Long-term application of organic matter improves soil properties and plant growth-promoting bacteria in soil communities of oil palm plantation

Hidayat, Fandi
Laboratory of Soil and Environmental Microbiology, Division of Systems Bioengineering, Department of Bioscience and Biotechnology, Graduate School of Bioresource and Bioenvironmental Science, Kyushu University

Pane, Rizki Desika Putri
Indonesian Oil Palm Research Institute

Sapalina, Fadilla
Indonesian Oil Palm Research Institute

Listia, Eka
Indonesian Oil Palm Research Institute

他

出版情報：Soil Science and Plant Nutrition. 70 (5-6), pp.393-405, 2024-07-30. 日本土壌肥料学会
バージョン：

Soil Science & Plant Nutrition
Japanese Society of Soil Science and Plant Nutrition

Long-Term Application of Organic Matter Improves Soil Properties and Plant Growth-Promoting Bacteria in Soil Communities of Oil Palm Plantation

Journal:	*Soil Science and Plant Nutrition*
Manuscript ID	SSPN-24-067-F.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	24-Jun-2024
Complete List of Authors:	Hidayat, Fandi; Kyushu University Faculty of Agriculture Graduate School of Bioresource and Bioenvironmental Sciences, Bioscience and Biotechnology; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Pane, Rizki Desika; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Sapalina, Fadilla; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Listia, Eka; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Koga, Tomonori; Kyushu University Faculty of Agriculture Graduate School of Bioresource and Bioenvironmental Sciences, Bioscience and Biotechnology Winarna, Winarna; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Lubis, M. Edwin; Indonesian Oil Palm Research Institute, Soil Science and Agronomy Oshiro, Mugihito; Kyushu University Faculty of Agriculture Graduate School of Bioresource and Bioenvironmental Sciences, Bioscience and Biotechnology sakai, kenji; Kyushu University Faculty of Agriculture Graduate School of Bioresource and Bioenvironmental Sciences, Bioscience and Bioengineering Utami, Sri; Universitas Gadjah Mada, Soil Science Tashiro, Yukihiro; Kyushu University Faculty of Agriculture Graduate School of Bioresource and Bioenvironmental Sciences, Bioscience and Biotechnology
Keywords:	microbiology and biology < Soil Biology, Soil Fertility, soil amendments < Fertilizers and Soil Amendments, environmental conservation < Environment, symbiosis < Soil Biology

Type of Contribution: Full-length paper

Division: Soil Biology

Title: Long-Term Application of Organic Matter Improves Soil Properties and Plant Growth-Promoting Bacteria in Soil Communities of Oil Palm Plantation

Running Title: Organic Matter Improves Oil Palm PGPB

Authors: Fandi Hidayat[a,b], Rizki Desika Putri Pane[b], Fadilla Sapalina[b], Eka Listia[b], Tomonori Koga[a], Winarna[b], M. Edwin Syahputra Lubis[b], Mugihito Oshiro[a], Kenji Sakai[a], Sri Nuryani Hidayah Utami[c], and Yukihiro Tashiro[a,*]

[a] *Laboratory of Soil and Environmental Microbiology, Division of Systems Bioengineering, Department of Bioscience and Biotechnology, Graduate School of Bioresource and Bioenvironmental Science, Kyushu University, West 5 744 Motooka, Nishiku, Fukuoka 819-0395*

[b] *Indonesian Oil Palm Research Institute, Jl. Brigjend Katamso No. 51 Kampung Baru, Medan, North Sumatera, Indonesia 20158*

[c] *Soil Science Department, Facuty of Agriculture, Gadjah Mada University, Jl. Flora, Bulaksumur, Depok, Sleman, Yogyakarta 55281*

**Corresponding author*

E-mail address: tashiro@agr.kyushu-u.ac.jp (Y. Tashiro)

CRediT authorship contribution statement:

Fandi Hidayat: Conceptualization, Methodology, Investigation, Writing-original draft. **Rizki Desika Putri Pane**: Data curation, Resources, Formal analysis. **Fadilla Sapalina**: Data curation, Resources, Formal analysis. **Eka Listia**: Data curation, Resources, Formal Analysis. **Tomonori Koga**: Formal analysis, Software. **Winarna**: Project administration, Validation, Supervision. **M. Edwin Syahputra Lubis**: Project administration, Validation, Supervision. **Mugihito Oshiro**: Conceptualization, Writing – review & editing. **Kenji Sakai**: Conceptualization, Writing – review & editing. **Sri Nuryani Hidayah Utami**: Validation, Supervision. **Yukihiro Tashiro**: Conceptualization, Supervision, Methodology, Validation, Writing – review & editing.

ABSTRACT

Oil palm (*Elaeis guineensis*) is a major contributor to global vegetable oil production; however, ensuring its sustainability remains a critical challenge, particularly concerning soil health. In this study, we investigated the impact of long-term organic matter application as part of good soil management (GSM) practices on oil palm plantations and compared it with poor soil management practices to determine the presence of plant growth-promoting bacteria (PGPB) in soil communities. The ten-years regular application of organic matter to the soil in the GSM plots led to notable improvements in soil chemical properties, including total organic carbon, total nitrogen, available phosphorus, available potassium, and cation exchange capacity. Metagenomic analysis revealed a significantly higher abundance of beneficial microbial species exclusively found in GSM plots, supporting oil palm growth. Furthermore, a novel finding emerged from this study, as it successfully predicted the metabolic function of PGPB in soil communities using Picrust2 provided by the soil microbiome. Picrust2 analysis indicated that the long-term application of organic matter in GSM plots increased functional enzymes related to PGPB activities, such as nitrogen fixation, phosphate solubilization, potassium solubilization, and phytohormone synthesis. This study underscores the significance of implementing GSM practices in oil palm plantations by incorporating eco-friendly materials, such as organic matter, to enhance soil health and fertility and ensure oil palm sustainability.

Keywords: *beneficial microbes, long-term organic matter application, microbial community, oil palm plantation, sustainability*

Abbreviations: AK, available potassium; AP, available phosphorus; ASV, amplicon sequence variant; CEC, cation exchange capacity; EFB, empty fruit bunches; GSM, good soil management; IAA, indole-acetic acid; ITS, internal transcribed spacer region; OM, organic matter; PGPB, plant growth-promoting bacteria; PICRUSt2, phylogenetic investigation of communities by reconstruction of unobserved state 2; PSM, poor soil management; TN, total nitrogen; TOC, total organic carbon.

1. Introduction

Indonesia has approximately 55.0 million hectares of agricultural land and plays a crucial role in the production of various crops (Pradana et al., 2019). Among these, the oil palm stands out as a significant annual crop, occupying a considerable portion of the country's agricultural landscape. Over the years, oil palm cultivation has seen tremendous growth, expanding from 3.6 million hectares in 1961 to an astonishing 15.1 million hectares in 2021 (Directorate General of Estate Crops, 2020). Oil palm cultivation is not without challenges, particularly in managing plantations effectively to achieve optimal productivity through adequate nutrients and other management practices (Foong et al., 2019; Makinde et al., 2011).

Currently, private companies (54%) manage the most oil palm plantations in Indonesia, followed by smallholders (42%), and the remaining area is managed by state-owned enterprises (Directorate General of Estate Crops, 2020). However, a recent study highlighted a significant yield gap between the actual and potential fresh fruit bunches (FFB) in large and smallholder plantations of 38% and 47%, respectively (Monzon et al., 2021). This gap can be attributed to various management practices, including difficulties in acquiring certified seedlings, fertilizers, and agrochemicals, as well as rarely practiced returning organic matter to the soil, especially in smallholder plantations (Comte et al., 2012).

Soil degradation has become a concern in oil palm plantations, with a decline in the soil carbon content observed with plantation age. Over time, erosion, soil compaction, and the absence of aboveground carbon input (organic matter return) contribute to this degradation (Guillaume et al., 2016). Furthermore, the excessive use of inorganic fertilizers accelerates the decrease in soil organic carbon (Guan Yi, 2019), negatively affecting soil health and contributing to the yield gap. Addressing these issues requires a focus on organic matter and its role in enhancing soil health. Recently, the application of organic matter is essential for increasing soil organic carbon, leading to improvements in soil physical, chemical, and

biological properties, which, in turn, enhances the attainable yield of oil palm trees (Hasputri et al., 2017; Rahman et al., 2021; Tao et al., 2017). Nevertheless, the effects of long-term application of organic matter on oil palm plantations remain poorly understood. Another crucial aspect of sustainable agriculture is the role of microbes, particularly plant growth-promoting bacteria (PGPB) and beneficial fungi in soil health. These beneficial microbes form symbiotic associations with plant roots, directly and indirectly enhancing plant growth and agricultural yield (Ali et al., 2021; Treseder and Lennon, 2015; Větrovský and Baldrian, 2013). The presence and diversity of these microbes in the soil rhizosphere play a vital role in determining soil health and, consequently, plant productivity and sustainability (Suman et al., 2022).

Over the last decade, several studies have explored the microbial communities in oil palm plantations using culture-independent techniques (Smets et al., 2016; Syarifain et al., 2019; Wong, 2021). These studies have primarily focused on soil microbial diversity in relation to land-use transformation (Brinkmann et al., 2019; Tin et al., 2017; Schneider et al., 2015; Lee-Cruz et al., 2013), soil-borne pathogenes (Hidayat et al., 2021; Goh et al., 2020; Lo and Chong, 2020), and various management practices, such as fertilizers and weeding (Berkelmann et al., 2020; Inayah et al., 2022; Ryadin et al., 2022).

In addition, advancing the use of organic matter in agriculture could reduce the global reliance on chemical fertilizers owing to environmental benefits, including the use of renewable and sustainable resources (e.g. empty fruit bunches (EFB)) as materials and low greenhouse gas emissions, compared with chemical fertilizers (Diacono and Montemurro, 2010; Hu et al., 2023; Walling and Vaneeckhaute, 2020; Wang et al., 2022). However, a knowledge gap persists regarding the long-term effects of organic matter application for good soil management (GSM) of soil bacterial and fungal communities in oil palm plantations. Furthermore, this is the first study to explore the use of the metabolic functions provided by

the microbiome to predict the presence of plant growth-promoting soil communities in the oil palm rhizosphere. By shedding light on these critical aspects, this study seeks to contribute to developing sustainable agricultural practices for oil palm plantations in Indonesia, ultimately bridging the yield gap and ensuring a more productive and ecologically balanced future for the country's agricultural sector.

