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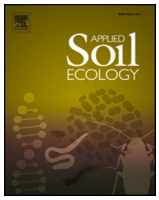

Core rhizosphere bacteria associated with banana (*Musa* spp.) across multiple continents

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ABSTRACT

Bananas (*Musa* spp.) are vital to the economy and food security of many nations but are constrained by multiple issues that often lack effective solutions. Banana microbiomes strongly influence host health and nutrition and may offer novel solutions to production constraints. Management of microbial communities is challenging, however, due to their variability across space and time. Despite this, a small number of 'core' taxa are almost always associated with their host irrespective of geographical and temporal differences. While country-level studies have defined core banana taxa, it remains unclear whether these taxa persist across multiple countries and continents. Establishing a multinational core microbiome of banana would help to focus research efforts to develop microbiome-based management strategies that are broadly applicable across diverse production systems. Here we used 16S rRNA gene sequencing to characterise bacterial communities associated with bulk soil and ectorhizosphere samples from banana grown in pots containing soil collected from 24 farms across Australia, Africa and Southeast Asia. By applying abundance-occupancy criteria, we identified 74 core bacterial taxa that were consistently associated with banana across these geographically distinct locations. These taxa represent logical targets for isolation and biobanking, which would support focussed ecological and functional studies and facilitate product development and the design of microbiome management approaches for growers.

1. Introduction

Bananas (*Musa* spp.) are among the most consumed fruits globally and contribute significantly to the gross domestic product of many nations (FAO, 2023). Commercial banana production is impacted by multiple abiotic and biotic constraints (Jones, 2019; Ploetz, 2003). In addition to maintaining yield and fruit quality, banana production systems are under increasing pressure to become more resilient and sustainable. Major challenges include the limited availability of effective control options for important soil-borne diseases, dependence on external inputs, and the difficulty of developing management strategies that remain effective across diverse edaphic and production conditions. These challenges have increased interest in management approaches that work with, rather than against, soil biological processes. In this context, microbiome-informed strategies are attracting attention as a potential complement to conventional agronomic and plant protection practices. Like other plants, bananas have evolved mutualistic relationships with soil microorganisms that greatly expand their

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functional repertoire (Brugman et al., 2018). Many of these associations benefit the host by enhancing nutrient availability, stress tolerance, and defence against pests and pathogens (Trivedi et al., 2020). Hence, these organisms may provide novel solutions to some of the production constraints that currently lack effective controls. Advising appropriate management strategies to utilise microbiomes across multiple farms is challenging, however, as microbiomes are spatially and temporally transient (Toju et al., 2018). Despite this, there are a small number of "core" lineages that could represent logical targets for further research efforts.

Core phylogenetic taxa are consistently associated with their host across a variety of environmental gradients and, due to this persistence, are thought to make important contributions to host fitness (Lay et al., 2018; Simonin et al., 2020). In addition, core taxa represent a disproportionately large fraction of the community and are therefore likely to influence the other taxa in a community, acting as keystone or "hub" species (Liu et al., 2017; Shade and Stopnisek, 2019). Consequently, core taxa may be considered logical targets for collection in biobanks and further ecological study, as they are more likely to be important in multiple locations over time (De Cáceres and Legendre, 2009). For example, Birt et al. (2022) identified that in Australia, bananas harbour 36 core bacterial operational taxonomic units (OTUs) that make up 30–40% relative abundance of the community despite representing only 0.002% of total OTUs observed. They also determined whether these core phylogenetic taxa were represented in datasets from 22 other banana microbiome studies globally (Birt et al., 2022). While matching sequences were found for all 36 core OTUs across all continents covered by these studies, the data did not enable them to determine whether the core OTUs in Australia were also core elsewhere.

Other studies that aim to identify the core taxa of *Musa* spp. have also focussed on a single country, such as China (Shen et al., 2022) and Tanzania (Kaushal et al., 2020). Hence, current lists of core taxa for banana are useful to prioritise research efforts within countries but lack compatibility between multiple countries. Identifying lists of core taxa across multiple countries would provide greater focus for industry engagement, product development and inform microbiome management approaches for growers. For example, it could help to direct international isolation efforts to build biobanks containing core lineages that strongly associate with banana irrespective of where they are grown. The development of these biobanks would facilitate more detailed study into the functioning and ecological preferences of core lineages and help inform the design of microbiome management approaches, thereby expediting impact from microbiome research to end user benefit.

Here, we sought to identify core bacterial lineages that were associated with banana plants across multiple nations. We used 16S rRNA gene sequencing to characterise the diversity of banana-associated bacterial communities in bulk and rhizosphere soil across Australia, Southeast Asia (Laos, Malaysia, and the Philippines), and Africa (Uganda and South Africa). By sampling multiple banana farms within each nation, we captured a wide range of edaphic conditions and were able to evaluate patterns of diversity across all sites. We tested the hypothesis that there would be a common bacterial core of *Musa* spp. across geographically distinct locations and diverse environmental gradients. Our study identified 74 bacterial lineages that are persistently associated with *Musa* spp. across diverse edaphic and geographical conditions. We propose that these taxa are likely important to the host and should be considered as a focus for future banana microbiome research.

2. Methods

2.1. Soil collection and experimental set up

To assess the impacts of edaphic conditions across geographical locations, bulk soil was collected from banana farms in Australia, Laos, Malaysia, Philippines, South Africa and Uganda (Fig. 1). All plants had no visible symptoms of diseases, and the farms had no reported instances of Fusarium wilt within the year prior to sampling. Bulk soil was collected with a shovel from multiple locations close to the base of banana plants, to a depth of approximately 0–20 cm, after clearing any leaf litter from the surface. Soil was then passed through a clean 8 mm sieve and pH was measured following the method described by Moody and Cong (2008).

Soils from Laos, Malaysia, Philippines and Uganda were assigned a number (e.g. Soil1 or S1). In Australia, soils of the region sampled are grouped into series (Cannon et al., 1992; Enderlin et al., 1997), so the series name for each soil was used in the label (Innisfail = In, Liverpool = Li, Pin Gin = Pg, Tolga = To, and Tully = Tu). In South Africa, soils were named after the area they were sampled from (Hebron = He, Langverwacht = La, Schoon Spruit = SS, Welgelegen = We). Sites were then denoted as the two letter ISO 3166 codes for each country followed by the soil label (e.g. LA.S1 = Laos Soil 1; or AU.Li = Australia Liverpool series). Detailed site information and soil properties are provided in Table S1.

In each country and within a week of soil collection, *Musa* (ABB) 'Pisang Awak' in vitro tissue culture (TC) plantlets, rinsed free of agar, were transplanted directly into sterilised 120 mm × 125 mm pots containing 1 kg (fresh weight) of soil. Given the high mortality rates typical of direct-to-soil tissue culture planting, 15 plantlets were grown for each treatment. We selected Pisang Awak as it was available in all countries, albeit with different names (Ducasse in Australia, Kayinja in Uganda, Kluai Nam Wa in Lao PDR, and Cardaba in the Philippines). To minimise cross contamination, when planting, benches and tools were sterilised with 4% bleach between each soil type and gloves were worn when handling tissue culture plantlets.

