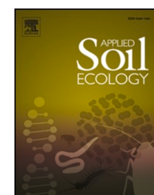
Applied Soil Ecology 223 (2026) 107040

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Research paper

Towards a global core mycobiome of banana (*Musa* spp.)

Anna-Belle C. Clarke[a], Christine Rose Ansale[b], Loren Banayag[b], Sheryl Bayang[b], Sheryl Bothma[c], Khonesavanh Chittarath[d], Merlina Juruena[b], Georgina Karamura[c,e], Hazel R. Lapis-Gaza[f], Cesar Limbaga Jr.[b], Rebecca Lyons[a], Jiarui Sun[a], Altus Viljoen[c], Diane Mostert[c], Noor Baity Saidi[g], Nurul Shamsinah Mohd Suhaimi[h], Anthony B. Pattison[f], Paul G. Dennis[a,*]

[a] *School of the Environment, The University of Queensland, Brisbane, QLD, 4072, Australia*
[b] *College of Agriculture and Related Sciences, University of Southeastern Philippines, Pindasan, Mabini, Davao de Oro, Philippines*
[c] *Department Plant Pathology, Stellenbosch University, Stellenbosch, South Africa*
[d] *Department of Agriculture, Ministry of Agriculture, the Lao People's Democratic Republic*
[e] *The Alliance of Bioversity-CIAT, Kampala, Uganda*
[f] *Department of Agriculture and Fisheries, Centre for Wet Tropics Agriculture, 24 Experimental Station Road, South Johnstone, QLD, 4859, Australia*
[g] *Department of Cell and Molecular Biology, Universiti Putra Malaysia, 43400, Selangor, Malaysia*
[h] *Institute of Biological Sciences, Universiti Malaya, 50603, Kuala Lumpur, Malaysia*

ARTICLE INFO

Keywords:
Banana
Core mycobiome
International
Global
Soil health
ITS2 metabarcoding
Musa spp.

ABSTRACT

Bananas (*Musa* spp.) are a staple for more than 400 million people and a major global commodity, yet production remains highly vulnerable to disease. Although healthy plants host diverse fungal communities, high diversity and strong site-to-site compositional turnover hinder efforts to understand and manage these mycobiomes. Identifying taxa that consistently persist across environments may therefore help prioritise targets for further investigation. We used ITS2 metabarcoding of bulk soil and the ectorhizosphere from a single banana cultivar grown in distinct plantation soils across six countries spanning Africa, Asia, and Australia. Across 24 sites, we identified 59 core fungal taxa that met prevalence–abundance criteria across multiple sites and compartments. Despite representing <1% of detected OTUs, these taxa accounted for up to 83% of total community relative abundance and showed strong concordance with our previously reported national core in Australia, indicating spatial and temporal stability. This curated multi-country core assemblage provides a tractable set of taxa for isolation and functional characterisation and establishes a shared reference for sequence-based tracking across studies, supporting future investigation of microbiome-informed approaches for sustainable banana production.

1. Introduction

Bananas (*Musa* spp.) are the most traded fruit in the world with over 100 million tonnes produced annually (FAO, 2023). They provide food security and income for more than 400 million people across South and Central America, Asia, and Africa (FAO, 2023). Owing to their low genetic diversity, commercial banana varieties are particularly susceptible to disease (Drenth and Kema, 2021). Fungal pathogens, including *Fusarium oxysporum* f. sp. *cubense*, are major constraints to production, often necessitating agrochemical inputs that are increasingly less effective (Gutierrez-Monsalve et al., 2015; Bubici et al., 2019; Drenth and Kema, 2021). However, not all fungi are pathogenic: many contribute to disease suppression, nutrient acquisition, and stress tolerance (Rodríguez-Romero et al., 2005; Ting et al., 2008; Ahmad et al., 2018). Improving management of commercial banana ecosystems therefore requires a more comprehensive understanding of fungal microbiomes (mycobiomes). This is challenging because mycobiomes exhibit strong spatial and temporal turnover and are shaped by land management practices (Birt et al., 2024), limiting the generalisability of findings from individual locations. Despite this variability, a subset of taxa consistently persists across environments. These “core” taxa tend to account for a substantial proportion of community abundance and are hypothesised to be ecologically relevant because of their stable host-associations across diverse environmental gradients (Liu et al., 2017;

* Corresponding author.
E-mail address: p.dennis@uq.edu.au (P.G. Dennis).

https://doi.org/10.1016/j.apsoil.2026.107040
Received 9 January 2026; Received in revised form 8 April 2026; Accepted 10 April 2026
Available online 18 April 2026
0929-1393/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Lay et al., 2018; Shade and Stopnisek, 2019; Simonin et al., 2020). These attributes make them useful candidates for further ecological and functional investigation.

In Australia, Birt et al. (2023) identified 21 core fungal operational taxonomic units (OTUs) associated with banana. Despite representing only 0.35% of detected OTUs, these taxa comprised 50–60% of the total community abundance. While that study demonstrated that these OTUs occurred in other published datasets, it did not assess whether they met the core criteria beyond Australia. As such, existing national lists of core taxa for banana are useful to prioritise research efforts within countries but remain uncertain over broader geographical scales. Identifying internationally persistent core taxa could strengthen industry collaboration, support coordinated biobanking initiatives (Ryan et al., 2023), and provide a basis for future investigation of microbiome-informed management strategies across regions.

Here, using ITS2 metabarcoding, we identified a multi-country core mycobiome associated with banana (*Musa* spp.) comprising 59 fungal taxa from the bulk and ectorhizosphere soil of a single banana variety ('Pisang Awak', *Musa* ABB). In each of six countries (Australia, Philippines, Lao PDR, Malaysia, South Africa, and Uganda), tissue-culture plantlets were grown in pots containing soils collected from banana plantations with distinct edaphic properties. DNA was then extracted from bulk and ectorhizosphere samples and sent to the University of Queensland for ITS2 metabarcoding and analysis. This standardised approach facilitated the identification of core taxa within and between countries and sites.

2. Methods

2.1. Soil collection and set up of the pot experiments

In each country (Australia, Philippines, Lao PDR, Malaysia, South Africa and Uganda), bulk soil was collected from up to five different farms (Fig. 1). At each farm, soil was sampled near the base of banana plants to a depth of c. 0–20 cm depth after removing surface leaf litter. Samples were passed through a clean 8 mm sieve, pH was measured using the method of Moody and Cong (2008), and 1 kg (fresh weight) was weighed into clean 120 mm × 125 mm pots. All farms had distinct edaphic properties, and no reported instances of Fusarium wilt within the year prior to sampling, and no visible disease symptoms at the time of collection. Site locations and soil properties are provided in Table S1.

Within seven days of soil collection, *Musa* (ABB) 'Pisang Awak' tissue culture (TC) plantlets were rinsed free of agar, then transplanted into the prepared pots. Pisang Awak was selected because it was available in all participating countries, albeit with different local names (Ducasse in Australia, Kayinja in Uganda, Kluai Nam Wa in Lao PDR, and Cardaba in the Philippines). To account for potential mortality, TC plantlets were transplanted into 15 replicate pots per soil in each country. To minimise contamination, benches and tools were sterilised with 4% bleach and new gloves were used between different soils.

2.2. Growth conditions

Prior to being exposed to full sunlight, TC banana plantlets were 'hardened' in shaded chambers with high humidity for one month, then moved to greenhouses, where they were regularly watered and exposed to full sunlight gradually over a few weeks. Plants were harvested when they were ≥ 10 cm tall, which took 12–16 weeks depending on country due to differences in climate and soils. Within countries, all plants were harvested at the same time with the slowest-growing treatment determining when sampling occurred. Ten plants were sampled per soil, except for treatments with higher mortality (e.g., Philippines Soil 4 and South Africa Soil 5), which were excluded if they had fewer than three replicates.

2.3. Bulk and ectorhizosphere soil sampling and DNA extraction

Samples of bulk soil and ectorhizosphere soil were collected using the protocol of Birt et al. (2021). Briefly, after removing a plant from its pot, bulk soil was shaken into a bag and a sub-sample collected in a 50 mL Falcon tube. Using sterile scissors, roots were then excised from the rhizome, cut into 2–3 cm apical, middle, and basal sections, and pooled