2. Materials and methods

2.1. Site and sample information

Soil samples (0 – 20 cm depth), including organic layer, were collected from the rhizosphere (bulky soil) and roots of oil palm plants under two contrasting soil management practices: GSM and poor soil management (PSM). Prior to sampling, leaf litters and grasses were removed from the soil surface. In August 2021, six-point sampling technique were employed from 100 × 100 m^2 plot in the middle of each block (20 Ha). The study area experiences an equatorial rainfall pattern which distributed a whole year. Both sites have a similar soil type, classified as Inceptisol, where oil palm trees were planted since 1984. The oil palm plantation in the GSM plot is located at coordinates 1.91007°N and 100.24472°E. Over the past 10 years, the GSM plot has consistently employed organic matter as a crucial part of soil management practices, specifically using empty fruit bunches (EFB) at a rate of 40 tons/ha/year and palm oil mill effluent. EFB without any treatments was applied raw as an organic mulch with single layer between the trees once a year. The total carbon, nitrogen, available P, and available K concentrations (per ha/year) derived from EFB application added to the GSM soil were approximately 17,120 kg, 320 kg, 88 kg, and 1,160 kg, respectively. Over the last five years, there has been a notable reduction in the use of inorganic fertilizers, showcasing a shift toward sustainable and organic-based practices. The practice of returning organic matter to the soil has never been implemented in the PSM plot. Instead, it has relied

heavily on the frequent application of inorganic fertilizers twice a year include the N, P, and K fertilizers. Over the past 10 years, the inorganic fertilizers usage history found that the GSM and PSM plots have used 113.75 kg/ha/year and 438.75 kg/ha/year of chemical compound fertilizers (N-P-K ratio of 15%-8%-23%), respectively. The oil palm yield and tree density in each site were calculated based on the average yield (kg/tree/year) and palm density (trees/ha) during last ten years according to management report data.

2.2. Soil chemical analysis

Various soil physicochemical properties were investigated, including soil texture, pH, total organic carbon (TOC), total nitrogen (TN), available phosphorus (AP), available potassium (AK), and cation exchange capacity (CEC). The soil texture was determined using the hydrometry method which involves dispersing soil particles such as sand, clay, and silt (Gee and Or, 2002), soil pH was measured using the potentiometry method by suspending the soil samples in the dH_2O with the ratio of 1:5 for 10 min (Thomas, 1996), TOC was quantified using the spectrometric method (Maestre et al., 2003), and TN was analyzed using the Kjeldahl method which involved pretreating the soil samples with 0.05 N H_2SO_4 before distillation and titration (Bremner, 1965). For AP, a spectrophotometric method using Bray's reagent was employed (Pierzynski, 2000). AK was measured using atomic absorption spectrophotometry after extraction with ammonium acetate (Mc Lean and Watson, 2015). The CEC was determined using the CEC-7 method, which involved percolation with a 1 N ammonium acetate (NH_4OAc) buffer at pH 7, followed by distillation with 1% (w/v) boric acid, and then titration with 0.005N H_2SO_4 (Soil Survey Staff, 2014). ~~The CEC was determined using a volumetric method with 10% sodium chloride extractant (Chapman, 1965).~~

2.3. *DNA extraction*

The total DNA extraction was conducted using the DNeasy® PowerSoil® Pro Kit (QIAGEN GmbH, QIAGEN Strasse 1, Hilden, Germany), according to the manufacturer's instructions. The concentration of the extracted DNA was determined using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). Subsequently, the DNA extracts (50 µl) were stored at −20°C until further use.

2.4. *Quantification of bacterial and fungal cells in soil samples*

For quantification of bacterial cell copy numbers, real-time PCR was performed using the CFX Connect System (Bio-Rad Laboratories, Inc., Hercules, CA, USA) with universal primers targeting a portion of the bacterial 16S rRNA gene (357F [5′-CCT ACG GGA GGC AGC AG-3′] and 518R [5′-ATT ACC GCG GCT GCT GG-3′]) (Nishi et al., 2015). PCR amplification was performed as described by Watanabe et al. (2019).

Fungal cell numbers were quantified using the primers FungiQuant-F (5′-GGR AAA CTC ACC AGG TCC AG-3′) and FungiQuant-R (5′-GSW CTA TCC CCA KCA CGA-3′) were used (Liu et al., 2012). The amplification was performed according to the protocol provided by Maza-Márquez et al. (2018). Bacterial and fungal cell copy numbers were calculated using the following equation:

$$Copies.g^{-1} of\ sample = qPCR\ copy.\mu l^{-1}\ of\ DNA \times\ elution\ volume\ (50\ \mu l) \times\ [1/sample\ weight\ (g)]$$

2.5. *Microbial community analysis*

The MiSeq platform (Illumina, San Diego, CA, USA) was used to analyze the microbial community structure, including bacteria and fungi. A two-stage PCR method was used to extract DNA. In the first-stage PCR, as previously described (Watanabe et al., 2019; Zhang et al., 2021), the V4 region of bacteria and the internal transcribed spacer region (ITS) of fungi

were targeted using universal primer sets. For bacterial amplification, the primer sequences were 1-515F (5′-TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG GTG CCA GCM GCC GCG GTA A-3′) and 1-806R (5′-GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA GGG ACT ACH VGG GTW TCT AAT-3′). For fungal amplification, the primer sequences were 1-ITS1F (5′-TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG TAG AGG AAG TAA AAG TCG TAA-3′) and 1-ITS2 (5′-GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA GTT YRC TRC GTT CTT ACT C-3′) (Toju et al., 2012). In the second-stage PCR, the purified 1st PCR amplicons were used with a primer set containing flow cell adapter, index, and tailed sequences (Forward primer 5′-AAT GAT ACG GCG ACC ACC GAG ATC TAC AC-Index sequence-TCG TCG GCA GCG TC-3′ and Reverse primer 5′-CAA GCA GAA GAC GGC ATA CGA GAT-Index sequence- GTC TCG TGG GCT CGG-3′). Finally, the purified PCR products from each sample were pooled, denatured, and subjected to sequencing on an Illumina MiSeq System (Illumina) using a MiSeq Reagent Kit v3 (300 × 2 cycles with paired ends; Illumina), according to the manufacturer's instructions. Illumina raw read sequences and the nucleotide sequences of 30 selected ASVs have been deposited under BioProject ID PRJDB16473 (bacterial) and PRJDB16380 (fungal) with accession numbers LC776194-LC776223 and LC7762224-LC776253 in the DNA Data Bank of Japan.

2.6. Bioinformatic analysis of MiSeq sequence data

The sequence data obtained from the MiSeq platform were subjected to bioinformatics analysis using QIIME 1.9.1 and QIIME2, following the approach described by Caporaso et al. (2010). Taxonomy-based analysis involved analyzing representative sequences for each amplicon sequence variant (ASV) using EzBioCloud (Yoon et al., 2017) for bacterial data and National Center for Biotechnology Information (Boratyn et al., 2019) for fungal data. To gain

insight into the functional potential of the bacterial community, a phylogenetic investigation of communities by reconstruction of unobserved state 2 (PICRUSt2) was utilized (Langille et al., 2013). PICRUSt2 enables the prediction of the number of functional genes responsible for plant growth promotion, such as those of nitrogen-fixing bacteria, phosphate-solubilizing bacteria, potassium-solubilizing bacteria, and phytohormone (indole-acetic acid (IAA)) producers. PGPB functional enzymes were quantified by multiplying the relative abundance of predicted genes by the copy number of each sample. Alpha diversity (Shannon index) was generated by employing QIIME alpha_rarefraction script meanwhile beta diversity (principal coordinate analysis) based on Weighted UniFrac method was generated using beta_diversity script in QIIME2 software package (Caporaso et al., 2010). The bacterial and fungal heatmaps were constructed using R-studio software (version 2022.07.2) based on the top 30 copy number in each sampling sites. Statistical analyses for Shannon index, quantifying microbial cell numbers and comparing microbial communities were conducted using the independent-samples T test. This analysis was performed using IBM SPSS Statistics software (version 29.0.1) to evaluate significant differences among the groups.

3. Results

3.1. Soil physiochemical properties and oil palm yield

In general, the GSM plots exhibited physical soil properties similar to those of the PSM plots, characterized by a sandy loam soil texture. However, notable differences emerged when considering the soil chemical characteristics, as indicated in Table 1. The long-term application of organic matter (over 10 years) in the GSM plots significantly improved the TOC content, with a remarkable increase of approximately 211% compared with the PSM plots (Table 1). Similarly, soil TN, AP, AK, and CEC were significantly higher in the GSM plots, with increments of approximately 100%, 749%, 160%, and 71%, respectively, than in the PSM plots

(Table 1). Furthermore, the soil management practices employed in the GSM plots led to a remarkable increase in oil palm yield, with ~~71~~23% higher production of fresh fruit bunches than the PSM plots (Table 1). Thus, long-term application of organic matter to oil palm plantations for over 10 years would improve soil properties and product yield.

3.2. Microbial copy number

The qPCR analysis of bacterial cell counts based on the copy number of the 16S rRNA gene revealed that GSM plots have a significantly higher copy number than PSM plots in soil and roots (Table 2). In more detail, the bacterial copy number in GSM soil was 171 times significantly higher than in PSM plots, with averages of 5.28×10^7 and 3.07×10^5 copy number per gram (Table 2), respectively. Similarly, in the roots, GSM plots exhibited 9.9 times higher bacterial copy number with averages of 1.47×10^8 than 1.48×10^7 in PSM plots (Table 2). Regardless of plot type, the bacterial copy number was consistently higher in the roots than in soils, although the difference was not statistically significant (Table 2, $p>0.05$, independent-samples T test). This suggests that prolonged application of organic matter increases the bacterial copy number in the roots and soils.