2.2. Growing conditions

As TC plantlets are fragile, it is common practice for them to first undergo a month of "hardening" before exposure to full sunlight. During this month, TC plantlets were matured in a shaded chamber with high humidity. Plants were then moved to a bench in the main greenhouse and gradually increased to full sunlight over a few weeks. On the same day as moving to the main greenhouse, plants received their first dose of fertiliser and were fertilised every two weeks thereafter. Watering frequency was based on the prevailing climate in each country, with plants in drier climates watered more frequently. Plants were grown for a minimum of six weeks in full sunlight.

Due to differing climates and soil types, plant growth rates varied between countries. Plants were sampled when they reached a height of ≥10 cm and had been growing for 12–16 weeks. Plants that failed to reach ≥10 cm in height by 16 weeks were sampled regardless of height. Sampling was conducted simultaneously for all soils per country, with the slowest growing treatment determining the sampling time. Of the 15 plants initially grown for each soil, only the 10 tallest and healthiest plants were sampled. In cases where mortality rates were higher and less than 10 plants survived, all remaining plants were sampled. High mortality rates were observed in some treatments. For instance, in the Philippines, only three replicates from Soil 4 survived to the time of sampling.

2.3. Sampling the bulk soil and ectorhizosphere

In each country, bulk soil and the ectorhizosphere were sampled from each plant using the standardized methods outlined by Birt et al. (2021). Briefly, bulk soil was gently shaken into a bin lined with a plastic bag (one per plant) and a sub-sample was collected in a 50 mL Falcon tube. Roots were then cut away from the rhizome with sterile scissors. Sections were cut from the base, middle and apex of the roots and placed together in a 50 mL Falcon tube. To loosen the soil from the roots, 40 mL of 1× phosphate buffered saline (PBS) was added to each tube and the

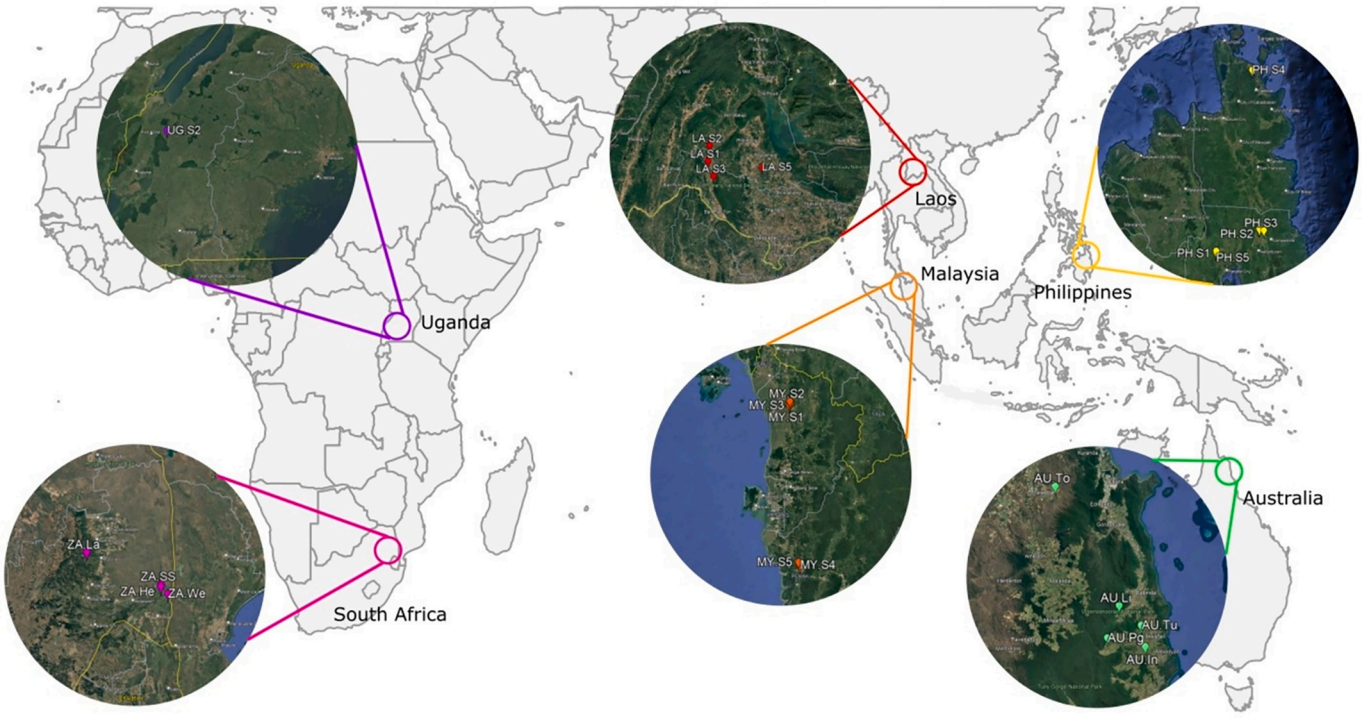

Fig. 1. Locations of the 24 banana farms (sites) where soils were collected.

contents were either vortexed for 2 min or shaken by hand for 5 min, depending on the equipment available. Following agitation, root material was removed with sterilised tweezers and the remaining slurry was centrifuged at 480 × g for 5 min. Excess PBS was removed until only the pellet of ectorhizosphere soil remained.

To prevent cross contamination, all tools (e.g. scissors, knives, tweezers) were sterilised with 4% bleach before and after processing each plant. Work surfaces were also sterilised with 4% bleach, and fresh gloves were used for handling each sample. Both the bulk soil and the ectorhizosphere samples were stored at −20 °C before DNA extraction.

2.4. DNA extraction and PCR of the 16S rRNA marker gene

To ensure consistency across countries, DNA was extracted using the DNeasy PowerSoil Pro Kits (Qiagen) as per the manufacturer's instructions. DNA samples from all countries were then shipped to the University of Queensland, Australia, where library preparation and sequencing was performed.