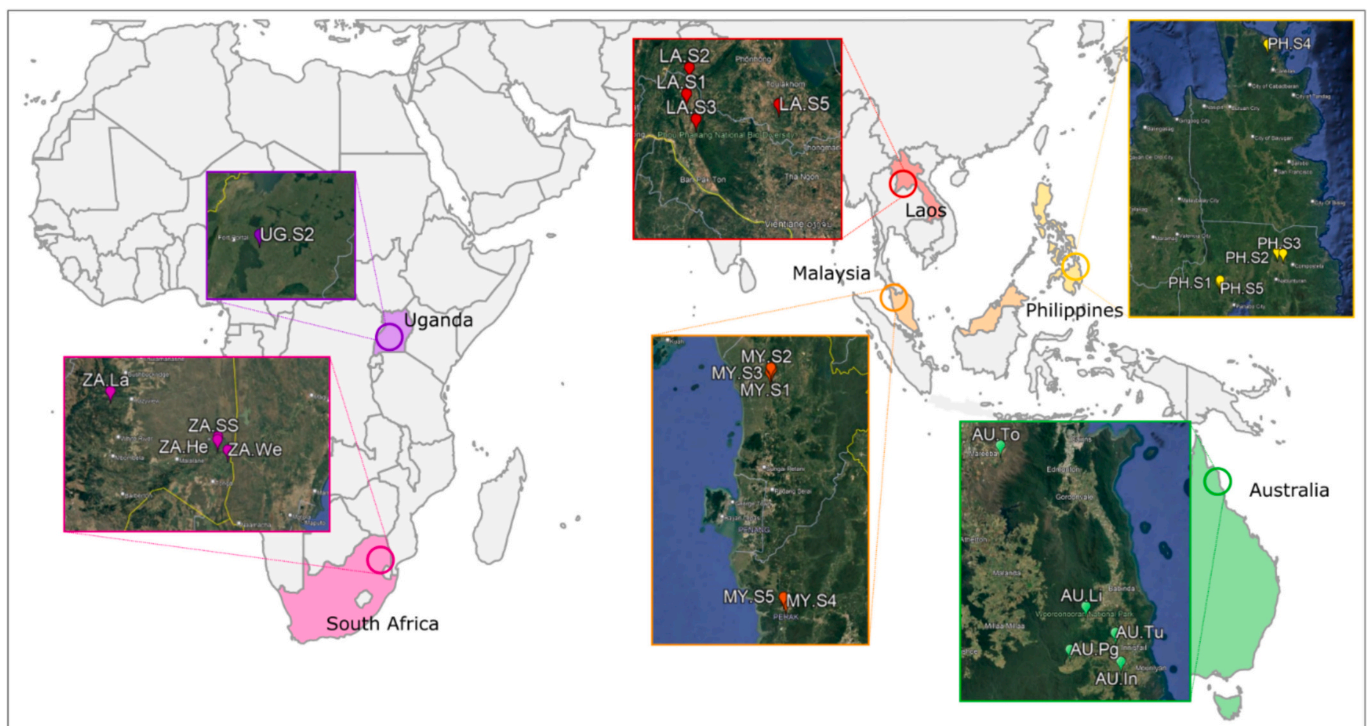


Fig. 1. Map of the 24 banana farms (sites) from which soils were collected.

in a 50 mL Falcon tube. Ectorhizosphere was then collected by shaking roots in 40 mL of 1× phosphate buffered saline (PBS) by hand for 5 min, or if available, by vortex for 2 min. Roots were then removed and ectorhizosphere soils were pelleted by centrifugation at 480 × g for 5 min. All samples were stored at −20 °C prior to DNA extraction.

2.4. PCR amplification and sequencing of ITS2 rRNA genes

In all countries, DNA was extracted using the DNeasy PowerSoil Pro Kits (Qiagen) as per the manufacturer's instructions, and then shipped to the University of Queensland, Australia, for ITS2 metabarcoding.

To PCR amplify fungal ITS2 regions without significant co-amplification of *Musa*, we used the semi-nested PCR described by Birt et al. (2023). Briefly, primers ITS-F_KYO1 (5′-CTH GGT CAT TTA GAG GAA STA A-‘3) (Toju et al., 2012) and ITS4 (5’-TCC TCC GCT TAT TGA TAT GC-‘3) (White et al., 1990) were used to generate full ITS amplicons (PCR 1), which were then used as template in PCR 2 to target the ITS2 region using gITS7 (5’- GTG AAT CAT CGA ATC TTT G-‘3) (Ihrmark et al., 2012) and ITS4. For PCR 1, reactions contained: 2.5 μL of DNA sample in 1× AmpliTaq Gold 360 master mix (Thermo Fisher) and 250 nM of each primer made to a total volume of 20 μL with molecular biology grade water. Amplifications were performed using a SimpliAmp™ 96-well Thermocycler (Applied Biosystems) under the following conditions: 95 °C for 8 min; then 15 cycles of 95 °C for 20 s, 56 °C for 30 s, 72 °C for 1 min, followed by 72 °C for 7 min. Amplicons were then purified using an 18% suspension of Sera-Mag Speed-beads Carboxyl Magnetic Beads (GE Healthcare), added in a ratio of 1.8:1 (*v*/*v*) (Rohland and Reich, 2012). Each PCR 2 reaction contained: 4.5 μL of the purified product from PCR 1, 1× AmpliTaq Gold 360 master mix (Thermo Fisher), and 250 nM of each primer made to a total volume of 20 μL with molecular biology grade water. The thermocycling conditions were identical to those used in PCR 1, except PCR 2 had 25 cycles. PCR 2 products were bead purified as described for those from PCR 1, and eight replicates per site were selected at random for sequencing. PCRs for Soil 4 from Lao PDR failed so it was excluded. Blank extraction controls and no-template PCR controls were included and verified by gel electrophoresis. Equimolar concentrations of each indexed sample were pooled and sequenced as a single batch on an Illumina MiSeq using 30% PhiX Control v3 (Illumina) and a MiSeq Reagent Kit v3 (600 cycles; Illumina) according to the manufacturer's instructions.

2.5. Sequence data processing

Sequence data were processed as described by Birt et al. (2023). Briefly, cutadapt from QIIME2 v2017.9 (Bolyen et al., 2019) was used to demultiplex samples, then fungal ITS2 sequences were extracted using ITSx v1.0.1 (Bengtsson-Palme et al., 2013). Chimeric sequences were removed using uchime2_ref from USEARCH (v10.0.240) (Edgar, 2010) against the UNITE v10 database (Abarenkov et al., 2024). The resulting ITS2 reads were then mapped against representative sequences using fastx_uniques and cluster_otus (sequence similarity = 0.97) from USEARCH to produce an OTU table. UNITE v10 taxonomy was assigned using BLASTN v2.3.0+ (Zhang et al., 2000) and data were then rarefied to a depth of 1000 reads per sample to normalise sequencing effort. This depth is sufficient to capture patterns of beta diversity (Lundin et al., 2012) and to reliably detect candidate core taxa based on the thresholds described in Section 2.7. All alpha diversity metrics were produced using QIIME2 v2017.9 (Bolyen et al., 2019). Lastly, ecological guilds were assigned using FUNGuild v1.x (Nguyen et al., 2016) with default parameters.

2.6. Matching sequences to previously identified banana core taxa

The ITS2 OTU sequences for our present study were compared to the sequences of the 21 core fungal OTUs identified by Birt et al. (2023) using USEARCH (Edgar, 2010). OTUs that were ≥ 97% similar were flagged as close matches.

2.7. Establishing a multi-country core assemblage

To operationally define core taxa, we first identified OTUs that consistently met biologically meaningful thresholds within each site. For each compartment at each site, OTUs present in ≥50% of biological replicates at a relative abundance of ≥0.5% were designated as candidate core OTUs (Fig. S1). Rather than imposing a binary definition of “core”, we quantified “coreness” as the number of sites in which an OTU satisfied these candidate criteria (i.e., cross-site occupancy). Candidate core OTUs were ranked within each compartment according to this occupancy measure, such that OTUs occurring in more sites were considered more core. The relationships between rank, occupancy, and country distribution were then examined to identify inflection points in the occupancy-rank distributions (Fig. 5A–C). OTUs within the upper occupancy tier defined by these inflection points were designated as the international core taxa reported in this study. For consistency across compartments, an equal number of highest-ranked OTUs were designated from bulk soil and the ectorhizosphere. This framework treats “coreness” as a continuous property reflecting geographic persistence rather than a strict categorical assignment. For full transparency, all candidate core OTUs, including their occupancy rank, number of sites, and number of countries in which they occurred, are provided in the Supplementary File.

2.8. Statistical analyses

The main and interactive effects of country (Australia, Lao PDR, Malaysia, Philippines, South Africa and Uganda), sites (sampling location) and compartments (ectorhizosphere and bulk soil) on univariate response variables (alpha diversity metrics, i.e., Shannon's Diversity Index and the numbers of observed (S_{obs}) and predicted (Chao1) OTUs, were evaluated using ANOVA with Tukey's HSD post hoc comparisons. The main and interactive effects of country, site and compartment on multivariate responses (Hellinger transformed OTU relative abundances) were assessed using PERMANOVA. All analyses were performed using R (v4.3.0; R Core Team, 2021). For alpha diversity models, the variance explained by each factor was estimated using partial η^2 derived from the ANOVA models, calculated using the *effectsize* package (Ben-Shachar et al., 2020). For community composition, the proportion of variance explained by each predictor was estimated as R^2 from the PERMANOVA models.

3. Results

3.1. Effects of country, site and compartment on fungal alpha diversity

The alpha diversity of fungal communities was significantly influenced by the main and interactive effects of country, site and compartment (Table 1). Country accounted for a larger proportion of variance in alpha diversity than site and compartment (Tables 1 and S2). Site had a significant effect on alpha diversity in all countries, except for South Africa (Table 1). In Australia, the interaction between site and compartment significantly influenced alpha diversity (Table 1), while in Laos, both the interactive and individual effects of compartment and site significantly influenced fungal alpha diversity. Compartment did not have a significant influence on the alpha diversity of fungal communities in Malaysia, Philippines, South Africa or Uganda (Table 1). ANOVAs on each individual site within Malaysia and Philippines, however, indicated that a few sites had significant differences between compartments (Fig. 2).