Contrary to the bacterial copy number, qPCR analysis of fungal cell counts based on the copy number of the 18S rRNA gene indicated that PSM plots had 3.4- and 2.2-times higher counts in soil and roots, respectively, than those in GSM plots (Table 2). Concerning soil fungal copy numbers, PSM showed significantly higher counts ($p < 0.05$, independent-samples T test) than GSM, with an average of 7.58×10^3 and 2.25×10^3 copy number per gram (Table 2), respectively. While there was no significant difference in root fungal copy numbers, it tended to be higher in PSM plots than in GSM plots, with averages of 2.07×10^5 and 9.33×10^4 copy numbers per gram, respectively (Table 2). Similar to the bacterial copy number, roots exhibited significantly higher fungal copy numbers than the soil systems ($p<0.05$, independent-samples

T test). This study highlights the increased fungal copy number in PSM plots, which is likely due to a decline in the bacterial copy number.

3.3. Microbial richness and diversity

The 16S rRNA gene amplicons targeting the V4 region were sequenced in the bacterial community analysis, resulting in 477,708 raw reads across all samples, including root and soil. After applying the QIIME2 standard pipeline to filter low-quality reads, 4,210–149,719 high-quality clean reads were obtained from the samples, comprising 3,489 ASVs with 99% sequence identity (Table S1). Alpha rarefaction analysis indicated good coverage, with values exceeding 0.9 at 3,200 sequences (Table S1). Regarding the fungal communities, 310,540 raw reads were obtained from the ITS region. After filtering, 2,029–41,951 high-quality clean reads were obtained (Table S1), comprising 777 ASVs with 99% sequence identity. Similar to the bacterial analysis, alpha rarefaction analysis showed coverage exceeding 0.9 for 2,000 sequences (Table S1).

Regarding microbial richness (Shannon index), no significant differences were observed between GSM and PSM plots in terms of bacterial and fungal α-diversity indices, both in roots and soils (Figure 1a and 1b, $p < 0.05$ by Tukey HSD). Moreover, bacterial richness was slightly higher in roots than in soils in both the GSM and PSM plots (Figure 1a). Moreover, in terms of fungal richness, the values were relatively similar in both sites (Figure 1b). The GSM plots showed a slightly higher bacterial richness, with an average Shannon index of 7.30, whereas the PSM plots exhibited a slightly higher average Shannon index for fungal richness (4.45).

In terms of β-diversity at species levels, bacterial communities exhibited marked distinctions between soil rhizosphere (root) and bulk soil, both in GSM and PSM plots (Figure 1c). Furthermore, GSM displayed diverse bacterial communities compared with the PSM plots (Figure 1c). Conversely, fungal species tended to be more distinct between the GSM and PSM

soils, whereas fungal communities in the roots were relatively similar at both sites (Figure 1d). Thus, long-term application of organic matter would result in diverse communities, not only of bacteria in roots and soil but also of fungi in soils in oil palm plantations.

3.4. Microbial community at the phylum level

The taxonomic assignment of reads from the GSM and PSM plots revealed members from the top 10 predominant bacterial phyla, namely Actinobacteria, Proteobacteria, Firmicutes, Acidobacteria, Chloroflexi, Verrucomicrobiota, Myxococcota, Planctomycetota, Bacteroidota, and Gemmatimonadota (Figure ~~2a~~ S1a and ~~2b~~S1b). Actinobacteria, Proteobacteria, and Firmicutes were particularly prevalent in the GSM and PSM plots, accounting for 22–43%, 6–24%, and 3–15% of the assigned reads, respectively. Proteobacteria was the most significant ($p < 0.05$) phylum in both sites followed by Actinobacteria in GSM sites (Figure ~~3a~~2a). The independent-samples T-test analysis indicated that the copy numbers of the top 10 bacterial phyla excluding Bacteroidota were significantly higher in the GSM plots than in the PSM plots ($p < 0.05$) (Figure ~~3c~~2c).

In terms of fungal communities at the phylum level, the top 10 fungal phyla were Ascomycota, Basidiomycota, Mucoromycota, Unclassified, Mortierellomycota, Aphelidiomycota, Chytridiomycota, Rozellomycota, and Kickxellomycota (Figure ~~2c~~ S1c and ~~2d~~S1d). Ascomycota emerged as the predominant fungal phylum, accounting for 34–97% relative abundance in the GSM and PSM plots. Ascomycota was found as the most significantly predominant phylum in GSM and PSM sites (Figure ~~3b~~2b). The independent-samples T test revealed that only the phylum Chytridiomycota exhibited a significantly higher abundance in the GSM plots ($p < 0.05$), whereas no statistically significant difference was observed in the copy number of other major fungal phyla (Figure ~~3d~~2d). Therefore, prolonged

application of organic matter is likely to enhance the abundance of common bacterial phyla and certain fungal phyla found in palm oil plantations.

3.5. Microbial community at species level

A comprehensive analysis of the microbial communities at the species level was conducted, and the results were visualized using a heat map depicting the relative abundances and copy numbers of the top 30 bacterial and fungal ASVs (Figure ~~4~~3). Overall, the relative bacterial and fungal abundance patterns displayed remarkable similarities between the GSM and PSM plots (Figure ~~S1~~S2). All 30 bacterial ASVs exhibited higher copy numbers in the GSM plots than in the PSM plots (Figure ~~4a~~3a). The roots harbored a greater abundance of fungi in both GSM and PSM plots (Figure ~~4b~~3b). Among the identified bacterial species, *Cytobacillus purgationiresistens* and *Bacillus yapensis* had the highest relative abundances, exceeding 8% in the GSM plots (Figure ~~S1a~~S2a). Similarly, several fungal species, including *Aspergillus niger* (~24.16%) and *Humicola seminuda* (~21.36%) (Figure ~~S1b~~S2b) were more abundant in GSM plots. Additionally, other fungal species such as *Pestalotiopsis mangifola* (~24.54%), *Apodus oryzae* (~37.71%), and *Arnium marcotheca* (~23.82%) (Figure ~~S1b~~S2b) exhibited notable relative abundances in PSM plots.

Among the top 30 bacterial ASVs, a subset of nine ASVs exhibited significantly higher abundance in the GSM plots than in the PSM plots ($p < 0.05$, independent-samples T test) based on their copy number (Figure ~~4a~~ 3a and Figure ~~S2a~~S3a). These ASVs correspond to important bacterial species, including *Nitrobacter alkalicus*, *Nitrobacter winogradsky*, *Bradyrhizobium kacangense*, *Hyphomicrobium holandicum*, *Mesorhizobium silamurunense*, *Bacillus coahuilense*, *Bacillus manliponensis*, *Cytobacillus purgationiresistens*, and *Nocardioides caricicola*.

In terms of fungal species, three ASVs from the top 30 ASVs were exclusively found in the GSM plots: *Aspergillus niger*, *Humicola seminuda*, and *Aspergillus fumigatus* (Figure ~~4b~~ 3b and Figure ~~S2b~~S3b), which have been reported as beneficial fungi (Table 3). Conversely, three other ASVs related to pathogenic fungi were detected in the PSM plots: *Fusarium proliferatum*, *Kalmusia longispora*, and *Talaromyces funiculosus* (Table 3). Hence, the long-term application of organic matter would result in an increased presence of beneficial bacteria and fungi while concurrently suppressing the occurrence of pathogenic fungi in oil palm plantations.

3.6. PGPB existence in soil communities

The abundance of genes related to PGPB in soil communities was analyzed using PICRUSt2, focusing on the prediction of PGPB functional enzymes involved in nitrogen fixation, phosphate solubilization, potassium solubilization, and IAA production, as indicated by their Enzyme Commission numbers. Among the functional enzymes, the genes encoding histidine kinase related to phosphate-solubilization showed the most significant abundance in GSM site (Figure ~~S3~~S4). Furthermore, the results revealed a significantly higher abundance of PGPB functional enzymes in the GSM plots than in the PSM plots (Figure ~~5~~4). GSM plots exhibited a significant abundance of predicted genes involved in PGPB activities, ranging from 1.54×10^6 to 6.80×10^8 copy numbers, whereas PSM had only 1.58×10^5 to 4.27×10^7 copy numbers.

Specifically, in terms of nitrogen-fixing bacteria, a 9.5 times higher abundance of genes encoding nitrogenase was observed in the GSM plots than in the PSM plots. Additionally, genes related to phosphate solubilization were significantly higher abundance in GSM plots than those in PSM plots. Exopolyphosphatase and alkaline phosphatase were the most

abundant among genes related to phosphate solubilization, followed by histidine kinase (Figure ~~5~~4).

Acetate kinase, citrate synthase, and malate dehydrogenase encode by the genes related to potassium solubilization were also significantly more abundant in GSM plots than those in PSM plots (Figure ~~5~~4). Additionally, GSM plots showed a higher abundance of indoleacetamide hydrolase and aldehyde dehydrogenase, known as the predominant enzymes involved in IAA production (Figure ~~5~~4). This study underscores the benefit of the long-term application of organic matter in enhancing the abundance of functional genes related to PGPB in oil palm plantations.

4. Discussion

4.1. Long-term application of organic matter improves the soil properties and oil palm yield

This study explored the influence of long-term EFB application in GSM of oil palm plantation on soil properties, yield, and microbial communities, emphasizing the significance of incorporating environmentally friendly and sustainable materials into the soil to enhance soil health and quality. Through the regular application of organic matter, a substantial improvement in the physicochemical properties of the soil in the GSM plots was observed (Table 1). The application of 40 tons/ha/year of EFB in GSM plots led to a remarkable 211% and ~~171~~23% increase in the TOC content and yield, respectively, compared with PSM plots. This aligns with prior research showing that EFB application enriches soil organic carbon (Boafo et al., 2020; Quezada et al., 2022; Rahman et al., 2021). Moreover, the higher organic carbon content in the GSM plots significantly affected other vital soil chemical properties, including TN, AP, AK, and CEC (Table 1). Although some studies have reported increased pH and TN with EFB application, the effects on other soil chemical properties, such as CEC, AP, and exchangeable potassium, are not significant (Budianta et al., 2013; Quezada et al., 2022).