Universal bacterial 16S rRNA genes were amplified by polymerase chain reaction (PCR) using the primers 799F (5′-AAC MGG ATT AGA TAC CCK G G-3′) and 1193R (5′-ACG TCA TCC CCA CCT TCC-3′) (Redford et al., 2010), each modified on the 5′ end to contain the Illumina overhang adapter for compatibility with the i5 and i7 Nextera XT indices, respectively. PCR reactions contained: 2.5 μL DNA template, 4 μL 5× Phire Green Reaction Buffer (Thermo Fisher), 0.4 μL of Phire Green Hot Start II DNA Polymerase (Thermo Fisher), 200 μM of each dNTP, and 250 nM of each primer made to a total volume of 20 μL with molecular biology grade water. Thermocycling conditions were as follows: 98 °C for 45 s; then 30 cycles of 98 °C for 5 s, 56 °C for 5 s, 72 °C for 6 s; followed by 72 °C for 1 min. Amplifications were performed using a SimpliAmp™ 96-well Thermocycler (Applied Biosystems). Blank extraction controls and negative amplification controls were verified by gel electrophoresis. PCR products were 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) PCR product. Indexed amplicons were then quantified using a PicoGreen dsDNA Quantification Kit (Invitrogen). Equimolar concentrations from eight randomly selected replicates per site were then pooled and sequenced 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

To ensure direct comparability with Birt et al. (2022), which defined the Australian banana core microbiome using an operational taxonomic unit (OTU)-based framework, sequence data were processed using the same modified UPARSE pipeline (Edgar, 2013). Briefly, forward reads were quality filtered using USEARCH (v10.0.240) (Edgar, 2010), and operational taxonomic units (OTUs) were clustered at a 97% sequence identity threshold. An OTU table was generated and taxonomy was assigned using BLASTN (v2.3.0+) (Zhang et al., 2000) within QIIME2 (Bolyen et al., 2019), referencing the Greengenes2 database (McDonald et al., 2023). Non-bacterial sequences were then filtered out using BIOM (McDonald et al., 2012). Samples were rarefied to a depth of 1400 reads per sample to normalise sequencing effort. All alpha diversity metrics were produced using QIIME2. To generate phylogenetic distance, the representative sequences were aligned using MAFFT (v7.221) (Katoh and Standley, 2013) and masked using QIIME2 (v2017.9) (Bolyen et al., 2019). A midpoint-rooted phylogenetic tree was generated from this alignment using FastTree (v2.1.9) (Price et al., 2010). To provide preliminary ecological context for the identified taxa, taxonomy-based functional annotation was also performed using FAPROTAX (Louca et al., 2016) based on 16S rRNA gene taxonomy. Relative abundances of functional traits in each sample were calculated as the proportion of total sequences assigned to each function after conversion to relative abundance. FAPROTAX outputs for both the full OTU table and the subset of 74 core OTUs are provided in the Supplementary file, together with an ASV table. These annotations were used only as putative functional predictions inferred from taxonomy.

2.6. Matching sequences to previously identified core bacterial taxa

Representative OTU sequences for our present study were compared to the sequences of the Australian 36 core bacteria (reported by Birt

et al. (2022)) using USEARCH (Edgar, 2010). Sequences that were ≥ 97% similar were included as potential matches.

2.7. Establishing a global core microbiome

To establish a global core, a similar approach to Birt et al. (2022) and Clarke et al. (2026) was used. For each site the prevalence (number of replicates an OTU appeared in) and relative abundance of each OTU was plotted (Fig. S1). Those that were present in ≥50% of the replicates at a relative abundance of ≥0.05% were selected as candidate core OTUs for each compartment, per site.

Candidate core OTUs were then ranked based on their occupancy (the number of sites in which each OTU was a candidate core) for each compartment (with the highest occupancy score being rank 1). OTUs with a rank score of ≤50 were then analysed further as this captured the majority of candidate core OTUs that were present in four or more countries. The top 50 taxa from the bulk soil and the ectorhizosphere were then combined, resulting in 74 non-redundant OTUs.

2.8. Statistical analyses

The main and interactive effects of country (Australia, Laos, Malaysia, Philippines, South Africa and Uganda), sites and compartments (ectorhizosphere and bulk soil) on univariate response variables (alpha diversity metrics, i.e., observed (Sobs) and predicted (Chao1) numbers of OTUs, as well as Shannon's and Faith's Phylogenetic Diversity (PD) Indices) 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)).

3. Results

3.1. The effects of country, site and compartment on bacterial alpha diversity

Bacterial alpha diversity was significantly influenced by the main and interactive effects of country, site and compartment (Table 1). Bacterial communities in samples from Laos had lower alpha diversity than those from other countries (Fig. 2). Within each country, the main and interactive effects of compartment and site explained a significant proportion of the variance in alpha diversity (Shannon's Diversity Index), except for Australia (Table 1). Compartment had a significant effect on bacterial alpha diversity within sites (indicated by asterisks in Fig. 2), especially in Laos (Table 1 and Fig. 2).

3.2. The effect of country and site on bacterial community composition

Bacterial communities from all sites were dominated by members of the Acidobacteriota, Actinobacteriota, Firmicutes, and Proteobacteria (Fig. 3). Gemmatimonadota were present across all sites at low relative abundance, while members from Bacteriodota were present in all countries except Australia. Laos, Australia, and Malaysia had larger relative abundances of Myxococcota while the Philippines, Uganda and South Africa had the largest representation of Nitrospirota. Soils with a pH <6.5 tended to have more Dormibacterota (Fig. 3).

At the OTU level, bacterial community composition was significantly influenced by the main and interactive effects of country, site, and compartment, with country and compartment explaining the most variance (Table 1). Bacterial community composition was more similar in more adjacent sites (i.e. sites from the same country and/or latitude), with those from the Philippines being the most distinct (Fig. 4A). When plotting weighted UniFrac distances, however, Philippines communities resembled those from other countries more closely (Fig. 4B). In countries from Southeast Asia (Laos, Malaysia, and the Philippines), compartment had a greater influence on community composition than site (Table 1), particularly in Laos, where the ectorhizosphere compartment was different from all other samples (Figs. 4B and S2B). Ordination indicated that sites within Australia, Malaysia and South Africa formed distinct groups, and within these, samples were clustered by compartment (Figs. 4A and S2A, C and F). The composition of bacterial communities within each site differed significantly except within site PH·S4, which had only three replicate plants rather than the eight for other sites due to high mortality during the pot experiment (Figs. 3 and S2D).

