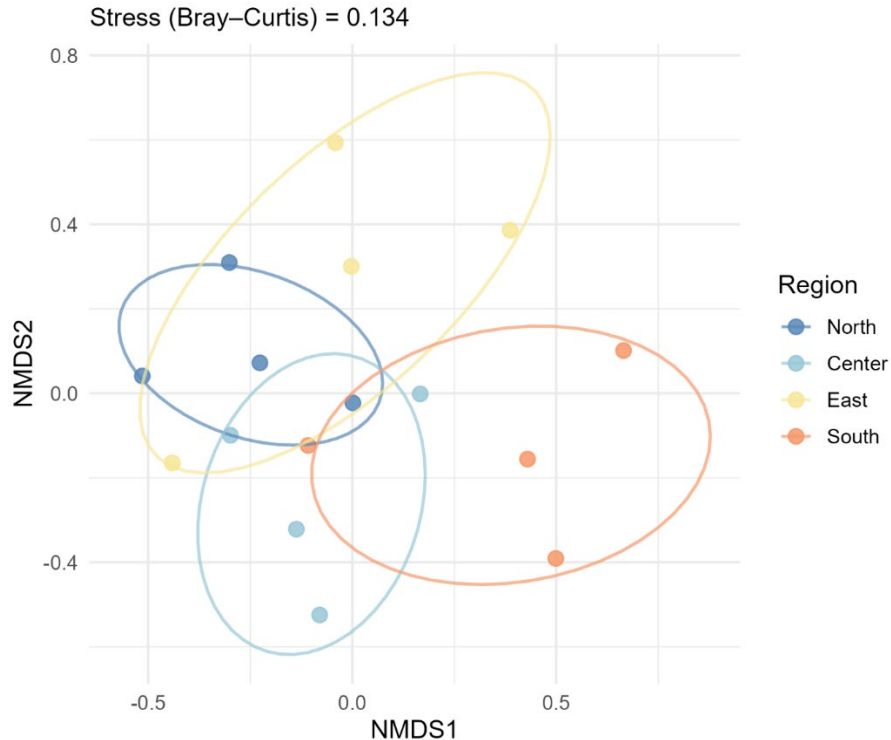


**Figure 2:** Cumulative generic richness of arbuscular mycorrhizal fungi (AMF) collected from four agroecological regions of Côte d'Ivoire

**Spatial structuring of AMF communities:  $\beta$ -diversity analysis**

**Inter-zone differentiation revealed by NMDS ordination and PERMANOVA:** The NMDS ordination (Figure 3), based on Bray–Curtis distances, revealed a structuring of fungal communities according to region, with partial overlap between groups but a more pronounced visual separation for certain regions. Notably, samples from the South projected on the positive side of NMDS axis 1, whereas those from the North, Centre, and East clustered around lower values. The two-

dimensional representation was deemed acceptable (stress = 0.134), indicating that the 2D configuration reasonably captures the dissimilarity relationships among sites. Finally, multivariate dispersion within regions (PERMDISP, 999 permutations) did not differ significantly between regions, neither for Bray–Curtis ( $F = 0.064$ ;  $p = 0.971$ ) nor for Jaccard ( $F = 0.766$ ;  $p = 0.527$ ), suggesting that the observed structuring is not an artefact of heterogeneous dispersion but primarily reflects differences in community composition and abundance between regions.



**Figure 3.** NMDS (Bray–Curtis) of arbuscular mycorrhizal fungal (AMF) community composition by region (stress = 0.134).

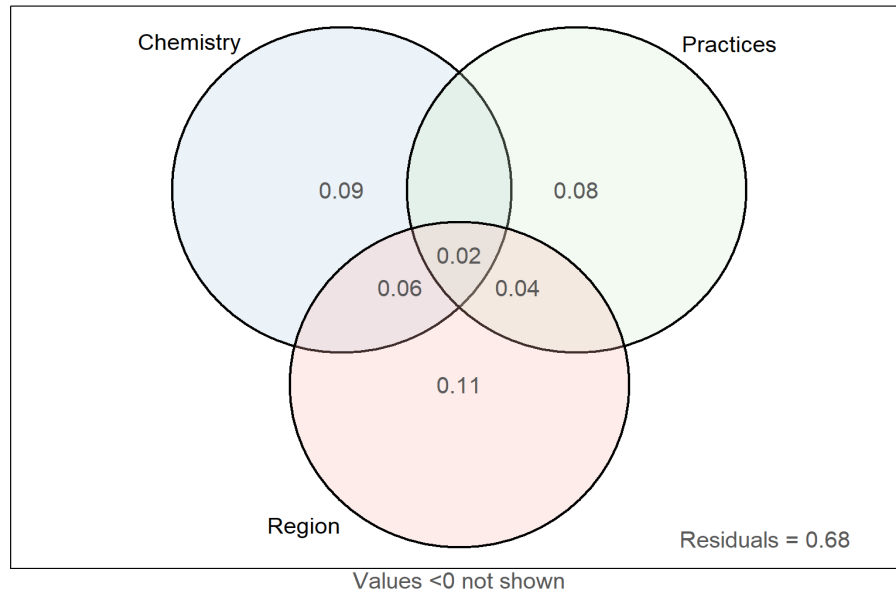
The ellipses indicate within-region dispersion around the centroids.