This study highlights the merits of the long-term application of organic matter in oil palm plantations to improve soil chemical properties and product yield.

4.2. The long-term organic matter application altered the microbial community structures

At the phylum level, Actinobacteria, Proteobacteria, and Firmicutes were the predominant bacterial phyla and were significantly more abundant in the GSM plots (Figure ~~2~~S1). These phyla have been reported as the common predominant phyla in the soils applied with organic matters such as sugarcane bagasse compost (Liu et al., 2023) and mushroom compost-cattle manure-rice straw (Sun et al., 2023). Moreover, ~~These~~ these findings are consistent with prior research that identified Actinobacteria, Proteobacteria, and Firmicutes as the dominant phyla under various conditions, including inorganic fertilizer application, weed management, and soils affected by *G. boninense*-induced basal stem rot diseases (Berkelmann et al., 2020; Goh et al., 2020; Lee-Cruz et al., 2013). The predominant fungal phylum was Ascomycota (Figure ~~2~~S1), which is consistent with a previous study on oil palm plantations in Jambi, Indonesia (Brinkmann et al., 2019). The relative abundance of Basidiomycota was higher in the PSM plots, to which the pathogenic fungus *G. boninense* belonged (Figure ~~2~~S1). Basidiomycota produces lignocellulolytic enzymes that are crucial for plant material decomposition (Boberg et al., 2011; Osono, 2020), which may be linked to the lower planting density and oil palm productivity observed in the PSM plots (Table 1). This study revealed the predominant indigenous bacterial and fungal phyla in oil palm plantations. Nevertheless, their communities underwent alterations primarily influenced by agricultural activities, particularly soil management involving organic matter application.

The presence of organic matter in the GSM plots also led to a noteworthy increase in bacterial copy numbers, likely due to the higher soil nutrient levels and pH observed in the GSM plots, which influenced the bacterial community (Hou et al., 2022; Liu et al., 2020).

Conversely, the lower bacterial copy numbers in the PSM plots could be attributed to lower pH, which negatively affects bacterial numbers (Xiang et al., 2021). Although no previous studies have explored the impact of organic matter application on bacterial richness and diversity in oil palm plantations, these findings are the first to be reported and are consistent with research on other crops, such as walnuts, arecanut, and rice, where organic matter application increased bacterial and fungal richness and diversity (Du et al., 2022; Liu et al., 2023; Sun et al., 2023). Fungal copy numbers tended to be higher in the PSM plots than in the GSM plots, which was the opposite trend for bacterial copy numbers (Table 2). This has the potential to negatively affect the growth and productivity of oil palm, as observed in the literature (Situmorang et al., 2016), which reported that an increase in the population of the pathogenic fungus *Ganoderma boninense* correlated with a decrease in the presence of indigenous beneficial bacteria. Our study detected an ASV closely related to *Ganoderma boninense* with a low relative abundance (0.15%, data not shown), which was only found in PSM soil. Thus, our finding underscores the vital role of organic matter in soil management in mitigating imbalances in bacterial and fungal communities within soil communities. This has the potential to induce changes in the overall microbial dynamics of the soil, with consequent implications for plant growth and productivity.

4.3. Organic matter application enhances the abundance of beneficial bacteria and fungi while suppressing the pathogenic fungi

Regular application of organic matter to GSM plots led to changes in the microbial communities, enriching the beneficial bacteria essential for oil palm plantations. The GSM plots exhibited a high abundance of nitrifying bacteria, including *Nitrobacter alkalicus*, *Nitrobacter winogradsky*, and *Bacillus manliponensis* (Table 3, Figure ~~S2a~~S3a), which play crucial roles in nitrogen cycling, enhancing soil fertility, and supporting plant growth (Babu

and Rengasamy, 2017; Edgar et al., 2018; Poly et al., 2008; Wang et al., 2012). Furthermore, the GSM plots exclusively harbored beneficial fungi, such as *Aspergillus niger*, *Aspergillus fumigatus*, *Humicola seminuda*, and *Humicola phialophoroides* (Table 3, Figure ~~S2b~~S3b). These fungi have been reported to contribute to disease suppression and the overall improvement of plant health (Galeano et al., 2021; Khan et al., 2011; Wen et al., 2022; Ko et al., 2011; Yang et al., 2014). In contrast, the PSM plot harbored pathogenic fungi, including *Fusarium proliferatum*, *Kalmusia longispora*, *Talaromyces funiculosus*, and *Arnium macrotheca* (Table 2, Figure ~~S2b~~S3b) and is associated with various plant diseases in cannabis, rice, *Vitis vinifera*, and peaches (Lei et al., 2019; Punja, 2021; Karácsony et al., 2021; Mukhtar et al., 2019; Udagawa et al., 1979). These findings suggest the importance of organic matter in boosting the abundance and activity of beneficial bacteria, with implications for promoting beneficial fungi while suppressing the population of pathogenic fungi.

4.4. Long-term application of organic matter led to increased genes that encode PGPB activities for sustainable agriculture

While previous studies explored microbial communities using various techniques in the soils of oil palm plantations (Berkelmann et al., 2020; Brinkmann et al., 2019; Goh et al., 2020; Schneider et al., 2015; Smets et al., 2016; Syarifain et al., 2019; Tin et al., 2017; Wong, 2021), this research first focused on functional diversity and its prediction of PGPB presence in the oil palm plantation using Picrust2 to predict functional composition in the several soils in literature (Breitkreuz et al., 2021; Kong and Liu, 2022; Volpiano et al., 2022; Samaddar et al., 2019; Farda et al., 2022). By predicting the potential functional genes of bacterial communities, we observed a significant enrichment of genes encoding enzymes that stimulate plant growth in GSM plots, including nitrogen fixation, phosphate solubilization, potassium solubilization, and IAA production (Figure ~~5~~4). Hence, the results of this study suggest that the long-term

application of organic matter in oil palm plantations serves to accumulate carbon sources, fostering the abundance and activity of PGPB. This has the potential to enhance soil health, quality, and fertility.

Several studies have reported that an increases in crop yield is linked to elevated soil nutrient levels (Gondwe et al., 2020; Liu et al., 2021). Furthermore, maintaining long-term soil nutrients is essential for stable yields, and these nutrients would be significantly influenced by the application of organic matter (Liang et al., 2012; Ozlu and Kumar, 2018). Additionally, a previous study indicated that long-term organic matter application increased beneficial bacteria and their PGP activities, leading to improved soil nutrient status in rice cultivation (Liu et al., 2021; Esitken et al., 2010). Balasundram et al. (2006) found that oil palm yield was positively correlated with soil nutrient levels, particularly phosphorus (P) and potassium (K), although there are few reports on investigation of relationship between PGPB and soil nutrient levels. Our study found the increases in oil palm yield, soil nutrient levels including total nitrogen, available phosphorus, available potassium, and functional genes related to enhancing available nutrients with PGPB in GSM plots (Table 1, Fig. 4). Linear correlation analysis indicated that the abundances of functional genes (nitrogen fixation, phosphate solubilization, potassium solubilization) with PGPB significantly showed positive correlations with total nitrogen (r=0.768), available phosphorus (r = 0.180–0.753) and available potassium (r = 0.567–0.709), respectively (Table S2). Therefore, our findings suggested that long-term organic matter application would enhance the abundances of functional genes and their activities with PGPB, which would contribute to not only an improvement of soil nutrient availability but also an increased oil palm yield.

In the context of sustainable agriculture, prolonged use of organic matter in oil plantations has prompted a shift in fertilization practices. A substantial reduction in the application of inorganic fertilizers was observed with the incorporation of OM. This practice

positively contributes to the economic, ecological, and environmental sustainability of oil palm plantations. A previous life cycle assessment study indicated that regularly returning palm oil mill effluent and EFB offers multiple benefits, including reduced greenhouse gas emissions, preserved carbon storage, and improved soil quality (Stichnothe and Schuchardt, 2011). Additionally, it has been suggested that replacing inorganic fertilizers with frequent organic matter application in organic farming systems not only improves soil properties but also decreases greenhouse gas emissions and promotes sustainable agricultural practices (Liem et al., 2022), which would enhance the application of organic matter in oil palm plantations.

5. Conclusion

This study underscores the importance of sustainable soil management practices, such as the long-term application of organic matter, to enhance soil health and quality in oil palm plantations. This approach supports current oil palm productivity and ensures soil fertility for future generations, contributing to sustainable agricultural practices and environmental preservation. Nurturing healthy soil can maintain a resilient and productive ecosystem that benefits farmers and the environment.

Acknowledgement

This work was partly supported by JSPS KAKENHI Grant-in-Aid for Scientific Research (B) [JP 23H03595]. We acknowledge Indonesian Oil Palm Research Institute (IOPRI) for providing the samples (administration and sample collection). We also would like to acknowledge Faculty of Agriculture, Gadjah Mada University (UGM) as the counterpart of this research and the Center for Advanced Instrumental and Educational Supports, the Faculty of Agriculture, Kyushu University for their support with MiSeq. This work was supported

partly by Japanese Government Monbukagakusho (Ministry of Education, Culture, Sports, Science, and Technology, MEXT) scholarship.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was partly supported by JSPS KAKENHI Grant-in-Aid for Scientific Research (B) [JP 23H03595].

Appendix A. Supplementary data

Supplementary data to this article can be found online at ….

References:

Ali, S.S., M. Kornaros, A. Manni, R. Al-Tohamy, A.E.R. El-Shanshoury, I.M. Matter, T. Elsamahy, M. Sobhy, and J. Sun. 2021. "Advances in Microorganisms-Based Biofertilizers: Major Mechanisms and Applications." *Biofertilizers* 1: 371–385.

Babu, S. and R. Rengasamy. 2017. "Isolation and Identification of *Bacillus* sp. from Seaweed Liquid Fertilizer (SLF)." *Journal of Marine Biosciences* 3: 167–174.