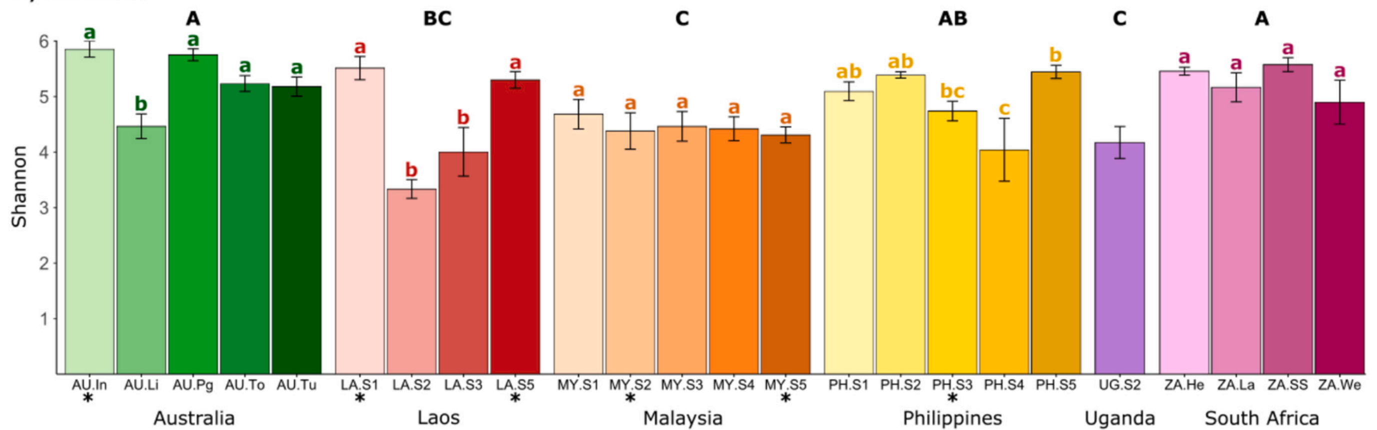
3.2. Changes in the composition of fungal communities

Fungal communities from all sites were dominated by members of

Table 1

Results from ANOVA and PERMANOVA models representing the main and interactive effects of country (Australia, Laos, Malaysia, Philippines, South Africa, and Uganda), site (sampling locations), and compartment (bulk vs. ectorhizosphere soil) on the alpha (Shannon's Diversity Index) and beta (Hellinger transformed OTU relative abundances) diversity of fungal communities, respectively. For alpha diversity, partial η^2 values are reported as estimates of variance explained, while for community composition R^2 values from PERMANOVA represent the proportion of variance explained by each predictor. Asterisks indicate significant differences where $P < 0.001^{(***)}$; $P < 0.01^{(**)}$; $P < 0.05^{(*)}$; $P < 0.10^{(.)}$.

Country	Predictor	Shannon Diversity Index					Community composition			
		df	*F* value	η^2 (%)	*P* value		*F* value	R^2 (%)	*P* value	
All	Country	5	31.20	33.91	<0.001	***	34.16	23.24	<0.001	***
	Site	18	3.60	17.57	<0.001	***	10.32	25.28	<0.001	***
	Compartment	1	14.96	4.69	<0.001	***	12.26	1.67	<0.001	***
	Country: Site: Compartment	23	3.18	19.40	<0.001	***	2.70	8.44	<0.001	***
Australia	Site	4	4.54	22.66	0.003	**	14.70	44.69	<0.001	***
	Compartment	1	1.80	2.82	0.185		4.95	3.76	<0.001	***
	Site: Compartment	4	2.69	14.78	0.039	*	1.45	4.42	0.017	*
Laos	Site	3	5.54	25.32	0.002	**	6.02	19.76	<0.001	***
	Compartment	1	19.44	28.40	<0.001	***	11.94	13.05	<0.001	***
	Site: Compartment	3	5.44	24.99	0.003	**	4.15	13.60	<0.001	***
Malaysia	Site	4	4.25	19.33	0.004	**	11.81	34.59	<0.001	***
	Compartment	1	3.06	4.13	0.085	.	8.61	6.31	<0.001	***
	Site: Compartment	4	2.37	11.80	0.060	.	2.42	7.10	<0.001	***
Philippines	Site	4	3.64	19.78	0.010	*	6.38	27.59	<0.001	***
	Compartment	1	2.29	3.74	0.135		2.63	2.84	<0.001	***
	Site: Compartment	4	1.30	8.11	0.280		1.33	5.74	0.0134	*
South Africa	Site	3	0.20	1.21	0.896		15.41	45.03	<0.001	***
	Compartment	1	2.34	4.55	0.133		2.92	2.85	0.002	**
	Site: Compartment	3	2.13	11.56	0.108		1.50	4.40	0.0352	*
Uganda	Compartment	1	2.32	14.19	0.150		1.25	8.22	0.189	



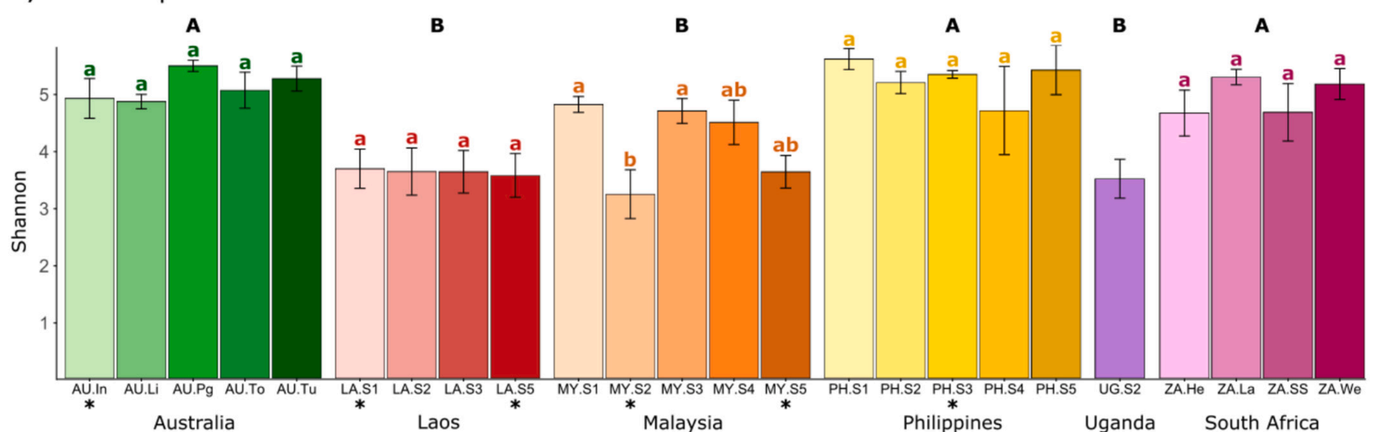


Fig. 2. The alpha diversity (Shannon's Diversity Index) of fungal communities in each site, grouped by country, within A) the bulk soil and B) the ectorhizosphere. Error bars represent the standard errors of the means. Capital letters represent significant differences between countries based on Tukey post hoc analysis of the average of all sites in each country. Lower case letters represent significant differences between sites within countries based on Tukey post hoc analysis. Asterisks indicate sites that differed significantly ($P < 0.05$) between compartments.

the Ascomycota, and to a lesser extent Basidiomycota and Mortierellomycota. Other fungal phyla were more sporadically represented and at lower relative abundances (Fig. 3). At the OTU level, fungal community composition (beta diversity) was significantly associated with the main and interactive effects of country, site, and compartment (Table 1). Country accounted for the greatest proportion of compositional variance (Table 1).

The composition of fungal communities was generally more similar among geographically closer sites (e.g., within the same country or latitude), while those from the Philippines were the most distinct (Fig. 4). Across most countries, variation among sites was greater than variation between compartments (Table 1). Ordination further showed that sites within each country formed distinct clusters, although in Laos, clustering was driven primarily by compartment and secondarily by site (Fig. 4; Fig. S2). By contrast, in Uganda (where only one site was investigated), compartment had no significant effect, and communities did not cluster by compartment (Table 1; Fig. S2).

3.3. *Defining international core taxa of Musa spp.*

Applying the ≥50% prevalence and ≥ 0.5% relative abundance thresholds at each site identified 328 OTUs in bulk soil and 293 in the ectorhizosphere as candidate core members across the 24 sites. Of these, 206 were shared between compartments, yielding 415 unique candidate core OTUs. Cross-site occupancy was positively associated with the number of countries in which an OTU occurred (Fig. 5A–B), indicating that geographically widespread taxa more frequently satisfied the candidate core criteria across sites.

Ranking candidate core OTUs by occupancy revealed a pronounced inflection in the occupancy-rank distribution around rank 50 for both compartments (Fig. 5C), separating a high-occupancy group from a larger pool of lower-occupancy taxa. All OTUs detected in four or more countries occurred within this upper occupancy tier (ranks ≤50; Fig. 5B), whereas OTUs restricted to a single country generally ranked below 50. This threshold therefore captured the inflection separating highly persistent taxa from the broader pool of lower-occupancy OTUs. A small number of exceptions (e.g., OTUs 59 and 126 in the ectorhizosphere; OTUs 77 and 36 in bulk soil) reached high ranks due to consistent presence across all five sampled sites within a single country (Fig. 5; Fig. S3), showing that strong within-country persistence was also associated with high coreness.