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 bacterial communities, respectively. 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	*P* value		*F* value	R^2 (%)	*P* value	
All	Country	5	208.7	<0.001	***	25.5	19.6	<0.001	***
	Site	18	18.3	<0.001	***	6.4	17.6	<0.001	***
	Compartment	1	192.2	<0.001	***	24.3	3.7	<0.001	***
	Country:Site:Compartment	23	25.8	<0.001	***	3.1	10.9	<0.001	***
Australia	Site	4	10.1	<0.001	***	6.4	25.4	<0.001	***
	Compartment	1	3.2	0.079	.	5.8	5.8	<0.001	***
	Site:Compartment	4	1.3	0.267		1.3	5.3	0.003	**
Laos	Site	3	10.9	<0.001	***	5.1	15.6	<0.001	***
	Compartment	1	169.2	<0.001	***	17.8	17.9	<0.001	***
	Site:Compartment	3	11.5	<0.001	***	4.0	12.1	<0.001	***
Malaysia	Site	4	52.6	<0.001	***	6.6	22.2	<0.001	***
	Compartment	1	11.9	<0.001	***	13.0	10.9	<0.001	***
	Site:Compartment	4	3.8	0.008	**	2.5	8.4	<0.001	***
Philippines	Site	4	21.6	<0.001	***	3.5	15.6	<0.001	***
	Compartment	1	14.6	<0.001	***	7.3	0.1	<0.001	***
	Site:Compartment	4	22.1	<0.001	***	2.0	0.1	<0.001	***
South Africa	Site	3	23.3	<0.001	***	11.6	35.8	<0.001	***
	Compartment	1	5.4	0.025	*	4.9	5.1	<0.001	***
	Site:Compartment	3	14.0	<0.001	***	1.8	5.6	<0.001	***
Uganda	Compartment	1	5.6	0.033	*	2.9	17.2	0.002	**

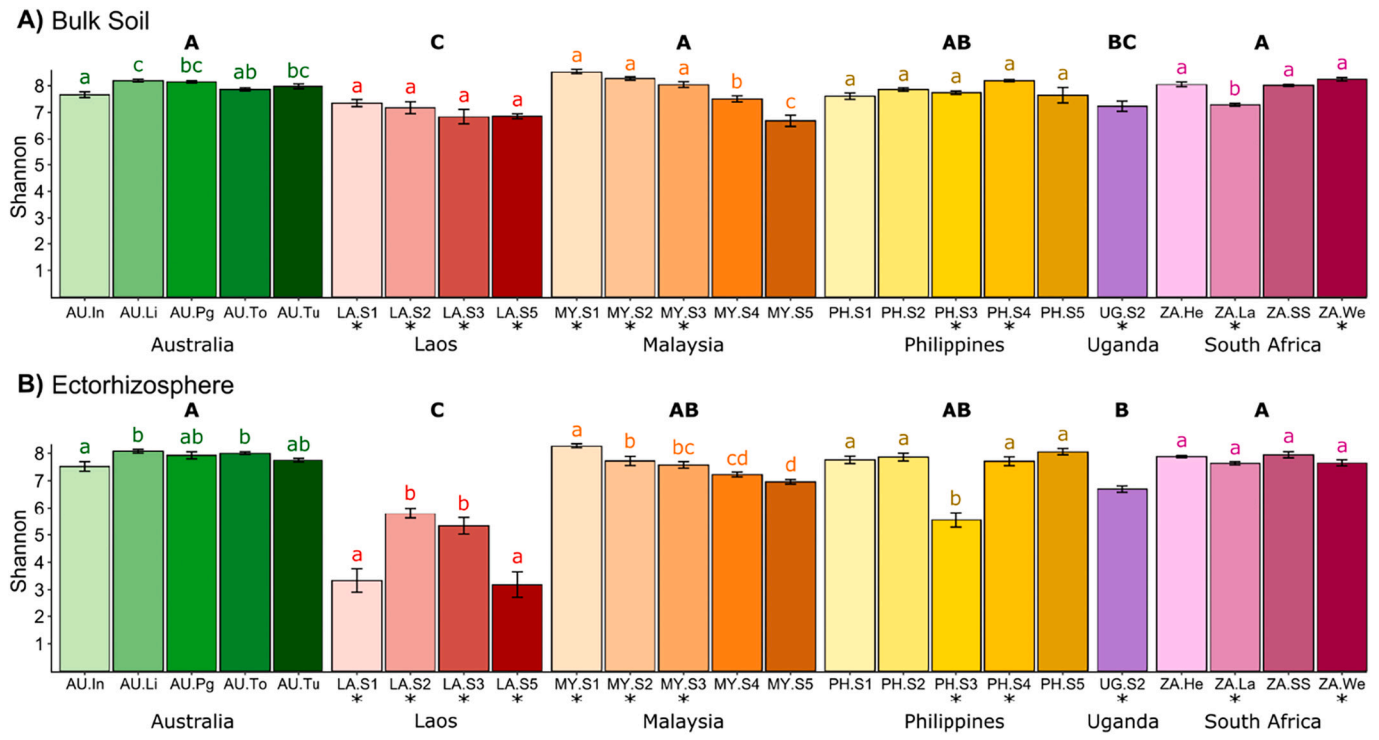

Fig. 2. The alpha diversity (Shannon's Diversity Index) of bacterial communities in each site, grouped by country, within A) the bulk soil and B) the ectorhizosphere. Error bars represent the standard errors of the means. Capital letters represent significant differences between countries based on Tukey 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.

3.3. Defining a multinational list of core Musa spp. associated bacterial taxa

After applying a threshold of ≥50% prevalence at ≥0.5% relative abundance to each site (Fig. S1), a total of 200 taxa for the bulk soil and 243 taxa for the ectorhizosphere were identified as candidate core OTUs across all 24 sites. Of these, 114 were in both compartments, resulting in 329 unique candidate core OTUs (Supplementary file).

We observed a positive correlation between the number of sites an OTU was a candidate core in (hereafter referred to as an OTU's "occupancy") and the number of countries occupied (Fig. 5A). Candidate taxa were ranked based on their occupancy, and there was a steep decline in OTU occupancy between rank 1 and 50, with the trend beginning to plateau after rank 50 (Fig. 5B). All OTUs detected in four or more countries were ranked within positions 1–50 (Fig. 5C), except for OTU 110 in the ectorhizosphere compartment, which was present in four countries but had a rank score of 54 due to occupancy in only four sites. Additionally, OTUs that were detected in only one country did not rank in the top 50 (Fig. 5C), apart from OTU158 and OTU222 in the bulk soil, which were ranked at positions 45 and 46, respectively, due to their occupancy in all five Philippines sites (Figs. 5C and S3).

3.4. The 74 core bacterial taxa of Musa spp.

The top 50 ranked core taxa from both the bulk soil and ectorhizosphere were then combined into a non-redundant list, resulting in 74 core OTUs (Supplementary file). These 74 core OTUs represented just 0.6% of all taxa (74 of 12,138 OTUs), but comprised 25–52% (mean = 35.8, SD = 5.8) and 24–74% (mean = 39.5, SD = 13.3) of the total relative abundance within the bulk soil and ectorhizosphere, respectively (Fig. 5E and F).

The 74 core taxa were dominated by members of the Acidobacteriota, Actinobacteriota, Firmicutes, and Proteobacteria, with many of the highest-ranking core OTUs being members of the Firmicutes, specifically within the order Bacilliales_B (Fig. 6). In addition, the core included representatives from the Chloroflexota, Desulfobacterota, Dormibacterota, Gemmatimonadota, Nitrospirota, and Verrucomicrobiota (Fig. 6).