Balasundram, S.K., P.C. Robert, D.J. Mulla, D.J., and D.L. Allan. 2006. "Relationship Between Oil Palm Yield and Soil Fertility as Affected by Topography in an Indonesian Plantation." *Communications in Soil Science and Plant Analysis* 37: 1321–1337. https://doi.org/10.1080/00103620600626817

Berkelmann, D., D. Schneider, N. Hennings, A. Meryandini, and R. Daniel. 2020. "Soil Bacterial Community Structures in Relation to Different Oil Palm Management Practices." *Scientific Data* 7: 421. https://doi.org/10.1038/s41597-020-00752-3.

Boafo, D.K., B. Kraisornpornson, S. Panphon, B.E. Owusu, and P.N. Amaniampong. 2020. "Effect of Organic Soil Amendments on Soil Quality in Oil Palm Production." *Applied Soil Ecology* 147: 103358. https://doi.org/10.1016/j.apsoil.2019.09.008.

Boberg, J.B., K. Ihrmark, and B.D. Lindahl. 2011. "Decomposing Capacity of Fungi Commonly Detected in *Pinus Sylvestris* Needle Litter." *Fungal Ecology* 4: 110–114. https://doi.org/10.1016/j.funeco.2010.09.002.

Boratyn, G.M., J. Thierry-Mieg, D. Thierry-Mieg, B. Busby, and T.L. Madden. 2019. "Magic-Blast, an Accurate RNA-Seq Aligner for Long and Short Reads." *BMC Bioinformatics* 20: 405. https://doi.org/10.1186/s12859-019-2996-x.

Breitkreuz, C., A. Heintz-Buschart, F. Buscot, S.F.M. Wahdan, M. Tarkka, and T. Reitz. 2021. "Can We Estimate Functionality of Soil Microbial Communities from Structure-Derived Predictions? A Reality Test in Agricultural Soils." *Microbiology Spectrum* 9 (1): e00278-21. https://doi.org/10.1128/Spectrum.00278-21.

Bremner, J.M. 1965. "Total Nitrogen, in: Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties." American Society of Agronomy, Inc., pp. 1149–1178.

Brinkmann, N., D. Schneider, J. Sahner, J. Ballauff, N. Edy, H. Barus, B. Irawan, et al. 2019. "Intensive Tropical Land Use Massively Shifts Soil Fungal Communities." *Scientific Reports* 9: 3403. https://doi.org/10.1038/s41598-019-39829-4.

Budianta, D., N. Gofar, and G.A. Andika. 2013. "Improvement of Sand Tailing Fertility Derived from Post Tin Mining Using Leguminous Crop Applied by Compost and Mineral Soil." *Journal of Tropical Soils* 18 (3): 217–223. https://doi.org/10.5400/jts.2013.18.3.217.

Caporaso, J.G., J. Kuczynski, J. Stombaugh, K. Bittinger, F.D. Bushman, E.K. Costello, N. Fierer, et al. 2010. "QIIME Allows Analysis of High-Throughput Community Sequencing Data." *Nature Methods* 7 (5): 335–336. https://doi.org/10.1038/nmeth.f.303.

~~Chapman, H.D. 1965. "Cation-Exchange Capacity, in: Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties." American Society of Agronomy, Inc., pp. 891–901.~~

Comte, I., F. Colin, J.K. Whalen, O. Grünberger, and J.-P. Caliman. 2012. "Agricultural Practices in Oil Palm Plantations and Their Impact on Hydrological Changes, Nutrient Fluxes and Water Quality in Indonesia, in: Advances in Agronomy." Elsevier, pp. 71–124. https://doi.org/10.1016/B978-0-12-394277-7.00003-8.

Diacono, M. and F. Montemurro. 2010. "Long-Term Effects of Organic Amendments on Soil Fertility." A review. *Agronomy for Sustainable Development* 30: 401–422. https://doi.org/10.1051/agro/2009040.

Directorate General of Estate Crops. 2020. "Statistical of National Leading Estate Crops Commodity 2019-2021." Secretariate of Directorate General of Estate Crops, Ministry of Agriculture Republic of Indonesia.

Du, T.-Y., H.-Y. He, Q. Zhang, L. Lu, W.-J. Mao, and M.-Z. Zhai. 2022. "Positive Effects of Organic Fertilizers and Biofertilizers on Soil Microbial Community Composition and Walnut Yield." *Applied Soil Ecology* 175: 104457. https://doi.org/10.1016/j.apsoil.2022.104457.

Edgar, M., A. Levi, C. Percy, and L. Gaddafi. 2018. "Analysis of Nitrifying Microbial Community for Organic Hydroponics." *African Journal of Microbiology Research* 12 (1): 1–8. https://doi.org/10.5897/AJMR2017.8635.

Esitken, A., H.E. Yildiz, S. Ercisli, M. Figen Donmez, M., Turan, and A. Gunes. 2010. "Effects of Plant Growth Promoting Bacteria (PGPB) on Yield, Growth and Nutrient Contents of

Organically Grown Strawberry." *Scientia Horticulturae* 124: 62–66. https://doi.org/10.1016/j.scienta.2009.12.012

Farda, B., A. Mattedi, R. Djebaili, L. Pace, M. Del Gallo, and M. Pellegrini.2022. "Microbial Community Investigation of Wild Brambles with Root Nodulation from a Calcareous Nitrogen-Deficient Soil." *Soil Systems* 6: 96. https://doi.org/10.3390/soilsystems6040096.

Foong, S.Z.Y., C.K.M., Goh, C.V. Supramaniam, and D.K.S. Ng. 2019. "Input–Output Optimisation Model for Sustainable Oil Palm Plantation Development." *Sustainable Production and Consumption* 17: 31–46. https://doi.org/10.1016/j.spc.2018.08.010.

Galeano, R.M.S., D.G. Franco, P.O. Chaves, G.C. Giannesi, D.C. Masui, R. Ruller, B.O. Corrêa, M. da Silva Brasil, and F.F. Zanoelo. 2021. "Plant Growth Promoting Potential of Endophytic *Aspergillus Niger* 9-P Isolated from Native Forage Grass in Pantanal of Nhecolândia Region, Brazil." *Rhizosphere* 18: 100332. https://doi.org/10.1016/j.rhisph.2021.100332.

Gee, G.W. and D. Or. 2002. "Particle-Size Analysis, in: Methods of Soil Analysis, Part 4: Physical Methods." Soil Science Society of America, Inc., Madison, WI, USA, pp. 255–293.

Goh, Y.K., M.Z.H.M. Zoqratt, Y.K., Goh, Q. Ayub, and A.S.Y. Ting. 2020. "Determining Soil Microbial Communities and Their Influence on *Ganoderma* Disease Incidences in Oil Palm (*Elaeis Guineensis*) via High-Throughput Sequencing." *Biology* 9: 424. https://doi.org/10.3390/biology9120424.

Gondwe, R.L., R. Kinoshita, T. Suminoe, D. Aiuchi, J.P. Palta, and M. Tani. 2020. "Available Soil Nutrients and NPK Application Impacts on Yield, Quality, and Nutrient Composition of Potatoes Growing during the Main Season in Japan." *American Journal of Potato Research* 97: 234–245. https://doi.org/10.1007/s12230-020-09776-2

Guan, Y.L. 2019. "Enhancing Sustainable Oil Palm Cultivation Using Compost." *Journal of Oil Palm Research* 31: 412–421. https://doi.org/10.21894/jopr.2019.0037.

Guillaume, T., A.M. Holtkamp, M. Damris, B. Brümmer, and Y. Kuzyakov. 2016. "Soil Degradation in Oil Palm and Rubber Plantations Under Land Resource Scarcity." *Agriculture, Ecosystems, and Environment* 232: 110–118. https://doi.org/10.1016/j.agee.2016.07.002.

Hasputri, R., Sudradjat, and Sugiyanta. 2017. "The Roles of Organic and NPK Compound Fertilizers for Four Year Old Mature Oil Palm (*Elaeis guineensis* Jacq)." *International Journal of Science* 36: 213–225.

Hidayat, F., R. Farrasati, I. Pradiko, E. Listia, M. Syarovy, S. Rahutomo, and Winarna. 2021. "Preliminary Study on The Bacterial Community Structure of *Ganoderma* Soil Under Oil Palm Plantation, in: Advances in Biological Sciences Research." Presented at the 10th International Seminar and 12th Congress of Indonesian Society for Microbiology (ISISM 2019), Atlantis Press International B.V., Surakarta, Indonesia, pp. 49–53. https://doi.org/10.2991/absr.k.210810.010.

Hou, Q., S. Lin, Y. Ni, L. Yao, S. Huang, T. Zuo, J. Wang, and W. Ni. 2022. "Assembly of Functional Microbial Communities in Paddy Soil With Long-Term Application of Pig Manure Under Rice-Rape Cropping System." *Journal of Environmental Management* 305: 114374. https://doi.org/10.1016/j.jenvman.2021.114374.

Hu, Y., D. Li, Y. Wu, S. Liu, L. Li, W. Chen, S. Wu, Q. Meng, H. Feng, and K.H.M. Siddique. 2023. "Mitigating Greenhouse Gas Emissions by Replacing Inorganic Fertilizer with Organic Fertilizer in Wheat–Maize Rotation Systems in China." *Journal of Environmental Management* 344: 118494. https://doi.org/10.1016/j.jenvman.2023.118494.

Inayah, M.N., Y. Lestari, and A. Meryandini. 2022. "Community of Soil *Actinobacteria* in PTPN VI Oil Palm Plantation Jambi (Sumatra, Indonesia) based on Amplicon Sequencing of 16S rRNA Gene." *Hayati Journal of Bioscience* 29 (3): 389–398. https://doi.org/10.4308/hjb.29.3.389-398.

Karácsony, Z., D.G., Knapp, S. Lengyel, G.M., Kovács, and K.Z. Váczy. 2021. "The Fungus *Kalmusia longispora* is Able to Cause Vascular Necrosis on *Vitis vinifera*." *PLoS ONE* 16: e0258043. https://doi.org/10.1371/journal.pone.0258043.