Consistent with this structural pattern, cumulative relative

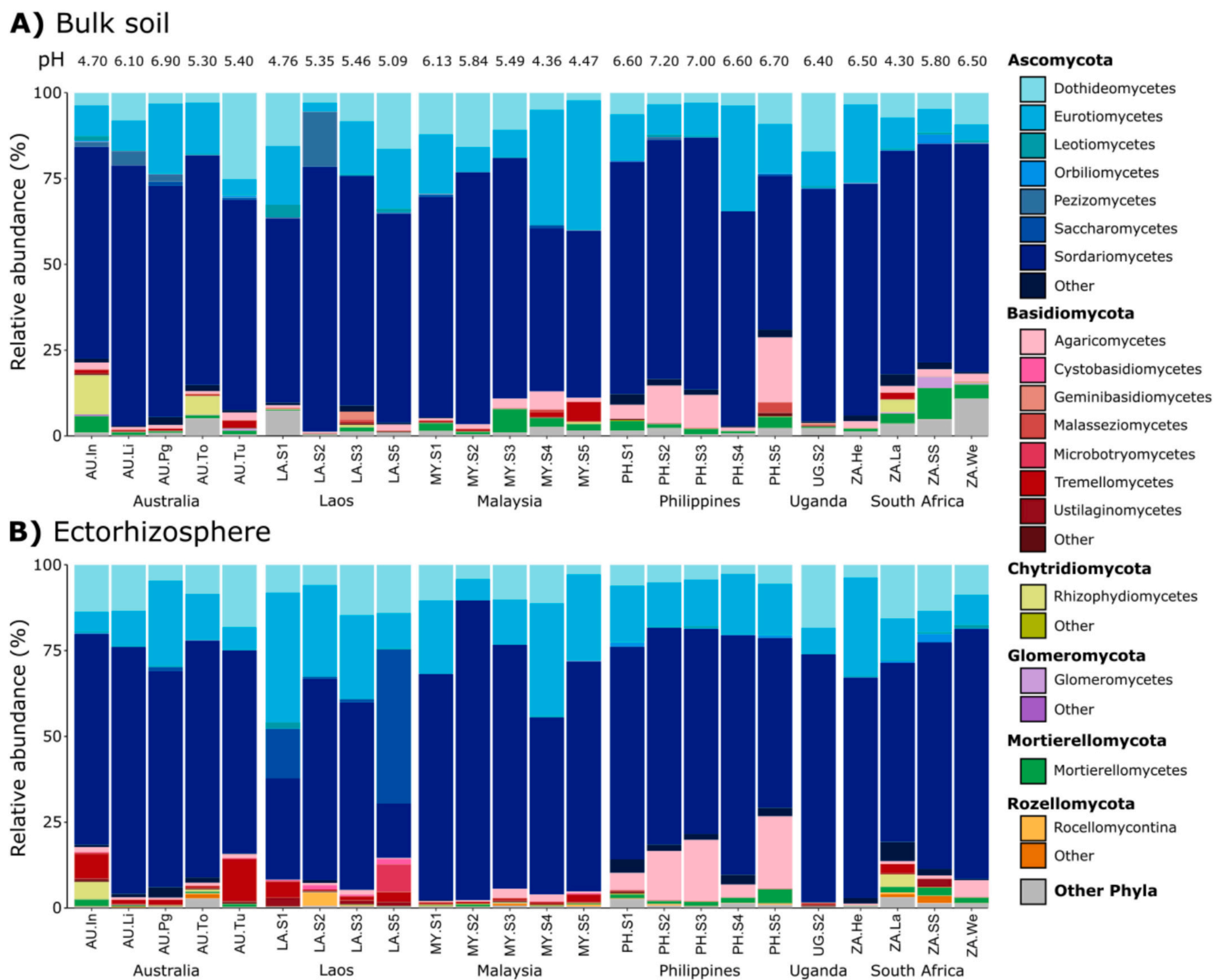


Fig. 3. Stacked bar graphs highlighting the relative abundances of fungal classes present at ≥1% mean relative abundance within at least one site for A) bulk soil, and B) ectorhizosphere samples. Within each phylum, classes representing <1% relative abundance were grouped as "Other". Phyla lacking any classes at ≥1% relative abundance were grouped as "Other phyla". The pH of each soil is shown above the bars in panel A.

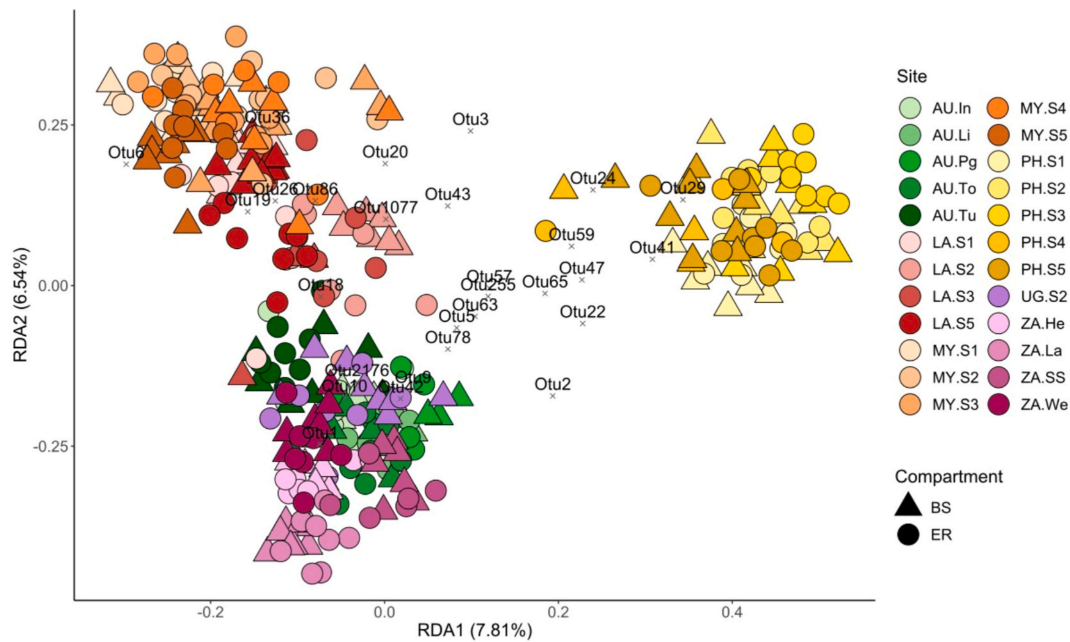


Fig. 4. Redundancy analysis (RDA) ordination highlighting differences in the composition of fungal communities as represented by Hellinger transformed OTU relative abundances constrained by country. Triangles represent bulk soil and circles represent the ectorhizosphere. The OTU IDs match those in the heatmap (Fig. 6).

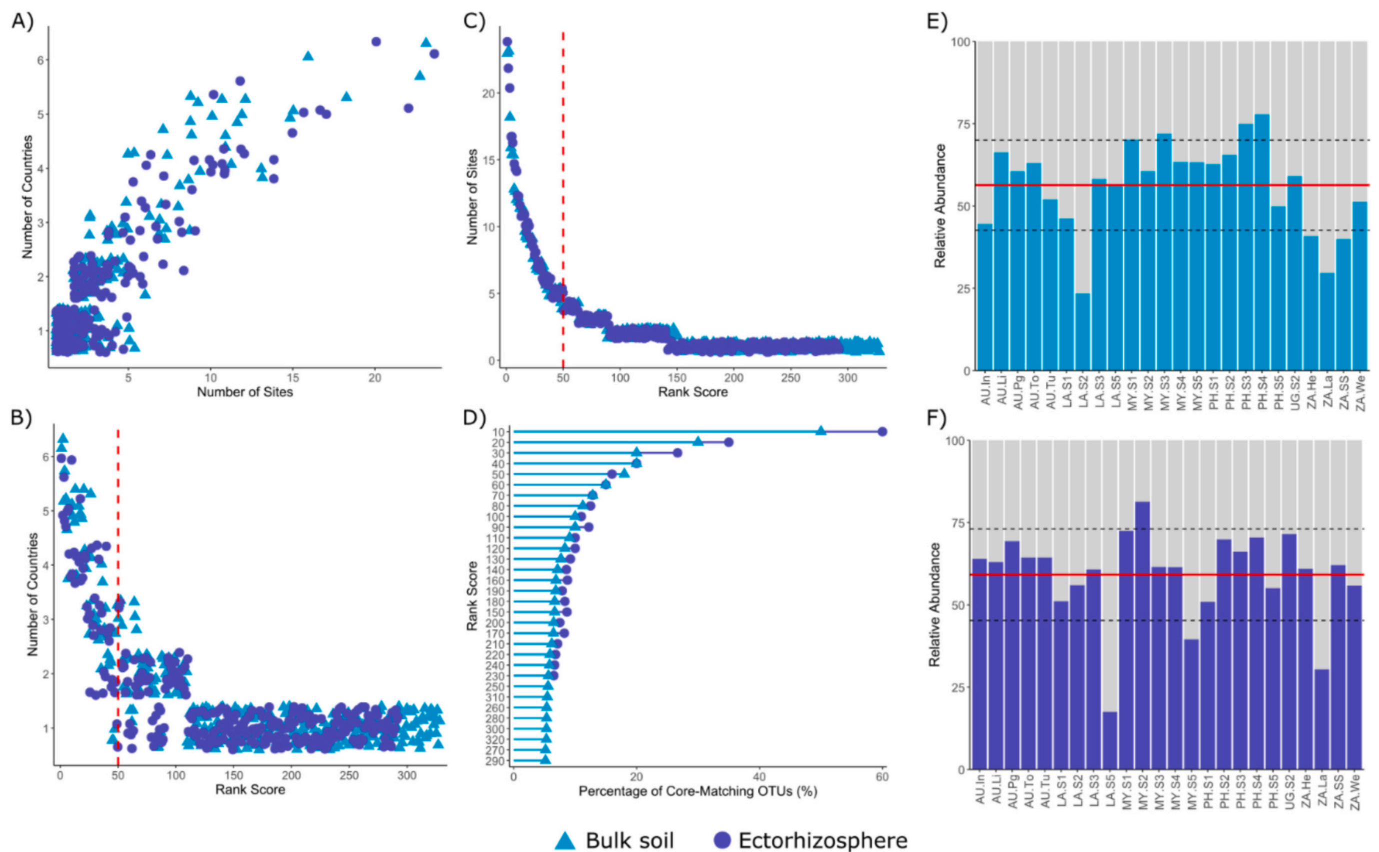


Fig. 5. A) The number of sites and countries in which each OTU was identified as a candidate core. B) The rank score of a candidate OTU and the number of countries it occupied, and C) Relationship between the rank score of an OTU and the number of sites in which it was identified as a candidate core; the dashed red line indicates the rank threshold (50) separating candidate core taxa from lower-ranked OTUs. D) Percentage of candidate core OTUs matching core fungal taxa from Birt et al. (2023), within the top 10, top 20, etc. ranked OTUs. E) Mean combined relative abundance of the identified core OTUs relative to the total OTU community in bulk soil samples; the red line indicates the mean relative abundance of all core OTUs and dashed lines represent ±1 standard deviation. F) Mean combined relative abundance of the identified core OTUs relative to the total OTU community in ectorhizosphere samples; the red line indicates the mean relative abundance of all core OTUs and dashed lines represent ±1 standard deviation.