Lastly, we aimed to determine if the 74 prominent OTUs in this study were identified as core taxa in our previous study, which defined core taxa in Australia only (Birt et al., 2022). As we only sampled the bulk soil and ectorhizosphere, we were not expecting to identify core taxa from other compartments sampled by Birt et al. (2022), such as the pseudostem and leaves. We confirmed the presence of closely related taxa (sequence similarity of ≥97%) of all seven of the Australian core OTUs in the bulk soil and 11 of 15 OTUs in the ectorhizosphere present within our list of 74 multinational OTUs (Figs. 6 and S4; Birt et al., 2022). In addition, we detected four core OTUs from other compartments, indicating 22 close relatives of the core OTUs identified by Birt et al. (2022) present in banana systems across multiple countries. The OTU sequences and details of all matches are provided in the Supplementary file, together with taxonomy-based putative functional annotations generated using FAPROTAX.

4. Discussion

Studies around the world consistently report the presence of similar bacterial genera within the microbiome of banana, suggesting that there may be core lineages that persist worldwide (Cabanás et al., 2021; Kaushal et al., 2020; Ong et al., 2024; Shen et al., 2022, 2015). For other crops, such as coffee (Bez et al., 2023), apple (Abdelfattah et al., 2021), barley (Zhou et al., 2024), wheat (Simonin et al., 2020) and citrus (Xu et al., 2018), formal analyses have identified core bacterial lineages across multiple nations. By contrast, studies of banana core bacteria have so far been geographically narrower in scope, meaning that while national or regional cores have been described, a multinational banana core microbiome has not previously been established. Here, we characterised the core bacterial microbiome of banana grown in soils

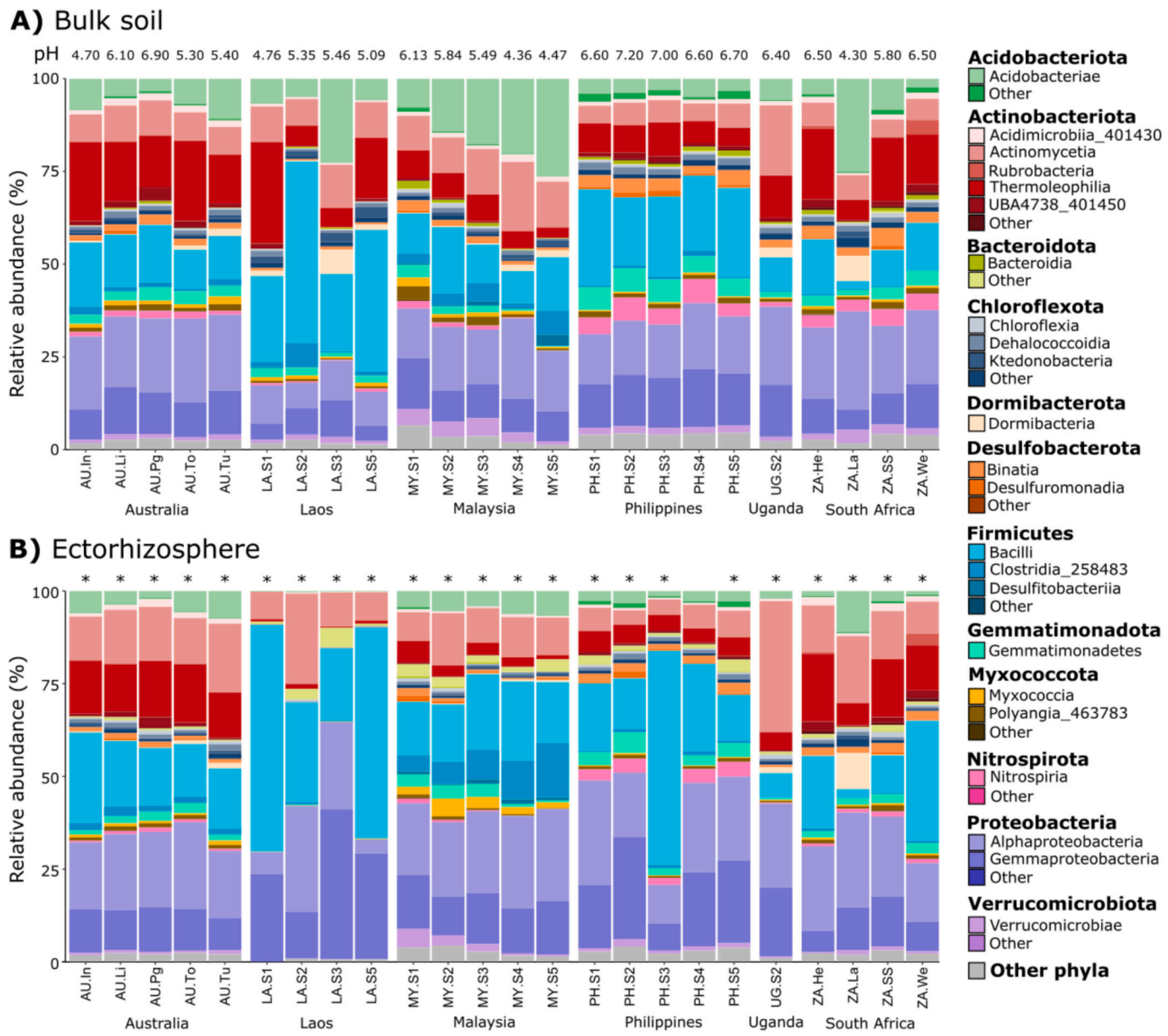

Fig. 3. Stacked bargraphs highlighting the frequencies of bacterial classes present at ≥1% mean relative abundance within at least one site for A) bulk soil, and B) ectorhizosphere samples. Within each phylum, classes representing <1% relative abundance were grouped as "Other". Phyla lacking any classes at ≥1% relative abundance were grouped as "Other phyla". The pH of each soil is shown above the bars in panel A. The asterisks above the bars in panel B indicate sites where bacterial community composition differed significantly between compartments.

collected from 24 farms across Australia, Africa and Asia. Our experimental design built upon the framework established by Birt et al. (2022) for characterising the core microbiome of banana in Australia, and encompassed a wide range of edaphic, climatic, and management conditions. Critically, we identified 74 core bacterial taxa, including 18 close relatives (≥97% sequence similarity) of the 22 core OTUs identified in the same compartments by Birt et al. (2022) (Supplementary file). These 74 core OTUs represent logical targets for biobanking, functional studies, and ecological research to harness the benefits of microbiomes in the form of bio-products that enhance banana production systems. Future work should investigate the extent to which banana core taxa overlap with those of other crops. Such comparisons would help determine whether some core lineages are broadly shared across plant hosts or are more strongly associated with particular crop lineages. In the case of banana, this question is especially interesting because cultivated *Musa* genotypes are closely related and clonally propagated, and previous work suggests that banana genotype has relatively little influence on bacterial community composition compared with edaphic variation (Birt et al., 2022). More broadly, however, host phylogenetic distance is often negatively associated with the similarity of root microbiomes (Yeoh et al., 2017). Clarifying the extent of overlap between banana and other crop core microbiomes could therefore help guide cross-crop biobanking, functional studies, and collaborative efforts to develop microbiome-based management strategies.