### Structuring of Arbuscular Mycorrhizal Fungal Communities along Environmental Gradients and Agricultural Practices:

Redundancy analysis (RDA) (Figure 4), performed on the Hellinger-transformed matrix ( $n = 16$ ) with four active variables (pH, phosphorus,  $P_2O_5$ , fungicide), explained  $R^2 = 0.421$  of the total variances, with an adjusted  $R^2 = 0.210$ , indicating a moderate proportion of variance explained after correcting for overfitting. The overall model was significant (permutations = 999:  $F = 1.997$ ;  $p = 0.010$ ), demonstrating a robust multivariate association between community composition and the selected environmental variables. The first two constrained axes captured most of the explained structure (RDA1 = 56.6%; RDA2 = 31.1%, cumulative 87.8%), supporting interpretation of the biplot along these two dimensions. Marginal tests (Type III, partial effects) indicated that phosphorus ( $F = 3.653$ ;

$p = 0.003$ ) and fungicide ( $F = 3.035$ ;  $p = 0.006$ ) were the main independent contributors, whereas pH ( $p = 0.331$ ) and  $P_2O_5$  ( $p = 0.549$ ) showed no detectable effect once the other variables were controlled for. Collinearity diagnostics suggested low to moderate collinearity ( $VIF \sim 1.19\text{--}1.80$ ), compatible with stable interpretation of coefficients and vectors. In passive projection (envfit, 999 permutations), carbon ( $r^2 = 0.601$ ;  $p = 0.004$ ), nitrogen ( $r^2 = 0.530$ ;  $p = 0.008$ ), C:N ratio ( $r^2 = 0.521$ ;  $p = 0.011$ ) and mulching ( $r^2 = 0.641$ ;  $p = 0.002$ ) were significantly aligned with the ordination, whereas weeding ( $p = 0.252$ ) and amendment ( $p = 0.627$ ) did not show a statistically detectable signal. Given the sample size ( $n = 16$ ), these results should be interpreted as robust multivariate associations, but with limited power to detect weak or strongly correlated effects.