abundance increased sharply across ranks 1–50 and stabilised thereafter (Fig. 5E–F), indicating that the upper coreness tier accounts for a substantial proportion of total community abundance. Together, the occupancy-rank inflection and the subsequent stabilisation of cumulative relative abundance provide complementary evidence for defining the upper coreness tier and the international core set reported here. Full occupancy rank, site-level presence, and country distribution data for all candidate core OTUs are provided in the Supplementary File.

3.4. An international core assemblage of fungal taxa associated with *Musa* spp.

The upper coreness tiers of taxa (ranks ≤50) identified in bulk soil and the ectorhizosphere were combined into a non-redundant set comprising 59 unique core fungal OTUs. This assemblage was dominated by Ascomycota, with only two Basidiomycota representatives and one Mortierellomycota representative (Fig. 6; Fig. S3). Although representing just 0.87% of all detected OTUs (59 of 6755), this core set represented a substantial proportion of total community abundance: 22–78% (mean = 56.3, SD = 13.7) in bulk soil and 17–83% (mean = 59.2, SD = 13.9) in the ectorhizosphere.

Highly ranked taxa corresponded closely with the core mycobiome of banana reported by Birt et al. (2023) (Figs. 5–6; Fig. S3). Of the 21 fungal OTUs they identified as core across eight compartments, we recovered ≥97% sequence similarity matches to 14 (67%), including eight of the nine (89%) OTUs they designated as core in bulk and ectorhizosphere soil (Supplementary file). The only bulk/ectorhizosphere soil core OTU not detected in our dataset was a representative of the *Colletotrichum siamense* (OTU 8). The remaining six matching taxa were reported by Birt et al. (2023) as core in other compartments, including the endorhizosphere, rhizome, pseudostem, or leaves (Supplementary file). Forty-one of the 59 core OTUs were assigned "probable" or "highly probable" guild classifications using FunGuild. The assemblage included many taxa classified as multifunctional pathotroph–saprotroph–symbiotrophs (37%) and pathotroph–saprotroph fungi (34%), and comprised predominantly plant-associated genera such as *Trichoderma*, *Aspergillus*, and *Penicillium* (Supplementary Information).

4. Discussion

Identifying internationally persistent core taxa provides a useful basis for future investigation of microbiome-informed approaches for sustainable agriculture (Toju et al., 2018). While regional studies provide valuable insights into local variation, broader sampling across contrasting environments is needed to identify taxa that consistently

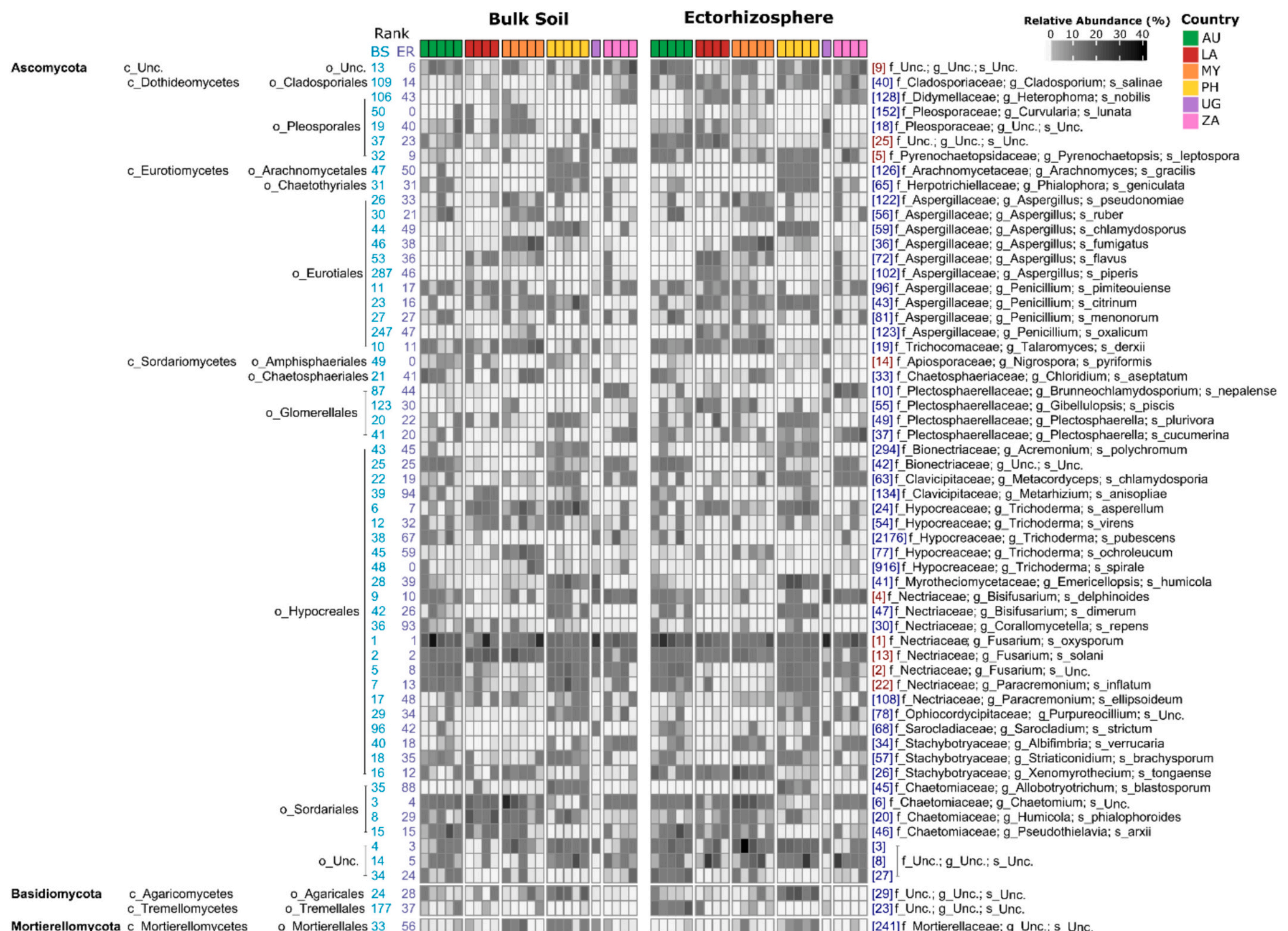


Fig. 6. Heatmap summarising the relative abundances of the 59 non-redundant core fungal OTUs identified using the occupancy–rank framework from bulk soil and the ectorhizosphere of *Musa* (ABB) 'Pisang Awak' across 24 farms in six countries (Australia (AU) = green, Laos (LA) = red, Malaysia (MY) = orange, Philippines (pH) = yellow, South Africa (ZA) = pink, and Uganda (UG) = purple). Rank scores are given in light blue (bulk soil) or purple (ectorhizosphere) on the left of the heatmap. A rank score of 0 indicates that the OTU was not a candidate core for that compartment in any site. OTU IDs are shown in square brackets next to the family and genus labels. OTUs shown in red match the sequences (≥97% similarity) of core OTUs identified by Birt et al. (2023).

persist across ecological gradients and to capture the diversity of farming systems across countries (Xu et al., 2018). By surveying banana systems across 24 sites in six countries spanning Africa, Asia, and Australia, we identified 59 fungal taxa with high cross-site occupancy that consistently met prevalence–abundance criteria in banana-associated soils. This multi-country design captured variation in climate, soil properties, and management practices, as well as ecological contrasts between bulk soil and the ectorhizosphere.

4.1. Similarities and differences between countries and sites

Across all countries, banana-associated mycobiomes were dominated by Ascomycota, in line with previous studies of *Musa* spp. fungal communities (Fu et al., 2017; Rames et al., 2018; Liu et al., 2019; Kaushal et al., 2020; Shen et al., 2022; Birt et al., 2023). Basidiomycota and Mortierellomycota were also well represented, whereas Chytridiomycota and Rozellomycota appeared sporadically, and Glomeromycota were only occasionally detected at appreciable abundance. The low representation of Glomeromycota in ITS metabarcoding studies contrasts with their frequent observation under the microscope in banana roots (Declerck et al., 1995; Van der Veken et al., 2008; Jefwa et al., 2012), suggesting that ITS-based approaches may underrepresent this group (Krüger et al., 2009). Targeted sequencing approaches may therefore be required to fully assess the occurrence of arbuscular mycorrhizal fungi in banana systems (Krüger et al., 2009).