4.1. Similarities and differences across countries and sites

When defining a core microbiome, capturing variation across known influential factors, such as geography and soil properties, is essential (Xu et al., 2018). Previous studies have shown that environmental and edaphic conditions have a particularly strong influence on microbial diversity and composition in banana (Souza et al., 2013; Kaushal et al.,

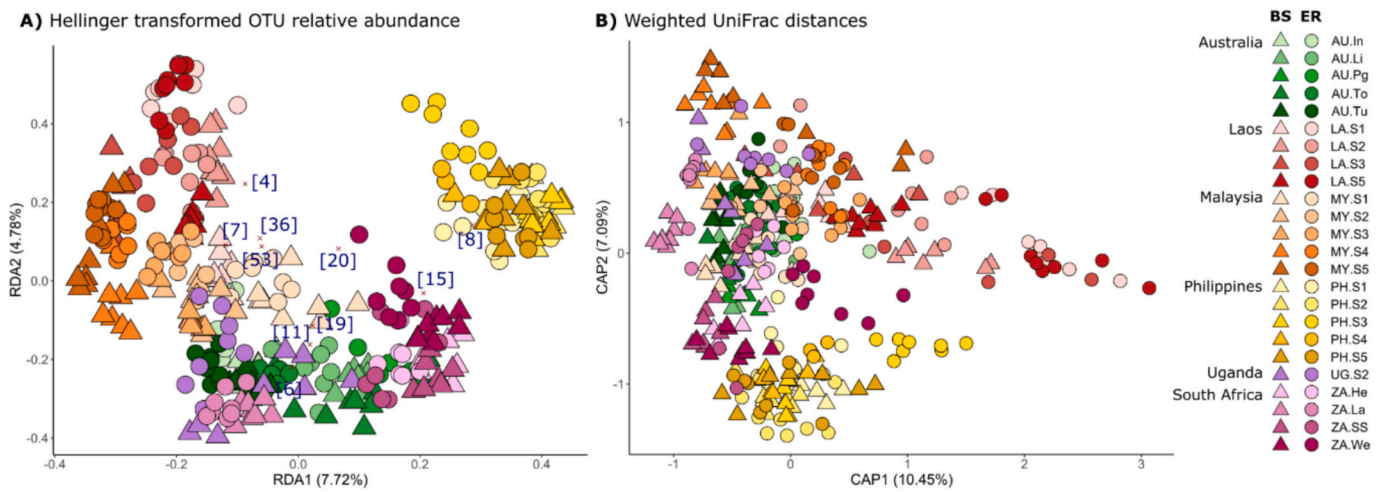

Fig. 4. A) Redundancy analysis (RDA) ordination highlighting differences in the composition of bacterial communities as represented by Hellinger transformed OTU relative abundances constrained by country. B) Constrained analysis of principle coordinates (CAP) ordination highlighting differences in the composition of bacterial communities as represented by weighted UniFrac distances constrained by country. Triangles and circles represent bulk soil (BS) and ectorhizosphere (ER) samples, respectively. In panel A the dark blue numbers in square brackets represent OTU IDs and are consistent with those in other figures.

2020; Birt et al., 2022; Shen et al., 2022). In contrast, differences between the microbiomes of different *Musa* spp. genotypes and cultivars appear to be relatively minor (Birt et al., 2022). Consequently, we characterised the microbiome of a single genotype (Pisang Awak, ABB) across multiple locations per country to capture representative variability in edaphic, climatic and management associated parameters.

The bacterial communities of *Musa* spp. across Australia, Laos, Malaysia, Philippines, Uganda, and South Africa, were all dominated by representatives of the Actinobacteriota, Firmicutes, and Proteobacteria, which is congruent with studies from Brazil (Souza et al., 2013), China (Zhou et al., 2019; Shen et al., 2022), India (Thomas and Soly, 2009), and Vietnam (Tran and Nguyen, 2024). Members of the Chloroflexota, Dormibacterota, Gemmatimonadota, and Nitrospirota were also common across countries, but were not detected in all. When considering the evolutionary distances between taxa within communities, the microbiomes of banana were less distinct, indicating that discriminating OTUs were members of closely related lineages (Fig. 4B).

At the OTU level, however, significant differences in the membership of bacterial communities between countries were observed, highlighting the importance of considering multiple nations (Table 1 and Fig. 4A). While historic details were not available for each site, the differences in banana microbiomes between countries may reflect, at least in part, differing management practices, landuses and cropping histories, as well as edaphic and climatic conditions. While our study was not designed as a comprehensive analysis of environmental drivers, soil pH was measured consistently across all countries and provided some additional context for patterns in community composition. Supplementary analyses showed that soil pH was significantly associated with variation in both the overall bacterial community and the subset comprising the 74 core taxa, while compartment also remained an important source of variation (Fig. S5). Because pH was measured at the site level rather than for individual pots, these analyses should be interpreted cautiously; nevertheless, they support the view that variation in soil chemistry, particularly pH, contributes to differences in banana-associated bacterial communities across countries.

4.2. The common bacterial lineages of Musa spp.

Using an abundance-prevalence threshold, we identified a total of 200 and 243 candidate core taxa from the bulk soil and ectorhizosphere, respectively. To prioritise the core taxa, we ranked candidate OTUs by their "coreness" (i.e. number of sites they occupied above the abundance-prevalence threshold). This approach avoids arbitrary core classifications and respects occupancy gradients where some taxa may be localised to one country. Furthermore, this approach could be applied more broadly, with taxa that are more likely to experience dispersal limitation, such as many protistan and metazoan taxa that are less easily dispersed passively due to their larger body size (Martiny et al., 2006). Focusing on the top 50 OTUs from each compartment, we generated a final list of 74 core taxa present across multiple countries (Fig. 6). Among the 74 core OTUs, we confirmed the presence of closely related taxa (sequence similarity of $\geq$97%) of all seven of the Australian core OTUs in the bulk soil and 11 of 15 OTUs in the ectorhizosphere originally identified by Birt et al. (2022; Figs. 6 and S4). Notably, these OTUs were some of the highest ranking OTUs (i.e., closer to rank 1) across all countries, reaffirming their spatial persistence and status as core taxa of *Musa* spp. (Figs. 5D and S4). Additionally, seven bulk soil and nine ectorhizosphere core OTUs previously detected in Australia (Birt et al., 2022) were once again identified as core in Australian soils, indicating not only spatial, but temporal consistency of these core taxa.