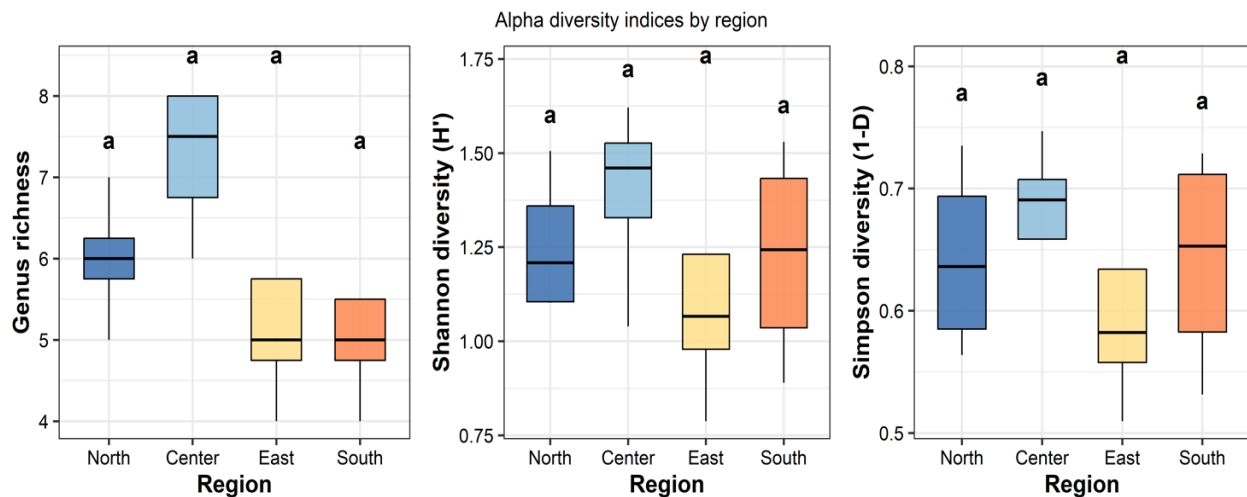




**Figure 5.** Variance partitioning of arbuscular mycorrhizal fungi community composition among soil chemistry, agricultural practices, and region (adjusted R<sup>2</sup>).

**α-Diversity of AMF Communities in the Surveyed Regions:** The α-diversity of Arbuscular Mycorrhizal Fungi (AMF) communities collected across the four studied regions was generally comparable. No statistically significant differences were detected among the regions for any of the α-

diversity indices considered (Figure 6;  $p > 0.05$ ). Figure 5 presents boxplots depicting genus richness as well as Shannon (H') and Simpson (1-D) diversity indices across regions. These results suggest a relatively homogeneous diversity structure of AMF communities on the national scale.

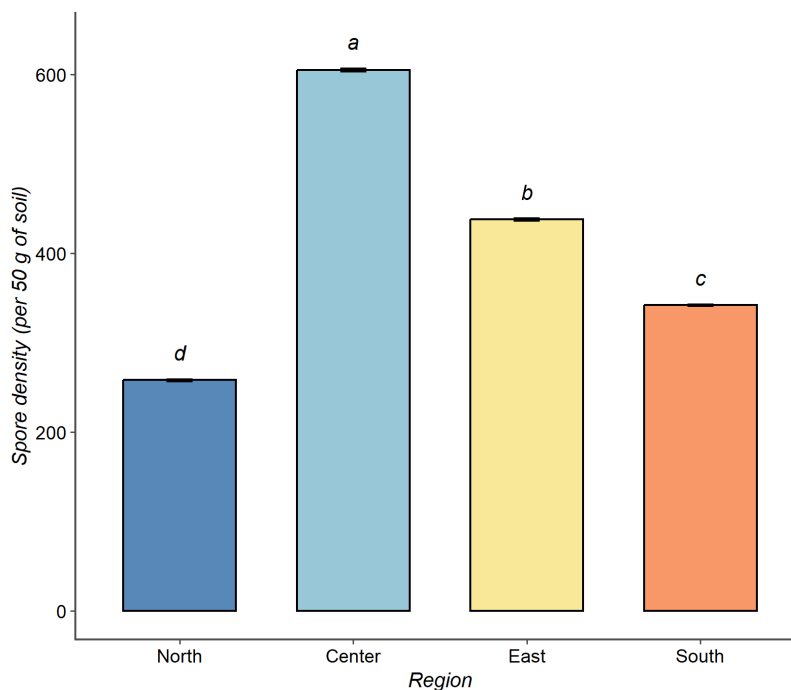


**Figure 6:** Diversity of arbuscular mycorrhizal fungal communities according to the eggplant production region in Côte d'Ivoire.

Identical letters indicate no significant differences between regions (Tukey HSD test,  $p > 0.05$ ).