Community-level analyses revealed a strong geographic signal, with clear differentiation among countries and additional structuring among sites within countries. These patterns are consistent with broader evidence that both geographic distance and local environmental factors are associated with fungal community composition (Bahram et al., 2018). Variation in climate, soil properties, and management practices likely interact to generate the regional differences in community composition observed here. Differences between bulk soil and the ectorhizosphere further reflect compartment-specific ecological filtering consistent with the distinct physicochemical and biological conditions associated with plant roots (Zheng et al., 2021; Birt et al., 2023).

Because this study involved sampling across multiple countries with differing analytical infrastructure and biosecurity constraints, it was not feasible to quantify a comprehensive suite of soil physicochemical properties using standardised methods across all sites. Soil pH, however, was measured consistently by all participating laboratories at the site level and is widely recognised as a key determinant of microbial community structure. Soil pH was significantly associated with variation in both the overall fungal community and the core assemblage (Fig. S4), consistent with the possibility that differences in soil conditions among sites are linked to regional variation in mycobiome structure. Understanding the ecological preferences of the banana mycobiome and its core taxa may also help guide future investigation of whether microbiome composition can be influenced indirectly through farm practices such as soil amendments and crop management (Clarke et al., 2024).

4.2. The international core taxa of *Musa* spp.

Applying prevalence–abundance criteria identified 328 candidate core OTUs in bulk soil and 293 in the ectorhizosphere across the 24 sites. Ranking these taxa by cross-site occupancy distinguished a highly persistent subset, and combining the upper occupancy tiers from each compartment yielded a non-redundant assemblage of 59 core fungal OTUs. This assemblage showed strong concordance with the core taxa previously reported in bulk soil and the ectorhizosphere by Birt et al. (2023), with all but one taxon recovered at ≥97% sequence similarity. As only bulk soil and ectorhizosphere were sampled here, the absence of taxa from other plant compartments (e.g., pseudostem, leaves) was expected. Notably, nearly all core OTUs from Birt et al. (2023) were again detected in Australian samples, consistent with the persistence of these OTUs across geographical and environmental gradients and over time. Although fungal diversity in banana production systems remains less well characterised than bacterial communities, particularly across multiple countries, the recurrence of these taxa across contrasting environments suggests that a relatively small subset of fungi consistently accounts for a substantial proportion of banana-associated fungal abundance.

While the 59 core fungal taxa represented only 0.87% of the total OTUs detected, they represented 22–83% of the total community relative abundance. Although formal diagnostic tests were not performed, all plants in this study lacked visible signs of disease or pest damage. Accordingly, this assemblage of core fungal OTUs was associated with visually healthy plants. Notably, functional guild assignments suggested that many of these taxa belong to genera that include plant pathogens (e.g., Fusarium). This pattern is not unexpected, as numerous fungal genera contain both pathogenic and non-pathogenic lineages, and ecological function often varies at the strain level. Consequently, the presence of taxa with pathogenic relatives does not necessarily imply disease risk, and some members of these groups may exist as commensals or latent symbionts in association with healthy plants. Identifying these persistent taxa therefore provides a useful foundation for future work aimed at clarifying their ecological roles and evaluating whether their abundances are associated with host health and productivity.

4.3. Future work with core taxa

Clarifying the ecological roles of these persistent taxa and evaluating whether their abundances are associated with host health and productivity represent important next steps for advancing banana mycobiome research. If these functions can be resolved, some core taxa may warrant consideration in future strategies aimed at supporting banana production and resilience, either through direct inoculation of beneficial isolates, or indirectly through farm management practices that influence their abundance and activity. Because the core assemblage comprises a relatively small and consistently detected subset of the broader fungal community, focusing on these 59 OTUs provides a tractable framework for hypothesis-driven investigation. Their consistent occurrence across sites also suggests that insights gained from studying these taxa may be relevant across multiple production systems.

One possible future application of these taxa is in microbiome-based approaches aimed at supporting plant health, including the potential use of microbial inoculants. The use of agrochemical inputs to support plant growth and control fungal pathogens and pests continues to rise, contributing to adverse environmental impacts and resistance in target organisms (Rahman et al., 2018). Biocontrol agents (i.e., microbes and/or their metabolites) represent a promising alternative and can be as effective as chemical pesticides (Gutierrez-Monsalve et al., 2015; Tyśkiewicz et al., 2022). The internationally persistent core taxa identified here may provide a useful starting point for future investigation of such approaches, as their recurrence across diverse soils, climates, and management systems suggests ecological robustness and consistent association with bananas (Zhou et al., 2024).

Circumstantial evidence from the literature indicates that close relatives of several core OTUs belong to genera that include strains with antagonistic or plant-promoting traits, such as *Aspergillus*, *Fusarium*, *Penicillium*, *Talaromyces*, and *Trichoderma* (Thambugala et al., 2020). While some members of the *Fusarium oxysporum* species complex are well-known pathogens, many lineages are non-pathogenic, commonly associated with healthy plants, and have been reported to suppress pathogenic strains (Forsyth et al., 2006; Nel et al., 2006a, 2006b; Belgrove et al., 2011; Zimmermann et al., 2016). Notably, the most dominant core fungal OTU in our present study (Fig. 6) and in Birt et al. (2023) was assigned to the *Fusarium oxysporum* species complex, indicating a recurrent association with *Musa* spp. Similarly, species within the genus *Trichoderma* include strains reported to stimulate plant growth, antagonise pathogens, and colonise the rhizosphere (Tyśkiewicz et al., 2022; Idbella et al., 2023). Members of both *Trichoderma* and

Penicillium have also been reported to be enriched in Fusarium wilt-suppressive soils (Puig and Cumagun, 2019; Win et al., 2021; Jamil et al., 2023), while representatives of *Aspergillus* have been shown to antagonise *Fusarium* spp. in vitro (Hidayat et al., 2019). The inverse abundance relationship observed here between *Trichoderma* OTU 2176 and *Fusarium* OTU 13 (Fig. 6) is consistent with the possibility of antagonistic interactions involving pathogenic *Foc*, although this remains to be tested directly.

Importantly, our study identifies several persistent lineages within the fungal tree that are consistently associated with banana across sites and environments. However, functional inference based on taxonomy or ITS2 sequence similarity alone provides only coarse ecological resolution, as closely related taxa, particularly within species complexes such as the *Fusarium oxysporum* species complex, can exhibit substantial functional variation. Because ITS markers generally do not resolve strain-level diversity, further targeted sequencing within these recurrent lineages may help determine whether specific strains are consistently associated with visually healthy plants or particular ecological traits. Isolation and culture of these taxa would then be required for direct characterisation of pathogenicity, beneficial traits, and ecological interactions. Such work may help evaluate whether pure or mixed-isolate inoculants could be developed for reintroduction into banana production systems. Alternatively, improved understanding of how these taxa respond to environmental gradients (e.g., soil pH; Fig. S4) and farm management practices may help assess whether their abundances can be influenced indirectly through microbiome-informed management.

5. Conclusion

This study provides the first large-scale multi-country survey of banana-associated mycobiomes, revealing clear geographic structuring and underscoring the importance of sampling across diverse soils, climates, and management systems. Using abundance–occupancy criteria, we identified 59 internationally persistent core fungal taxa that, while representing less than 1% of detected OTUs, accounted for up to 83% of total community relative abundance. Their recurrence across continents, environmental gradients, and time points indicates that they are stable components of banana-associated fungal communities and supports their prioritisation for future investigation.

By defining a reproducible, cross-country core assemblage, this study establishes a practical framework for advancing research on the banana mycobiome. These taxa provide a tractable foundation for isolation, functional characterisation, and future evaluation as candidate taxa of potential relevance to microbiome-informed management strategies. Anchoring future studies to a shared set of core taxa may improve consistency, facilitate collaboration, and help guide the development and assessment of microbiome-informed strategies for sustainable banana production.

CRediT authorship contribution statement

Anna-Belle C. Clarke: Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Christine Rose Ansale:** Writing – review & editing, Project administration. **Loren Banayag:** Writing – review & editing, Methodology. **Sheryl Bayang:** Writing – review & editing, Methodology. **Sheryl Bothma:** Writing – review & editing, Methodology. **Khonesavanh Chittarath:** Writing – review & editing, Methodology, Conceptualization. **Merlina Juruena:** Writing – review & editing, Methodology. **Georgina Karamura:** Writing – review & editing, Project administration, Methodology. **Hazel R. Lapis-Gaza:** Writing – review & editing, Project administration, Methodology. **Cesar Limbaga:** Writing – review & editing, Project administration, Methodology. **Rebecca Lyons:** Writing – review & editing, Project administration, Methodology. **Jiarui Sun:** Writing – review & editing, Formal analysis. **Altus Viljoen:** Writing – review & editing, Project administration. **Diane Mostert:** Writing – review & editing, Project administration. **Noor Baity Saidi:** Writing – review & editing, Project administration, Methodology. **Nurul Shamsinah Mohd Suhaimi:** Writing – review & editing, Project administration, Methodology. **Anthony B. Pattison:** Writing – review & editing, Project administration, Conceptualization. **Paul G. Dennis:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Conceptualization.

Funding

We gratefully acknowledge the funding and support from the Australian Centre for International Agricultural Research through the research project HORT/2018/192.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The sequence data associated with this study is available from NCBI under BioProject: PRJNA1321393. The sequences of core and candidate-core fungal OTUs, together with their similarities to those reported by Birt et al. (2023), are provided in the Supplementary file. The Supplementary file also includes FUNGuild assignments and information on the occupancy rank of each core and candidate-core OTU, along with the number of sites and countries in which they occur.