Given that plants in this study were sampled from plants without diseases, the core taxa are likely members of a "healthy" microbiome and are either beneficial or benign. The core taxa were highly abundant, representing 24–74% of the total relative abundance, while only accounting for 0.6% of the total OTUs detected (Fig. S4). The fact that core taxa are highly abundant across diverse environments suggests that they play an important role in host fitness (Lasa et al., 2019). Additionally, their prominence in the community suggests that they are likely to have influence over other taxa. Furthermore, deciphering the specific roles of individual taxa within microbiomes, and their interactions with the host plant, is challenging due to the complexity and variability of these ecosystems. Hence, the 74 core OTUs identified in this study provide a focused starting point for future research to explore their potential contributions to sustainable agricultural practices.

4.3. Core taxa act as a logical focus for future work

There is a growing consensus that to leverage the benefits of microbiomes in agriculture, we need to identify the core taxa associated with each crop species (Toju et al., 2018). Identifying core taxa provides a focus for isolation efforts and subsequent ecological studies, which can inform product development and industry engagement. Hence, identifying taxa that are members of the core banana microbiome in multiple countries is a crucial first step toward microbiome-based management

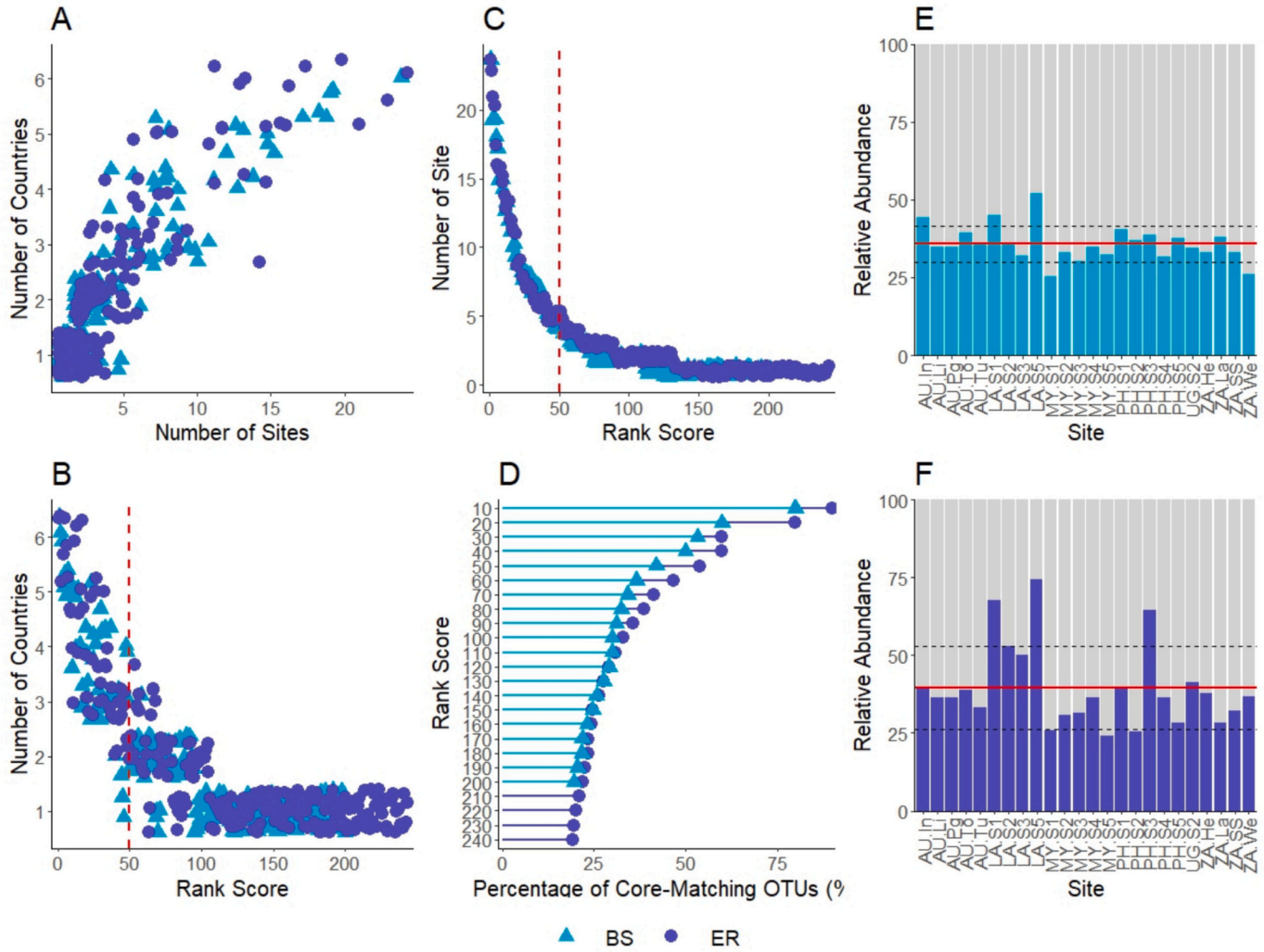

Fig. 5. A) The number of sites and countries in which each OTU was identified as a candidate core. B) The rank score of an OTU and the number of countries it occupied, and C) relationship between the rank score of an OTU and the number of sites in which it was identified as a candidate core; the dashed red line indicates the rank threshold (50) separating candidate core taxa from lower-ranked OTUs. D) Percentage of candidate core OTUs matching core taxa from Birt et al. (2022), within the top 10, top 20, etc. ranked OTUs. 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.

strategies. From a management perspective, our results suggest that efforts to manipulate banana microbiomes should prioritise persistent core taxa as candidates for isolation, biobanking and functional testing. The next step is to determine which of these taxa contribute desirable functions and how agronomic practices such as fertilisation, cover crop management, organic amendments, and disease-suppressive rotations influence their abundance and activity under field conditions.

This emphasis on core taxa is important because the competitive nature of the rhizosphere often limits the ability of introduced bacteria to establish, leading to variable effectiveness and longevity (Trivedi et al., 2020). In contrast, taxa that repeatedly occur as core members across geographically distinct production systems may provide more robust targets for microbiome-informed management (Fig. 5). Culturing the core taxa is therefore a critical next step. Paterson (2024) has already isolated 24 close relatives of 36 core banana-associated taxa from Australia (Birt et al., 2022), most of which we have now shown to be prevalent and core across multiple countries. Such isolates will allow more detailed study into the ecology and function of core OTUs, helping to identify the ecosystem services they may provide to banana production systems and the ways in which they might be managed.

Circumstantial evidence from the literature, or putative functional inferences provided in the Supplementary file, could be used in conjunction with core taxa lists to guide researchers on where to begin. For example, members of the *Sphingomonas* (i.e. OTU 16), *Sphingobium* (i.e. OTU 10), and *Streptomyces* (i.e. OTUs 18 and 12) genera have been shown to have antifungal properties and, given their consistent presence in disease suppressive soils of *Musa* spp., are thought to be candidates for bio-control against *Fusarium* wilt (Shen et al., 2019; Hong et al., 2020; Qi et al., 2021; Zhu et al., 2021). Hence, if a researcher wanted to identify a core taxon likely capable of suppressing *Fusarium* wilt, they would logically begin with pot or field studies on isolate cultures of core OTU 10, 12, 16 and 18 rather than other core taxa. For this to be achieved, however, we must first generate core taxa lists for each crop species, obtain isolate cultures, and store isolates in internationally available biobanks.