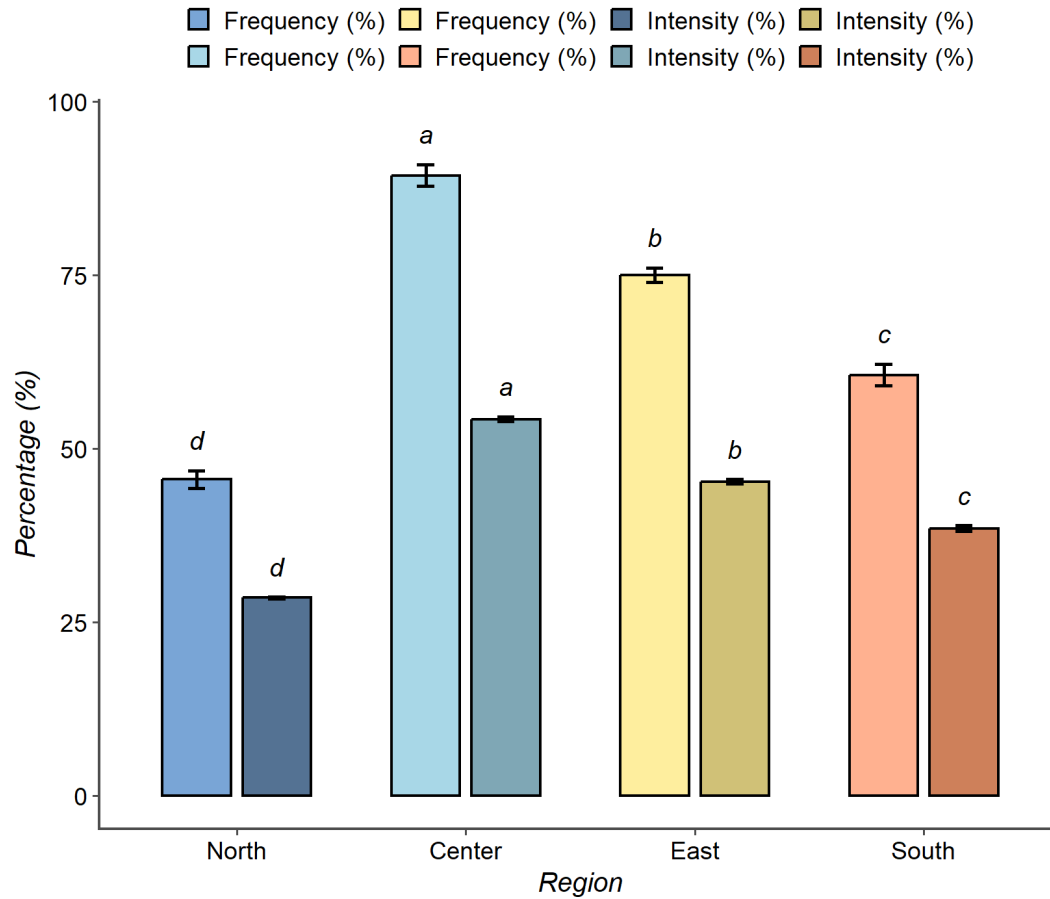
**Variability of functional mycorrhizal parameters (spore density, root colonization):** The density of arbuscular mycorrhizal fungi (AMF) spores measured in soil samples collected from *Solanum aethiopicum* fields varied significantly among regions (Figure 7). Mean spore density ranged from 258 to 605 spores·g<sup>-1</sup> of soil. A significant regional effect was detected for spore density (Tukey's test;  $p < 0.01$ ). The Centre region exhibited the highest values, followed by the East, whereas the South and particularly the North showed lower levels. Non-parametric analyses (Kruskal–Wallis test followed by pairwise Mann–Whitney comparisons) further supported the presence of spatial differences among regions, consistent with a gradient of Centre > East > South > North across all mycorrhizal parameters. Figure 8 highlights marked variations in mycorrhizal colonization of *S. aethiopicum* across production zones. Mean root colonization intensity and frequency

ranged from 28.5 to 54.3% and from 46.6 to 89.4%, respectively. Both the frequency and intensity of root colonization increased overall from the North towards the Centre, where maximum values were recorded. The Eastern zone also displayed high levels, intermediate between those of the Centre and the South. In contrast, the Northern zone showed the lowest values for both parameters. As shown in Figure 9, colonization intensity was strongly associated with colonization frequency across all samples (Spearman's  $\rho = 0.939$ ,  $n = 16$ ,  $p = 6.85 \times 10^{-8}$ ; 95% bootstrap CI: 0.771–0.986). However, this association was not detected within regions after controlling for the “region” effect (Spearman correlation on residuals:  $\rho = -0.093$ ,  $p = 0.732$ ), and the effect of frequency was not significant in a model adjusted for region ( $\beta = -0.021 \pm 0.067$ ,  $p = 0.763$ ). These results suggest that the overall relationship is primarily driven by inter-regional differences rather than by within-region variation.