Acknowledgements

We gratefully acknowledge all banana growers and landholders for allowing us access to their properties. Furthermore, we appreciate technical assistance from Shahnaz Sultana in Australia; Carlito, Hindoy Jr., and Nelvin Villason in the Philippines; and Joseph Ssekandi and Felix Tuyisabe in Uganda. We would also like to acknowledge the students who assisted with the pot trial in Malaysia: Azlee Hafizy Piliang Johari, Noraini Nazri, Hayatun Nabila Norjan, Ong Jia Xin, Nurulhuuda binti Ahmad Sharafae, Ang Shin Huey. We would like to acknowledge Connie Fraser from Banana Growers Association of South Africa who assisted with collection of soils. Michael Tobe, Tim Shuey and Wayne O'Neill are gratefully acknowledged for their help navigating import and export permits and handling.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107040.

References

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., May, T.W., Frøslev, T.G., Pawlowska, J., Lindahl, B., Põldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T.E., Ishigami, Y., Kõljalg, U., 2024. The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. Nucleic Acids Res. 52 (D1), D791–D797. https://doi.org/10.1093/nar/gkad1039.

Ahmad, M., Pataczek, L., Hilger, T.H., Zahir, Z.A., Hussain, A., Rasche, F., Schafleitner, R., Solberg, S.Ø., 2018. Perspectives of microbial inoculation for sustainable development and environmental management. Front. Microbiol. 9, 2992. https://doi.org/10.3389/fmicb.2018.02992.

Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundra, S., Olsson, P.A., Pent, M., Põlme, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. Nature 560, 233–237. https://doi.org/10.1038/s41586-018-0386-6.

Belgrove, A., Steinberg, C., Viljoen, A., 2011. Evaluation of nonpathogenic *fusarium oxysporum* and *Pseudomonas fluorescens* for Panama disease control. Plant Dis. 95, 951–959. https://doi.org/10.1094/PDIS-06-10-0409.

Bengtsson-Palme, J., Ryberg, M., Hartmann, M., Branco, S., Wang, Z., Godhe, A., De Wit, P., Sánchez-García, M., Ebersberger, I., de Sousa, F., Amend, A., Jumpponen, A., Unterseher, M., Kristiansson, E., Abarenkov, K., Bertrand, Y.J.K., Sanli, K., Eriksson, K.M., Vik, U., Veldre, R., Nilsson, R.H., 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods Ecol. Evol. 4, 914–919. https://doi.org/10.1111/2041-210X.12073.

Ben-Shachar, M.S., Lüdecke, D., Makowski, D., 2020. Effectsize: estimation of effect size indices and standardized parameters. J. Open Source Softw. 5 (56), 2815. https://doi.org/10.21105/joss.02815.

Birt, H.W.G., Pattison, A.B., Dennis, P.G., 2021. Sampling microbiomes associated with different plant compartments. In: Carvalhais, L.C., Dennis, P.G. (Eds.), The Plant Microbiome: Methods and Protocols. Springer, New York, NY, pp. 23–29.

Birt, H.W.G., Pattison, A.B., Skarshewski, A., Daniells, J., Raghavendra, A., Dennis, P.G., 2023. The core fungal microbiome of banana (*Musa* spp.). Front. Microbiol. 14, 1127779. https://doi.org/10.3389/fmicb.2023.1127779.

Birt, H.W.G., Pattison, A.B., Carrillo, Y., Lieske, S.N., Lyons, R., Lapis-Gaza, H., Sun, J., Dennis, P.G., 2024. Relative to rainforests and grasslands, banana and sugarcane soils have half the microbial biomass and highly distinct bacterial and fungal communities. Appl. Soil Ecol. 204, 105750. https://doi.org/10.1016/j.apsoil.2024.105750.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J.E., Bittinger, K., Brejnrod, A., Brislawn, C.J., Brown, C.T., Callahan, B.J., Caraballo-Rodríguez, A.M., Chase, J., Cope, E.K., Da Silva, R., Diener, C., Dorrestein, P.C., Douglas, G.M., Durall, D.M., Duvallet, C., Edwardson, C.F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J.M., Gibbons, S.M., Gibson, D.L., Gonzalez, A., Gorlick, K., Guo, J., Hillmann, B., Holmes, S., Holste, H., Huttenhower, C., Huttley, G.A., Janssen, S., Jarmusch, A.K., Jiang, L., Kaehler, B.D., Kang, K.B., Keefe, C.R., Keim, P., Kelley, S.T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M.G.I., Lee, J., Ley, R., Liu, Y.X., Loftfield, E., Lozupone, C., Maher, M., Marotz, C., Martin, B.D., McDonald, D., McIver, L.J., Melnik, A.V., Metcalf, J.L., Morgan, S.C., Morton, J.T., Naimey, A.T., Navas-Molina, J.A., Nothias, L.F., Orchanian, S.B., Pearson, T., Peoples, S.L., Petras, D., Preuss, M.L., Pruesse, E., Rasmussen, L.B., Rivers, A., Robeson, M.S., Rosenthal, P., Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S.J., Spear, J.R., Swafford, A.D., Thompson, L.R., Torres, P.J., Trinh, P., Tripathi, A., Turnbaugh, P.J., Ul-Hasan, S., van der Hooft, J.J.J., Vargas, F., Vázquez-Baeza, Y., Vogtmann, E., von Hippel, M., Walters, W., Wan, Y., Wang, M., Warren, J., Weber, K.C., Williamson, C.H.D., Willis, A.D., Xu, Z.Z., Zaneveld, J.R., Zhang, Y., Zhu, Q., Knight, R., Caporaso, J.G., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat. Biotechnol. 37, 852–857. https://doi.org/10.1038/s41587-019-0209-9.

Bubici, G., Kaushal, M., Prigigallo, M.I., Gómez-Lama Cabanás, C., Mercado-Blanco, J., 2019. Biological control agents against fusarium wilt of banana. Front. Microbiol. 10, 616. https://doi.org/10.3389/fmicb.2019.00616.

Clarke, A.B.C., Lapis-Gaza, H.R., Irvine-Brown, S., Lyons, R., Sun, J., Pattison, A.B., Dennis, P.G., 2024. Moderate phosphorus addition to field-grown bananas enhanced soil microbial enzyme activities but had negligible impacts on bacterial, fungal, and nematode diversity. Appl. Microbiol. 4, 1582–1599. https://doi.org/10.3390/applmicrobiol4040108.

Declerck, S., Plenchette, C., Strullu, D.G., 1995. Mycorrhizal dependency of banana (*Musa acuminata*, AAA group) cultivar. Plant and Soil 176, 183–187. https://doi.org/10.1007/BF00017688.

Drenth, A., Kema, G., 2021. The vulnerability of bananas to globally emerging disease threats. Phytopathology 111, 2146–2161. https://doi.org/10.1094/PHYTO-07-20-0311-RVW.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26, 2460–2461. https://doi.org/10.1093/bioinformatics/btq461.

FAO, 2023. Bananas: Commodity in Focus. Food and Agriculture Organization of the United Nations. https://www.fao.org/markets-and-trade/commodities/bananas/en/. (Accessed 25 July 2023).

Forsyth, L.M., Smith, L.J., Aitken, E.A.B., 2006. Identification and characterization of non-pathogenic *fusarium oxysporum* capable of increasing and decreasing fusarium wilt severity. Mycol. Res. 110, 929–935. https://doi.org/10.1016/j.mycres.2006.03.008.

Fu, L., Penton, C.R., Ruan, Y., Shen, Z., Xue, C., Li, R., Shen, Q., 2017. Inducing the rhizosphere microbiome by biofertilizer application to suppress banana fusarium wilt disease. Soil Biol. Biochem. 104, 39–48. https://doi.org/10.1016/j.soilbio.2016.10.008.

Gutierrez-Monsalve, J.A., Mosquera, S., González-Jaramillo, L.M., Mira, J.J., Villegas-Escobar, V., 2015. Effective control of black Sigatoka disease using a microbial fungicide based on *Bacillus subtilis* EA-CB0015 culture. Biol. Control 87, 39–46. https://doi.org/10.1016/j.biocontrol.2015.04.012.

Hidayat, I., Dewi, L.C., Sukmawati, D., 2019. Antagonistic activity of three *aspergillus* isolates against fusarium wilt of banana. J. Microb. Syst. Biotechnol. 1, 16. https://doi.org/10.37604/jmsb.v1i1.16.

Idbella, M., Mazzoleni, S., Bonanomi, G., 2023. Plant Mycobiome. Springer International Publishing, Cham.

Ihrmark, K., Bödeker, I.T.M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K.E., Lindahl, B.D., 2012. New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiol. Ecol. 82, 666–677. https://doi.org/10.1111/j.1574-6941.2012.01437.x.

Jamil, F.N., Hashim, A.M., Yusof, M.T., Saidi, N.B., 2023. Association of soil fungal community composition with incidence of fusarium wilt of banana in Malaysia. Mycologia 115, 178–186. https://doi.org/10.1080/00275514.2023.2180975.

Jefwa, J.M., Kahangi, E., Losenge, T., Mung'atu, J., Ngului, W., Ichami, S.M., Sanginga, N., Vanluawe, B., 2012. Arbuscular mycorrhizal fungi in the rhizosphere of banana and plantain and the growth of tissue culture cultivars. Agric. Ecosyst. Environ. 157, 24–31. https://doi.org/10.1016/j.agee.2012.03.014.