Khan, A.L., M., Hamayun, Y.-H. Kim, S.-M. Kang, J.-H. Lee, and I.-J. Lee. 2011. "Gibberellins Producing Endophytic *Aspergillus fumigatus* sp. LH02 Influenced Endogenous Phytohormonal Levels, Isoflavonoids Production and Plant Growth in Salinity Stress." *Process Biochemistry* 46: 440–447. https://doi.org/10.1016/j.procbio.2010.09.013.

Ko, W.-H., C.-H. Yang, M.-J. Lin, C.-Y. Chen, and Y.-J. Tsou. 2011. "*Humicola phialophoroides* sp. nov. from Soil with Potential for Biological Control of Plant Diseases. *Botanical Studies* 52: 197–202.

Kong, Z. and H. Liu. 2022. "Modification of Rhizosphere Microbial Communities: a Possible Mechanism of Plant Growth Promoting Rhizobacteria Enhancing Plant Growth and Fitness." *Frontier in Plant Science* 13: 920813. https://doi.org/10.3389/fpls.2022.920813.

Langille, M.G.I., J. Zaneveld, J.G. Caporaso, D. McDonald, D. Knights, J.A. Reyes, J.C. Clemente, et al. 2013. "Predictive Functional Profiling of Microbial Communities using 16S rRNA Marker Gene Sequences." *Nature Biotechnology* 31: 814–821. https://doi.org/10.1038/nbt.2676.

Lee-Cruz, L., D.P. Edwards, B.M., Tripathi, and J.M. Adams. 2013. "Impact of Logging and Forest Conversion to Oil Palm Plantations on Soil Bacterial Communities in Borneo." *Applied and Environmental Microbiology* 79 (23): 7290–7297. https://doi.org/10.1128/AEM.02541-13.

Lei, S., L., Wang, L. Liu, Y. Hou, Y. Xu, M. Liang, J. Gao, Q. Li, and S. Huang. 2019. "Infection and Colonization of Pathogenic Fungus *Fusarium proliferatum* in Rice Spikelet Rot Disease." *Rice Science* 26 (1): 60–68. https://doi.org/10.1016/j.rsci.2018.08.005.

Liang, Q., H. Chen, Y. Gong, M. Fan, H. Yang, R. Lal, and Y. Kuzyakov. 2012. "Effects of 15 Years of Manure and Inorganic Fertilizers on Soil Organic Carbon Fractions in a Wheat-Maize System in the North China Plain." *Nutrient Cycling in Agroecosystems* 92: 21–33. https://doi.org/10.1007/s10705-011-9469-6

Liem, L.T.T., Y. Tashiro, P.V.T. Tinh, and K. Sakai. 2022. "Reduction in Greenhouse Gas Emission from Seedless Lime Cultivation Using Organic Fertilizer in a Province in Vietnam Mekong Delta Region." *Sustainability* 14: 6102. https://doi.org/10.3390/su14106102.

Liu, C.M., S. Kachur, M.G. Dwan, A.G. Abraham, M. Aziz, P.-R. Hsueh, Y.-T. Huang, J.D. Busch, et al. 2012." FungiQuant: a Broad-Coverage Fungal Quantitative Real-Time PCR Assay." *BMC Microbiology* 12: 255. https://doi.org/10.1186/1471-2180-12-255.

Liu, H., D. Li, Y. Huang, Q. Lin, L. Huang, S. Cheng, S. Sun, and Z. Zhu. 2023. "Addition of Bacterial Consortium Produced High-Quality Sugarcane Bagasse Compost as an Environmental-Friendly Fertilizer: Optimizing Arecanut (*Areca catechu* L.) Production, Soil Fertility and Microbial Community Structure." *Applied Soil Ecology* 188: 104920. https://doi.org/10.1016/j.apsoil.2023.104920.

Liu, J., A. Shu, W. Song, W. Shi, M. Li, W. Zhang, Z. Li, G. Liu, F. Yuan, S. Zhang, Z. Liu, and Z. Gao. 2021. "Long-term Organic Fertilizer Substitution Increases Rice Yield by Improving Soil Properties and Regulating Soil Bacteria." *Geoderma* 404: 115287. https://doi.org/10.1016/j.geoderma.2021.115287

Liu, Z., X. Ma, N. He, J. Zhang, J. Wu, and C. Liu. 2020. "Shifts in Microbial Communities and Networks are Correlated with the Soil Ionome in A Kiwifruit Orchard Under Different Fertilization Regimes." *Applied Soil Ecology* 149: 103517. https://doi.org/10.1016/j.apsoil.2020.103517.

Lo, R.K.S. and K.P. Chong. 2020. "Metagenomic Data of Soil Microbial Community in Relation to Basal Stem Rot Disease." *Data in Brief* 31: 106030. https://doi.org/10.1016/j.dib.2020.106030.

Maestre, S.E., J. Mora, V. Hernandis, and J.L. Todolí. 2003. "A System for the Direct Determination of the Nonvolatile Organic Carbon, Dissolved Organic Carbon, and Inorganic Carbon in Water Samples Through Inductively Coupled Plasma Atomic Emission Spectrometry." *Analytical Chemistry* 75: 111–117. https://doi.org/10.1021/ac025980f.

Makinde, E.A., L.S. Ayeni, and S.O. Ojeniyi. 2011. "Effects of Organic, Organomineral and NPK Fertilizer Treatments on the Nutrient Uptake of *Amaranthus cruentus* (L) on Two Soil Types in Lagos, Nigeria." *Journal of Central European Agriculture* 12 (1): 114–123. https://doi.org/10.5513/JCEA01/12.1.887.

Maza-Márquez, P., R. Vílchez-Vargas, A. González-Martínez, J. González-López, and B. Rodelas. 2018. "Assessing the Abundance of Fungal Populations in a Full-Scale Membrane Bioreactor (MBR) Treating Urban Wastewater by Using Quantitative PCR (qPCR)." *Journal of Environmental Management* 223: 1–8. https://doi.org/10.1016/j.jenvman.2018.05.093.

Mc Lean, E.O. and M.E. Watson. 2015. "Soil Measurements of Plant-Available Potassium," in: Munson, R.D. (Ed.), ASA, CSSA, and SSSA Books. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI, USA, pp. 277–308. https://doi.org/10.2134/1985.potassium.c10.

Monzon, J.P., M.A. Slingerland, S. Rahutomo, F. Agus, T. Oberthür, J.F. Andrade, A. Couëdel et al. 2021. "Fostering a Climate-Smart Intensification for Oil Palm." *Nature Sustainability* 4: 595–601. https://doi.org/10.1038/s41893-021-00700-y.

Mukhtar, I., X. Quan, T. Chou, Q. Huang, J. Yan, B. Chen, S. Jiang, F. Liu, Z. Wen, and B. Xie. 2019. "First Report of *Talaromyces funiculosus* Causing Fruit Core Rot of Peach

(Prunus *persica*) in China." *Plant Disease* 103: 2124–2125. https://doi.org/10.1094/PDIS-11-18-2050-PDN.

Nishi, E., Y. Tashiro, and K. Sakai. 2015. "Discrimination Among Individuals Using Terminal Restriction Fragment Length Polymorphism Profiling of Bacteria Derived from Forensic Evidence." *International Journal of Legal Medicine* 129: 425–433. https://doi.org/10.1007/s00414-014-1092-z.

Osono, T. 2020. "Functional Diversity of Ligninolytic Fungi Associated with Leaf Litter Decomposition." *Ecological Research* 35: 30–43. https://doi.org/10.1111/1440-1703.12063.

Ozlu, E. and S. Kumar. 2018. "Response of Soil Organic Carbon, pH, Electrical Conductivity, and Water Stable Aggregates to Long-Term Annual Manure and Inorganic Fertilizer." *Soil Science Society of America Journal* 82: 1243–1251. https://doi.org/10.2136/sssaj2018.02.0082

Pierzynski, G.M. 2000. "Methods of Phosphorus Analysis for Soils, Sediments, Residuals, and Waters." North Carolina State University, North Carolina.

Poly, F., S. Wertz, E. Brothier, and V. Degrange. 2008. "First Exploration of *Nitrobacter* Diversity in Soils by a PCR Cloning-Sequencing Approach Targeting Functional Gene *nxrA*: *nxrA* Diversity in Soils." *FEMS Microbiology Ecology* 63: 132–140. https://doi.org/10.1111/j.1574-6941.2007.00404.x.

Pradana, A., I. Pujiastuti, and P.P. Paramita. 2019. "Regionalization of Agricultural Based Leading Sectors and Food Security in Indonesia. " *IOP Conf. Ser.: Earth Environmental Science* 338: 012015. https://doi.org/10.1088/1755-1315/338/1/012015

Punja, Z.K. 2021. "First Report of *Fusarium proliferatum* Causing Crown and Stem Rot, and Pith Necrosis, in Cannabis (Cannabis *sativa* L., marijuana) Plants." *Canadian Journal of Plant Pathology* 43 (2): 236–255. https://doi.org/10.1080/07060661.2020.1793222.

Quezada, J.C., T. Guillaume, C. Poeplau, J. Ghazoul, and A. Buttler. 2022. "Deforestation‐Free Land‐Use Change and Organic Matter‐Centered Management Improve the C Footprint of Oil Palm Expansion." *Glob. Change Biology* 28: 2476–2490. https://doi.org/10.1111/gcb.16069.

Rahman, N., K.E. Giller, A. de Neergaard, J. Magid, G. van de Ven, and T.B. Bruun. 2021. "The Effects of Management Practices on Soil Organic Carbon Stocks of Oil Palm Plantations in Sumatra, Indonesia." *Journal of Environmental Management* 278: 111446. https://doi.org/10.1016/j.jenvman.2020.111446.

Ryadin, A.R., D. Janz, D. Schneider, A. Tjoa, B. Irawan, R. Daniel, and A. Polle. 2022. "Early Effects of Fertilizer and Herbicide Reduction on Root-Associated Biota in Oil Palm Plantations." *Agronomy* 12: 199. https://doi.org/10.3390/agronomy12010199.

Samaddar, S., J. Truu, P. Chatterjee, M. Truu, K. Kim, S. Kim, S. Seshadri, and T. Sa. 2019. "Long-term Silicate Fertilization Increases the Abundance of Actinobacterial Population in Paddy Soils." *Biology and Fertility of Soils* 55 (2): 109–120. https://doi.org/10.1007/s00374-018-01335-6.