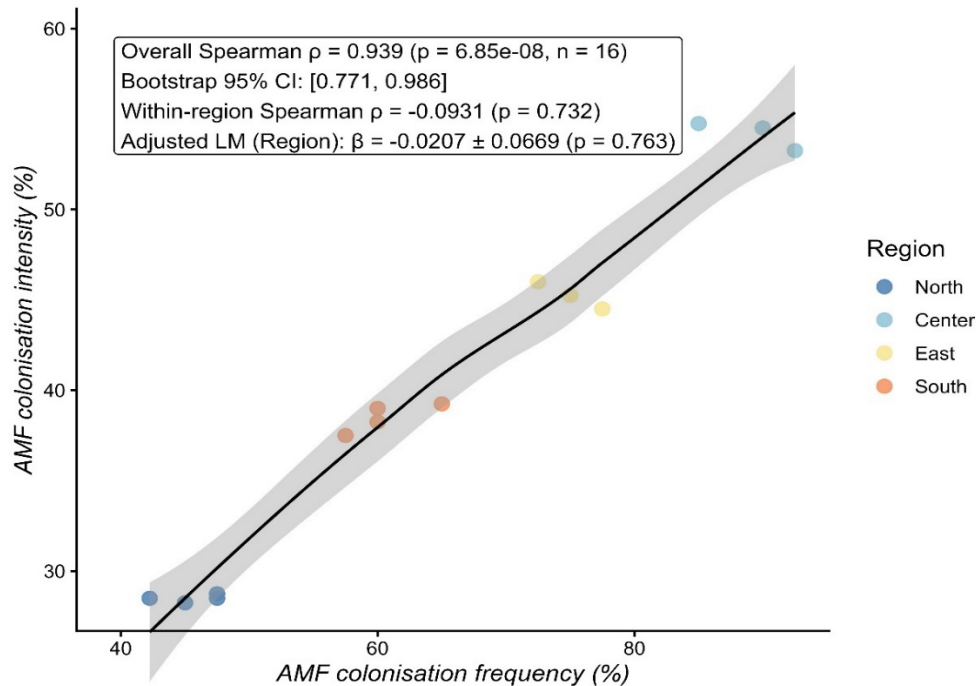


**Figure 7.** Density of arbuscular mycorrhizal fungal spores in rhizospheric soil samples collected from the surveyed plots.

Different letters indicate statistically significant differences among zones (Tukey's test,  $p < 0.01$ ).



**Figure 8.** Frequency and intensity of mycorrhizal colonization of African eggplant (*Solanum aethiopicum*) roots from plots across the four surveyed regions. Different letters indicate statistically significant differences among zones (Tukey's test,  $p < 0.01$ ).



**Figure 9.** Relationship between the frequency and intensity of arbuscular mycorrhizal fungal colonization across regions.

## DISCUSSION

This study demonstrates a non-random structuring of arbuscular mycorrhizal fungi (AMF) communities associated with *Solanum aethiopicum* in Côte d'Ivoire. The results reveal a hierarchy dominated by soil properties and certain agricultural practices (notably phosphorus and fungicide application), while gradients of organic matter and mulching align with the ordination. Conversely, the regional effect appears moderate. Overall, soil chemistry/fertility constitutes the primary filter, with agricultural management modulating the local composition of AMF.

**Spatial variability of functional mycorrhizal parameters:** Spore density and root colonization varied markedly along the gradient Centre > East > South > North, indicating a spatially heterogeneous mycorrhizal potential, influenced by the combination of edaphic factors (pH, organic carbon, nutrients), agroclimatic conditions, and management practices (Tchabi *et al.*, 2008; Thanni *et al.*, 2022). Higher densities in

the Centre and East are consistent with soils richer in carbon and with mulching/residue retention practices, generally associated with increased inoculum and/or colonization through improved soil microclimate and resource availability (Nyamwange *et al.*, 2018). Conversely, lower densities in the North correspond to more restrictive soils, particularly those low in organic carbon, often linked to reduced inoculum, which is biologically plausible given that AMF rely on host-derived carbon (Soka & Ritchie, 2018).

Overall, levels of *S. aethiopicum* mycorrhization ( $\approx 54\%$ ; intensity  $\approx 42\%$ ) are comparable to those reported for other Solanaceae, while varying according to soil conditions, phenology, and AMF community composition (Liu *et al.*, 2016; Yildiz, 2010). Globally, intensity was strongly correlated with colonization frequency ( $\rho = 0.939$ ), consistent with these indices describing closely related aspects of mycorrhization (Trouvelot *et al.*, 1986). However, the absence

of correlation after controlling for the “region” effect indicates that this relationship is largely driven by an interregional gradient (edaphic conditions/practices) and should therefore be interpreted as a joint response to shared factors rather than a direct causal link between the metrics.