Kaushal, M., Swennen, R., Mahuku, G., 2020. Unlocking the microbiome communities of banana (*Musa* spp.) under disease-stressed (fusarium wilt) and non-stressed conditions. Microorganisms 8, 443. https://doi.org/10.3390/microorganisms8030443.

Krüger, M., Stockinger, H., Krüger, C., Schüßler, A., 2009. DNA-based species level detection of Glomeromycota: one PCR primer set for all arbuscular mycorrhizal fungi. New Phytol. 183, 212–223. https://doi.org/10.1111/j.1469-8137.2009.02835.x.

Lay, C.Y., Bell, T.H., Hamel, C., Harker, K.N., Mohr, R., Greer, C.W., Yergeau, É., St-Arnaud, M., 2018. Canola root–associated microbiomes in the Canadian prairies. Front. Microbiol. 9, 1118. https://doi.org/10.3389/fmicb.2018.01188.

Liu, H., Carvalhais, L.C., Crawford, M., Singh, E., Dennis, P.G., Pieterse, C.M.J., Schenk, P.M., 2017. Inner plant values: diversity, colonization and benefits from endophytic bacteria. Front. Microbiol. 8, 2552. https://doi.org/10.3389/fmicb.2017.02552.

Liu, Y., Zhu, A., Tan, H., Cao, L., Zhang, R., 2019. Engineering banana endosphere microbiome to improve fusarium wilt resistance in banana. Microbiome 7, 74. https://doi.org/10.1186/s40168-019-0690-x.

Lundin, D., Severin, I., Logue, J.B., Ostman, O., Andersson, A.F., Lindström, E.S., 2012. Which sequencing depth is sufficient to describe patterns in bacterial α- and β-diversity? Environ. Microbiol. Rep. 4, 367–372. https://doi.org/10.1111/j.1758-2229.2012.00345.x.

Moody, P.W., Cong, P.T., 2008. Soil Constraints and Management Package (SCAMP): Guidelines for Sustainable Management of Tropical Upland Soils. Australian Centre for International Agricultural Research, Canberra.

Nel, B., Steinberg, C., Labuschagne, N., Viljoen, A., 2006a. Isolation and characterization of nonpathogenic *fusarium oxysporum* isolates from the rhizosphere of healthy banana plants. Plant Pathol. 55, 207–216. https://doi.org/10.1111/j.1365-3059.2006.01343.x.

Nel, B., Steinberg, C., Labuschagne, N., Viljoen, A., 2006b. The potential of non-pathogenic *fusarium oxysporum* and other biological control organisms for suppressing fusarium wilt of banana. Plant Pathol. 55, 217–223. https://doi.org/10.1111/j.1365-3059.2006.01344.x.

Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol. 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.

Puig, C.G., Cumagun, C.J.R., 2019. Rainforest fungal endophytes for the bio-enhancement of banana toward *fusarium oxysporum* f. sp. *cubense* tropical race 4. Arch. Phytopathol. Plant Protect. 52, 776–794. https://doi.org/10.1080/03235408.2018.1560652.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rahman, S.F., Singh, E., Pieterse, C.M.J., Schenk, P.M., 2018. Emerging microbial biocontrol strategies for plant pathogens. Plant Sci. 267, 102–111. https://doi.org/10.1016/j.plantsci.2017.11.012.

Rames, E.K., Pattison, A.B., Czislowski, E., Smith, M.K., 2018. Soil microbial community changes associated with ground cover management in cultivation of Ducasse banana (*Musa* sp. ABB, Pisang Awak subgroup) and suppression of *fusarium oxysporum*. *Australas*. Plant Pathol. 47, 449–462. https://doi.org/10.1007/s13313-018-0578-4.

Rodríguez-Romero, A., Sol Piñero Guerra, M., Jaizme-Vega, M. del C., 2005. Effect of arbuscular mycorrhizal fungi and rhizobacteria on banana growth and nutrition. Agron. Sustain. Dev. 25, 395–399. https://doi.org/10.1051/agro:2005039.

Rohland, N., Reich, D., 2012. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Nat. Protoc. 7, 862–871. https://doi.org/10.1038/nprot.2012.043.

Ryan, M.J., Mauchline, T.H., Malone, J.G., et al., 2023. The UK crop microbiome cryobank: a utility and model for supporting phytobiomes research. CABI Agric. Biosci. 4, 53. https://doi.org/10.1186/s43170-023-00190-2.

Shade, A., Stopnisek, N., 2019. Abundance–occupancy distributions to prioritize plant core microbiome membership. Curr. Opin. Microbiol. 49, 50–58. https://doi.org/10.1016/j.mib.2019.09.008.

Shen, Z., Thomashow, L.S., Ou, Y., Tao, C., Wang, J., Xiong, W., Liu, H., Li, R., Shen, Q., Kowalchuk, G.A., 2022. Shared core microbiome and functionality of key taxa suppressive to banana fusarium wilt. Research 2022, 9818073. https://doi.org/10.34133/2022/9818073.

Simonin, M., Dasilva, C., Terzi, V., Ngonkeu, E.L.M., Diouf, D., Kane, A., Béna, G., Moulin, L., 2020. Influence of plant genotype and soil on the wheat rhizosphere microbiome: evidence for a core microbiome across eight African and European soils. FEMS Microbiol. Ecol. 96, fiaa067. https://doi.org/10.1093/femsec/fiaa067.

Thambugala, K.M., Daranagama, D.A., Phillips, A.J.L., Kannangara, S.D., Promputtha, I., 2020. Fungi vs. fungi in biocontrol: an overview of fungal antagonists applied against fungal plant pathogens. Front. Cell. Infect. Microbiol. 10, 604923. https://doi.org/10.3389/fcimb.2020.604923.

Ting, A.S.Y., Meon, S., Kadir, J., Radu, S., 2008. Endophytic microorganisms as potential growth promoters of banana. BioControl 53, 541–553. https://doi.org/10.1007/s10526-007-9093-1.

Toju, H., Tanabe, A.S., Yamamoto, S., Sato, H., 2012. High-coverage ITS primers for the DNA-based identification of ascomycetes and basidiomycetes in environmental samples. PloS One 7, e40863. https://doi.org/10.1371/journal.pone.0040863.

Toju, H., Peay, K.G., Yamamichi, M., Narisawa, K., Hiruma, K., Naito, K., Fukuda, S., Ushio, M., Nakaoka, S., Onoda, Y., Yoshida, K., Schlaeppi, K., Bai, Y., Sugiura, R., Ichihashi, Y., Minamisawa, K., Kiers, E.T., 2018. Core microbiomes for sustainable agroecosystems. Nat. Plants 4, 247–257. https://doi.org/10.1038/s41477-018-0139-4.

Tyśkiewicz, R., Nowak, A., Ozimek, E., Jaroszuk-Ściseł, J., 2022. *Trichoderma*: the current status of its application in agriculture for the biocontrol of fungal phytopathogens and stimulation of plant growth. Int. J. Mol. Sci. 23, 2329. https://doi.org/10.3390/ijms23042329.

Van der Veken, L., Win, P.P., Elsen, A., De Waele, D., 2008. Susceptibility of banana intercrops for rhizobacteria, arbuscular mycorrhizal fungi and the burrowing nematode *Radopholus similis*. Appl. Soil Ecol. 40, 283–290. https://doi.org/10.1016/j.apsoil.2008.05.003.

White, T., Bruns, T., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), PCR Protocols: A Guide to Methods and Applications. Academic Press, San Diego, pp. 315–322.

Win, T.T., Bo, B., Malec, P., Fu, P., 2021. The effect of a consortium of *Penicillium* sp. and *Bacillus* spp. in suppressing banana fungal diseases caused by *fusarium* sp. and *Alternaria* sp. J. Appl. Microbiol. 131, 1890–1908. https://doi.org/10.1111/jam.15067.

Xu, J., Zhang, Y., Zhang, P., Trivedi, P., Riera, N., Wang, Y., Liu, X., Fan, G., Tang, J., Coletta-Filho, H.D., Cubero, J., Deng, X., Ancona, V., Lu, Z., Zhong, B., Roper, M.C., Capote, N., Catara, V., Pietersen, G., Vernière, P., Al-Sadi, A.M., Yang, F., Xu, X., Wang, J., Yang, H., Jin, T., Wang, N., 2018. The structure and function of the global citrus rhizosphere microbiome. Nat. Commun. 9, 4894. https://doi.org/10.1038/s41467-018-07343-2.

Zhang, Z., Schwartz, S., Wagner, L., Miller, W., 2000. A greedy algorithm for aligning DNA sequences. J. Comput. Biol. 7, 203–214. https://doi.org/10.1089/10665270050081478.

Zheng, Y., Li, X., Cao, H., Lei, L., Zhang, X., Han, D., Wang, J., Yao, M., 2021. The assembly of wheat-associated fungal community differs across growth stages. Appl. Microbiol. Biotechnol. 105, 7427–7438. https://doi.org/10.1007/s00253-021-11550-1.

Zhou, Y., Liu, D., Li, F., Dong, Y., Jin, Z., Liao, Y., Li, X., Peng, S., Delgado-Baquerizo, M., Li, X., 2024. Superiority of native soil core microbiomes in supporting plant growth. Nat. Commun. 15, 6599. https://doi.org/10.1038/s41467-024-50685-3.

Zimmermann, J., Musyoki, M.K., Cadisch, G., Rasche, F., 2016. Biocontrol agent *fusarium oxysporum* f. sp. *strigae* has no adverse effect on indigenous total fungal communities and specific AMF taxa in contrasting maize rhizospheres. Fungal Ecol. 23, 1–10. https://doi.org/10.1016/j.funeco.2016.05.007.