Schneider, D., M. Engelhaupt, K. Allen, S. Kurniawan, V. Krashevska, M. Heinemann, H. Nacke, et al. 2015. "Impact of Lowland Rainforest Transformation on Diversity and Composition of Soil Prokaryotic Communities in Sumatra (Indonesia)." *Frontiers in Microbiology* 6: 1339. https://doi.org/10.3389/fmicb.2015.01339.

Situmorang, E.C., Y.A. Nugroho, A. Prameswara, E. Andarini, Hartono, R.H. Setyobudi, N. Toruan-Mathius, and T. Liwang. 2016. "The Bacterial Diversity Investigation in Oil Palm Plantation Using Terminal Restriction Length Polymorphism." Presented at the The 4th International Conference on Biological Science, Yogyakarta, Indonesia, p. 020017. https://doi.org/10.1063/1.4953491.

Smets, W., J.W. Leff, M.A. Bradford, R.L. McCulley, S. Lebeer, and N. Fierer. 2016. "A Method for Simultaneous Measurement of Soil Bacterial Abundances and Community Composition via 16S rRNA Gene Sequencing." *Soil Biology and Biochemistry* 96: 145–151. https://doi.org/10.1016/j.soilbio.2016.02.003.

Soil Survey Staff. 2014. "Soil Survey Field and Laboratory Methods Manual", in Soil Survey Investigations Report No. 51; Version 2. U.S. Department of Agriculture, Nebraska, US, pp. 184-189.

Stichnothe, H. and F. Schuchardt. 2011. "Life Cycle Assessment of Two Palm Oil Production Systems." *Biomass and Bioenergy* 35: 3976–3984. https://doi.org/10.1016/j.biombioe.2011.06.001.

Suman, J., A. Rakshit, S.D. Ogireddy, S. Singh, C. Gupta, and J. Chandrakala. 2022. "Microbiome as a Key Player in Sustainable Agriculture and Human Health." *Frontiers in Soil Science* 2: 821589. https://doi.org/10.3389/fsoil.2022.821589.

Sun, T., X. Mao, Q. Ma, K. Han, X. Wang, Q. Cheng, X. Sheng, W. Mi, and L. Wu. 2023. "Response of Rice Yield to Organic Amendments was Regulated by Soil Chemical Properties, Microbial Functional Genes and Bacterial Community Rather than Fungal Community." *Applied Soil Ecology* 188: 104923. https://doi.org/10.1016/j.apsoil.2023.104923.

Syarifain, R.I., E.D. Anggrainy, R. Sudirja, E.T. Sofyan, and T. Simarmata. 2019. "The Change of Microbial Communities in Rhizomicrobiome Due to the Land Management." *IOP Conference Series: Earth and Environmental Science* 393: 012043. https://doi.org/10.1088/1755-1315/393/1/012043.

Tao, H.-H., J.L. Snaddon, E.M. Slade, J.-P. Caliman, R.H. Widodo, Suhardi, and K.J. Willis. 2017. "Long-term Crop Residue Application Maintains Oil Palm Yield and Temporal

Stability of Production." *Agronomy for Sustainable Development* 37: 33. https://doi.org/10.1007/s13593-017-0439-5.

Thomas, G.W. 1996. "Soil pH and Soil Acidity", in: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E. (Eds.), SSSA Book Series. Soil Science Society of America, American Society of Agronomy, Madison, WI, USA, pp. 475–490. https://doi.org/10.2136/sssabookser5.3.c16.

Tin, H.S., K. Palaniveloo, J. Anilik, M. Vickneswaran, Y. Tashiro, C.S. Vairappan, and K. Sakai. 2017. "Impact of Land-Use Change on Vertical Soil Bacterial Communities in Sabah." *Microbial Ecology* 75: 459–467. https://doi.org/10.1007/s00248-017-1043-6.

Toju, H., A.S. Tanabe, S. Yamamoto, and H. Sato. 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.

Treseder, K.K. and J.T. Lennon. 2015. "Fungal Traits that Drive Ecosystem Dynamics on Land." *Microbiology and Molecular Biology Reviews* 79: 243–262. https://doi.org/10.1128/MMBR.00001-15.

Udagawa, S., Y. Tsuzaki, and H. Uehada. 1979. "Growth Damage Caused by Ascopore Dispersal of *Arnium macrotheca* from Cultivated Carnation." *Trans. Mycol. Soc*. Japan 20: 357–369.

Větrovský, T. and P. Baldrian. 2013. "Analysis of Soil Fungal Communities by Amplicon Pyrosequencing: Current Approaches to Data Analysis and the Introduction of the Pipeline SEED." *Biology and Fertility of Soils* 49 (8): 1027–1037. https://doi.org/10.1007/s00374-013-0801-y.

Volpiano, C.G., B.B. Lisboa, J.F.B.D.S. José, A. Beneduzi, C.E. Granada, and L.K. Vargas. 2022. "Soil-Plant-Microbiota Interactions to Enhance Plant Growth." *Revista Brasileira de Ciencia do Solo*. 46: e0210098. https://doi.org/10.36783/18069657rbcs20210098.

Walling, E. and C. Vaneeckhaute. 2020." Greenhouse Gas Emissions from Inorganic and Organic Fertilizer Production and Use: A Review of Emission Factors and Their Variability." *Journal of Environmental Management* 276: 111211. https://doi.org/10.1016/j.jenvman.2020.111211.

Wang, C., X. Ma, J. Shen, D. Chen, L. Zheng, T. Ge, Y. Li, and J. Wu. 2022. "Reduction in Net Greenhouse Gas Emissions Through a Combination of Pig Manure and reduced Inorganic Fertilizer Application in a Double-Rice Cropping System: Three-Year Results." *Agriculture, Ecosystems and Environment* 326: 107799. https://doi.org/10.1016/j.agee.2021.107799.

Wang, F., Y. Liu, J. Wang, Y. Zhang, and H. Yang. 2012. "Influence of Growth Manner on Nitrifying Bacterial Communities and Nitrification Kinetics in Three Lab-Scale Bioreactors." *Journal of Industrial Microbiology and Biotechnology* 39: 595–604. https://doi.org/10.1007/s10295-011-1065-x.

Watanabe, K., E. Nishi, Y. Tashiro, and K. Sakai. 2019. "Mode and Structure of the Bacterial Community on Human Scalp Hair." *Microbes and Environments* 34: 252–259. https://doi.org/10.1264/jsme2.ME19018.

Wen, J., S.K. Okyere, S. Wang, J. Wang, L. Xie, Y. Ran, and Y. Hu. 2022. "Endophytic Fungi: an Effective Alternative Source of Plant-Derived Bioactive Compounds for Pharmacological Studies." *Journal of Fungi* 8: 205. https://doi.org/10.3390/jof8020205.

Wong, S. 2021. "Soil Fungal Composition and Diversity in Oil Palm Plantation at Sungai Asap, Sarawak, Malaysia." *Journal of Oil Palm Research* 33: 215–226. https://doi.org/10.21894/jopr.2021.0014.

Xiang, X., J.M. Adams, C. Qiu, W. Qin, J. Chen, L. Jin, C. Xu, and J. Liu. 2021. "Nutrient Improvement and Soil Acidification Inducing Contrary Effects on Bacterial Community Structure Following Application of Hairy Vetch (*Vicia villosa Roth* L.) in Ultisol."

Agriculture, Ecosystems and Environment 312: 107348. https://doi.org/10.1016/j.agee.2021.107348.

Yang, C.-H., M.-J. Lin, H.-J. Su, and W.-H. Ko. 2014. "Multiple Resistance-Activating Substances Produced by *Humicola phialophoroides* Isolated from Soil for Control of Phytophthora Blight of Pepper." *Botanical Studies* 55: 40. https://doi.org/10.1186/1999-3110-55-40.

Yoon, S.-H., S.-M. Ha, S. Kwon, J. Lim, Y. Kim, H. Seo, and J. Chun. 2017. "Introducing EzBioCloud: a Taxonomically United Database of 16S rRNA Gene Sequences and Whole-Genome Assemblies." *International Journal of Systematic and Evolutionary Microbiology* 67: 1613–1617. https://doi.org/10.1099/ijsem.0.001755.

Zhang, M., Y. Tashiro, Y. Asakura, N. Ishida, K. Watanabe, S. Yue, M.-N. Akiko, and K. Sakai. 2021. "Lab-Scale Autothermal Thermophilic Aerobic Digestion Can Maintain and Remove Nitrogen by Controlling Shear Stress and Oxygen Supply System." *Journal of Bioscience and Bioengineering* 132: 293–301. https://doi.org/10.1016/j.jbiosc.2021.05.008.