**$\alpha$ -Diversity, taxonomic composition, and functional stability:**  $\alpha$ -Diversity (Shannon index) did not differ between zones despite environmental heterogeneity, compatible with compensatory turnover: composition changes, but the richness–evenness combination remains similar (Pereira *et al.*, 2022). This decoupling may be explained by a large regional AMF pool with low endemism (Davison *et al.*, 2015) combined with fine-scale spatial heterogeneity (Davison *et al.*, 2012), which may reduce the detectability of differences. Finally, the dominance of generalist genera (e.g., *Glomus*, *Acaulospora*, *Funneliformis*) suggests potential functional redundancy, which could stabilize symbiotic functions despite local compositional variation (Masebo *et al.*, 2023 ; Gosling *et al.*, 2016).

**Hierarchy of environmental determinants and role of agricultural practices:** The results highlight a hierarchy of determinants dominated by soil fertility and agricultural practices. Redundancy analysis (RDA) indicates a significant association between AMF composition and selected variables, though with moderate explained variance (adjusted  $R^2 = 0.210$ ), consistent with previous work showing that a substantial part of AMF variability is linked to soil microheterogeneity and unmeasured factors (Hazard *et al.*, 2013). Phosphorus emerged as an independent factor, aligning with experimental studies in tropical environments showing that moderate P additions alter AMF community composition, with responses differing between soil and roots depending on the edaphic context (Dueñas *et al.*, 2020; Liu *et al.*, 2016). The association with fungicide is also consistent with the

literature, which reports possible pesticide effects on mycorrhizal symbioses, though highly dependent on molecule type, dose, and soil conditions, limiting causal inference in observational studies (Hage-Ahmed *et al.*, 2019). Passive correlations with C, N, C: N, and mulching suggest gradients of organic matter and management, to be interpreted as covariation rather than causality. Finally, the regional signal appears at best moderate (non-significant PERMANOVA, homogeneous dispersion), and the variance partitioning (pure region fraction  $\sim 0.11$ ; high residual) aligns with a weak regional effect and/or limited statistical power (Peres-Neto *et al.*, 2006).

**Ecological and agronomic implications:** Overall, our results indicate a hierarchy of controls in which soil properties act as the primary filter structuring AMF communities associated with *S. aethiopicum*, while agricultural practices modulate variability at the local scale. The independent contribution of phosphorus and fungicide suggests these management levers can directly influence community composition, whereas alignment of organic matter and mulching variables (C, N, C:N, mulching) should be interpreted as concomitant gradients in an observational framework (Hazard *et al.*, 2013 ; Liu *et al.*, 2016 ; Hage-Ahmed *et al.*, 2019). The moderate regional signal and high residual fraction are consistent with structuring dominated by within-field processes and/or limited power to detect weak spatial effects (Peres-Neto *et al.*, 2006). Agronomically, these findings support integrated management of vegetable systems based on: (i) targeted phosphorus application, (ii) optimization of plant protection to minimize impacts on mycorrhizal symbioses, and (iii) maintenance or enhancement of organic matter (notably via mulching/cover crops) to preserve AMF functional diversity and sustain symbiotic services in tropical contexts.

## CONCLUSION AND APPLICATION OF RESULTS

This study demonstrates that the structuring of AMF communities associated with *Solanum aethiopicum* in Côte d'Ivoire results from a hierarchy of filters combining edaphic properties, agricultural practices, and spatial gradients. Soil properties and certain agricultural practices, particularly phosphorus and fungicide application, appear as the determinants most directly associated with AMF composition. Variables linked to organic matter and mulching align with the ordination as concomitant gradients, indicating a role for organic management in modulating soil conditions and, consequently, local community dynamics. Conversely, the regional effect remains moderate, indicating that observed structuring is primarily driven by local contrasts in soil and management rather than regionalization alone. The dominance of generalist genera such as *Glomus*,

*Acaulospora*, and *Funneliformis* suggests high functional redundancy, conferring ecological resilience to fungal communities against environmental and anthropogenic disturbances. This pattern indicates that functional stability of AMF in tropical agroecosystems relies on a complementarity between edaphic filtering and ecological plasticity. These findings underscore the importance of integrating mycorrhizal management into sustainable agricultural strategies, notably through soil quality preservation, reduction of chemical inputs, and promotion of favourable practices such as mulching and organic amendments. In the longer term, improved understanding of soil–plant–microbiome interactions could optimize AMF symbiotic functions, thereby contributing to food security and the resilience of African agroecosystems.

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**Data Availability Statement:** The data that support the findings of this study are available from the corresponding author upon reasonable request.

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