Given the high relative abundance and known role of core taxa to act as hub or "keystone" species (Birt et al., 2022), it is equally important to further investigate how agricultural management practices influence these taxa. This can be achieved with culture independent approaches, particularly when culturing is not feasible. Future and existing studies

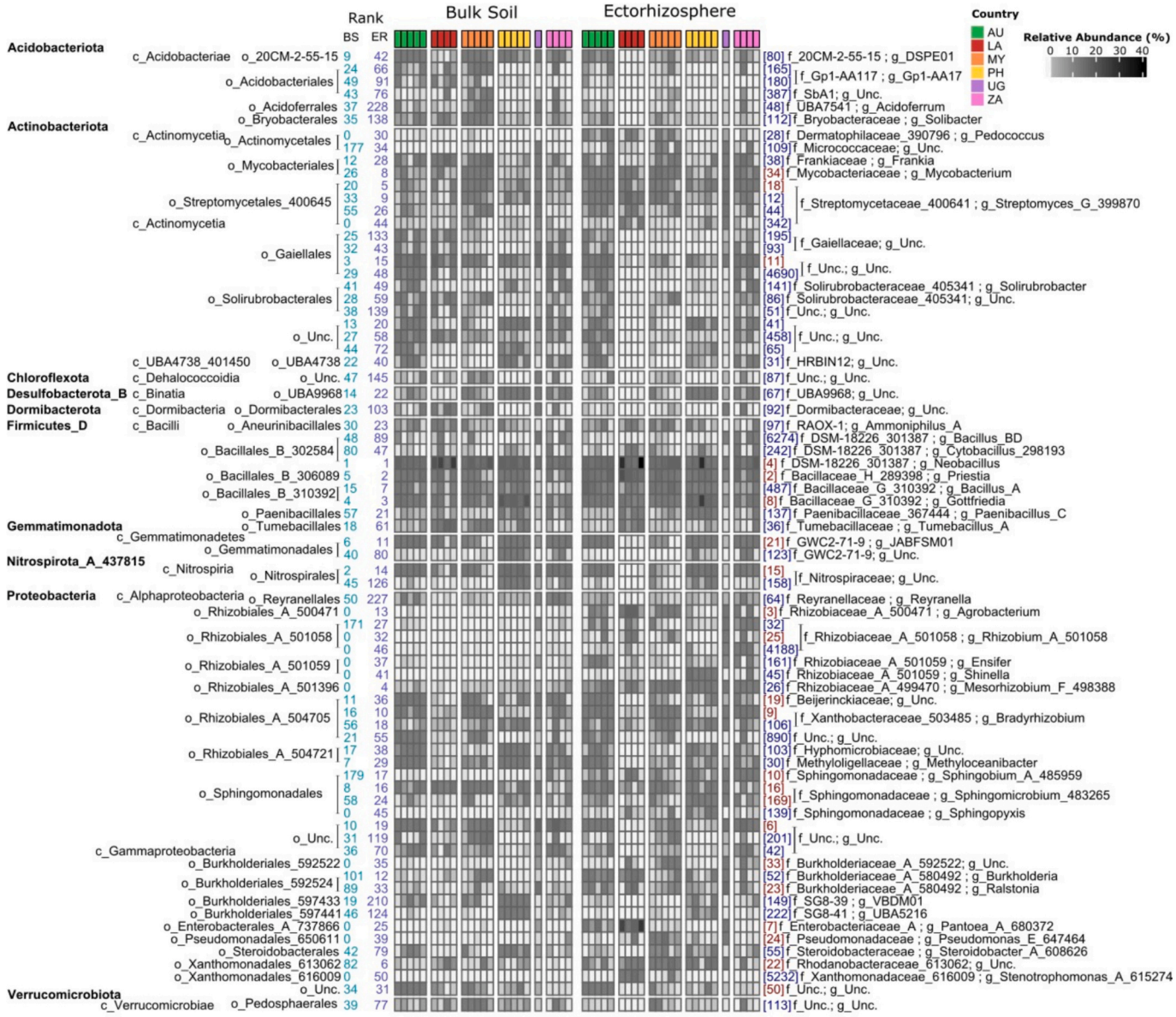

Fig. 6. Heatmap summarising the relative abundances of the 74 non-redundant core bacterial OTUs identified using the occupancy–rank framework from bulk soil and the ectorhizosphere of *Musa* (ABB) 'Pisang Awak' across 24 farms in six countries (Australia (AU) = green, Laos (LA) = red, Malaysia (MY) = 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 Birt et al. (2022).

can sequence match against the core taxa to enhance research into banana microbiome dynamics. For example, Clarke et al. (2024), examined the effects of phosphorus fertilisation on banana-associated microbiomes and sequence matched to the core list provided by Birt et al. (2022), enhancing the impact of the study. In this way, lists of core taxa facilitate informal global collaboration.

5. Conclusion

Here we have conducted a large-scale ecological study of the microbiomes associated with the bulk soil and ectorhizosphere of *Musa* spp. across 24 farms from multiple countries and continents. Our results revealed significant country-level differences in banana microbiomes emphasising the importance of defining core taxa across a broad range of edaphic, climate and management conditions. By applying abundance-occupancy criteria, we identified 74 core taxa that represented a large proportion (24–74%) of the overall community in the bulk soil and ectorhizosphere. The overlap of 22 OTUs with previous research by Birt et al. (2022) demonstrates that they are persistent across space and time. As Birt et al. (2022) demonstrated, different plant compartments have different core taxa and we are only capturing the core taxa from the bulk soil and the ectorhizosphere, future work should investigate other compartments from the endosphere and phyllosphere to define a plant-wide, multinational core microbiome. This list can guide international efforts to establish biobanks for *Musa* spp. core taxa, enabling research into ecological roles and practical applications in crop production. As a part of this study, all collaborating laboratories generated glycerol stocks of bulk soil and ectorhizosphere samples to facilitate isolation efforts, providing the foundation for an international biobank for *Musa* spp. microbiomes. Lastly, even without isolates, any researcher of *Musa* spp. microbiomes can compare sequences to the 74 core taxa to analyse the ecology of these taxa in a broad range of

experimental and environmental conditions. By applying these methods across crop ecosystems, we can begin to build a comprehensive understanding of how and when to implement specific management practices to effectively manipulate microbial communities, advancing sustainable agriculture.

CRediT authorship contribution statement

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

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107107.

Data availability

The data have been uploaded to NCBI SRA

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