Figure 1. The bacterial richness and diversity among GSM vs PSM based on the alpha and beta diversity (a and c); fungal richness and diversity in GSM vs PSM (b and d). The bacterial and fungal Shannon index indicates no significant difference among the sub-sites ($p>0.05$ by Tukey HSD); the bacterial and fungal beta diversity were generated by principal component analysis in QIIME2 software package

~~**Figure 2.** Comparison of bacterial and fungal community structure at phylum level in soil and root of oil palm plantations in GSM and PSM plots. Top 10 bacterial phyla in GSM (a) and PSM (b); Top 10 fungal phyla in GSM (c) and PSM (d)~~

Figure ~~3~~2. Comparison of the phylum copy numbers in each site (a and b) and phylum copy number between GSM and PSM sites (c and d). The different letter above the bacterial and fungal abundant phylum bars (a and b) indicates significant difference among the sub-sites ($p<0.05$ by Tukey HSD); and single asterisk (*) above bacterial and fungal copy numbers (c and d) shows a significantly difference on each phylum between GSM and PSM ($p<0.05$ by independent-samples T test)

Figure ~~4~~3. Top 30 bacterial heatmap (a) and fungal heatmap (b) based on the copy number in each sample and each site. The asterisk (*) shows significant difference of the bacterial and fungal ASV between GSM and PSM sites ($p<0.05$ by independent-samples T test)

Figure ~~5~~4. The abundance of plant growth-promoting bacteria (PGPB) functional enzymes comparison between Good Soil Management (GSM) and Poor Soil Management (PSM). NFB: nitrogen fixing bacteria; PSB: phosphate-solubilizing bacteria; KSB: potassium-solubilizing bacteria; IAA: indole acetic acid. The single asterisk (*) shows a significantly different of each PGPB functional enzymes in GSM plots compared to PSM plots ($p<0.05$ by independent-samples T test)

Table 1

Comparison of physical and chemical properties of soils between good soil management (GSM) and poor soil management (PSM)

Site	Texture	pH	TOC (%)	TN (%)	AP (~~mc.100g~~$^{-1}$mg/kg)	AK (~~mc.100g~~$^{-1}$mg/kg)	CEC (~~mc.100g~~$^{-1}$cmol/kg)	Yield*) (kg/tree/year)	PD/~~ha~~*) (trees/ha)
GSM	Sandy loam	5.93[a]	3.05 [a]	0.28[a]	55.62 [a]	~~1.74~~678.6 [a]	13.60 [a]	187.8 [a]	136 [a]
PSM	Sandy loam	5.80[a]	0.98 [b]	0.14[a]	6.55 [b]	~~0.67~~261.3 [b]	7.97 [b]	152.6 [b]	97 [b]

Notes: Means followed by the different letter for treatment is significantly different according to independent-samples T test at p <0.05.
TOC: total organic carbon; TN: total Nitrogen; AP: soil available P; AK: soil available K; CEC: cation exchange capacity
**) Yield and PD (palm density/~~ha~~) was calculated based on the average yield or palm density at the last ten years in both sites.*

Table 2

The comparison of bacterial and fungal copy number between GSM and PSM

Sub-sites	Sites	Bacterial			Fungal		
		Copy number. g^{-1}	Average	*p-value**	Copy number. g^{-1}	Average	*p-value**
Soil	GSM	6.97×10^7	5.28×10^7	0.017	4.44×10^3	2.25×10^3	0.041
	GSM	2.63×10^7			8.84×10^2		
	GSM	6.25×10^7			1.43×10^3		
	PSM	3.08×10^5	3.07×10^5		7.20×10^3	7.58×10^3	
	PSM	5.85×10^5			1.02×10^4		
	PSM	2.77×10^4		0.083	5.34×10^3		0.009
Root	GSM	2.00×10^8	1.47×10^8	0.010	8.08×10^4	9.33×10^4	0.110
	GSM	1.35×10^8			7.40×10^4		
	GSM	1.05×10^8			1.25×10^5		
	PSM	2.40×10^7	1.48×10^7		2.66×10^5	2.07×10^5	
	PSM	1.56×10^7			1.01×10^5		
	PSM	4.90×10^6			2.53×10^5		

*Notes: * significancy value among the sites by independent-samples T test (p<0.05: significantly different; p>0.05: not significant different)*

Table 3

Comparison of the dominant bacterial and fungal species and their function in GSM and PSM

Species	Copy number. g^{-1}		Function	Reference
	GSM	PSM		
Bacteria:				
Nitrobacter alkalicus	4.02×10^5	2.38×10^4	Nitrifying bacteria	(Poly et al., 2008; Wang et al., 2012)
Nitrobacter winogradsky	2.24×10^5	9.46×10^3	Nitrite-oxidizing bacteria	(Edgar et al., 2018)
Bacillus manliponensis	8.73×10^5	1.91×10^4	Nitrogen fixing bacteria	(Babu and Rengasamy, 2017)
Fungi:				
Aspergillus niger	1.89×10^2	0	Multifunctional PGP	(Galeano et al., 2021)
Aspergillus fumigatus	9.68×10^1	0	Gibberellin producers	(Khan et al., 2011)
Humicola seminuda	3.15×10^1	0	Endophytic fungi	(Wen et al., 2022)
Humicola phialophoroides	3.20×10^3	4.86×10^1	Biocontrol agents of *Phytophthora*	(Wen et al., 2022)
Fusarium proliferatum	0	2.93×10^2	Pathogenic fungi of crown and spikelet rot diseases	(Lei et al., 2019; Punja, 2021)
Kalmusia longispora	0	1.40×10^2	Pathogenic fungi of vascular necrosis	(Karácsony et al., 2021)
Talaromyces funiculosus	0	2.16×10^2	Pathogenic fungi of fruit core rot	(Mukhtar et al., 2019)
Arnium macrotheca	1.95×10^0	6.76×10^3	Pathogenic fungi of Asco-spore dispersal	(Udagawa et al., 1979)

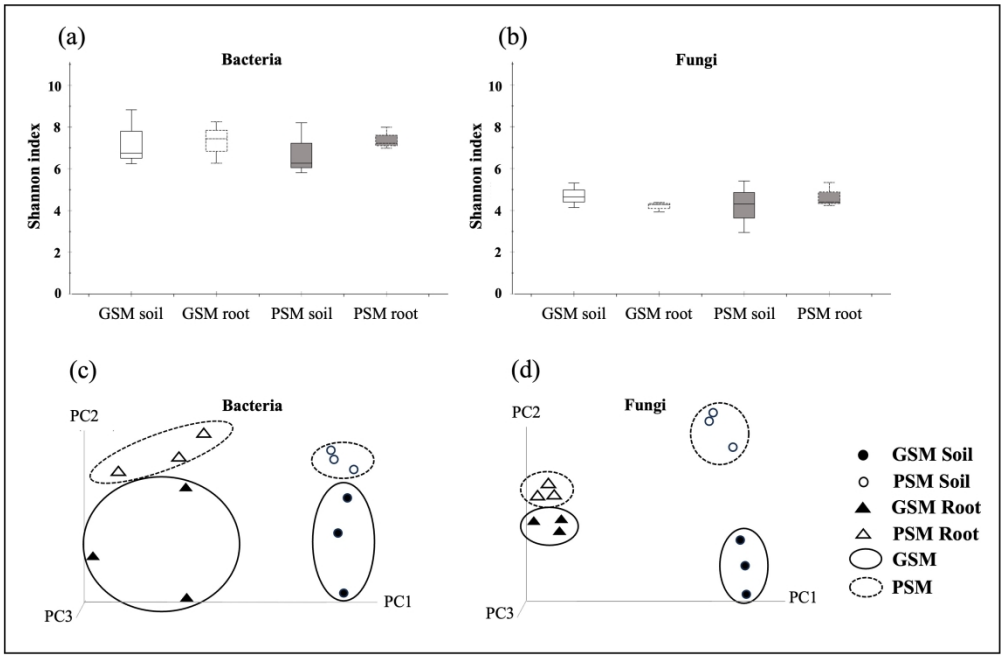

Figure 1. The bacterial richness and diversity among GSM vs PSM based on the alpha and beta diversity (a and c); fungal richness and diversity in GSM vs PSM (b and d). The bacterial and fungal Shannon index indicates no significant difference among the sub-sites (*p>0.05* by Tukey HSD); the bacterial and fungal beta diversity were generated by principal component analysis in QIIME2 software package

252x164mm (330 x 330 DPI)

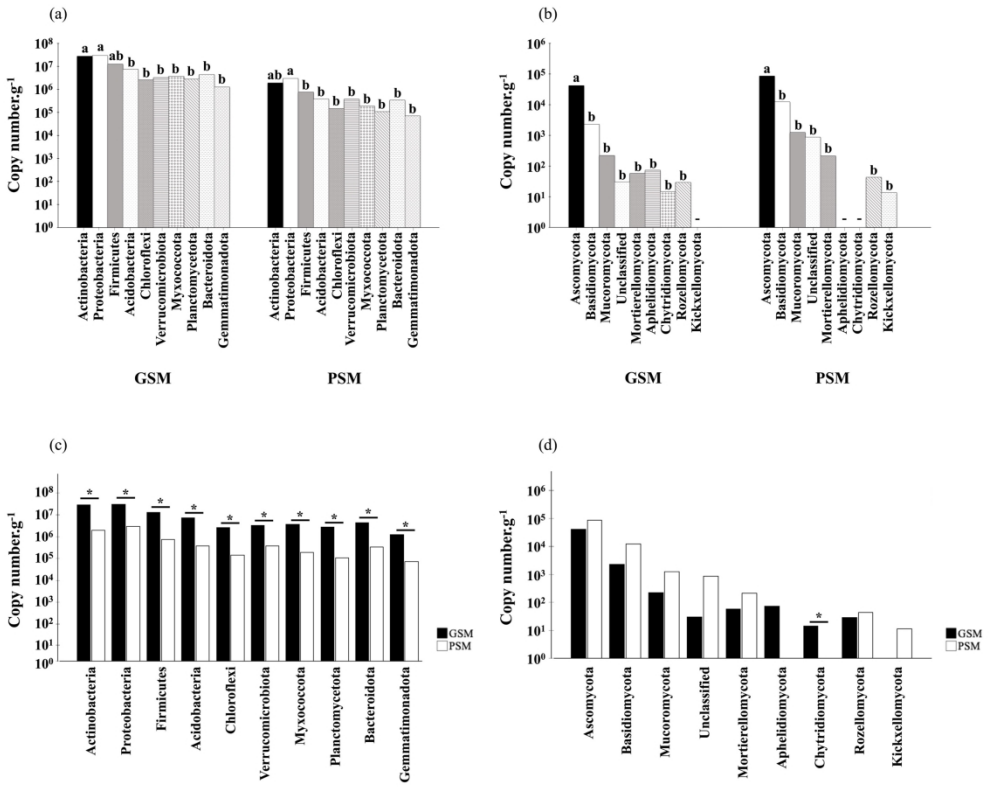

Figure 2. Comparison of the phylum copy numbers in each site (a and b) and phylum copy number between GSM and PSM sites (c and d). The different letter above the bacterial and fungal abundant phylum bars (a and b) indicates significant difference among the sub-sites ($p<0.05$ by Tukey HSD); and single asterisk (*) above bacterial and fungal copy numbers (c and d) shows a significantly difference on each phylum between GSM and PSM ($p<0.05$ by independent-samples T test)

566x456mm (132 x 132 DPI)

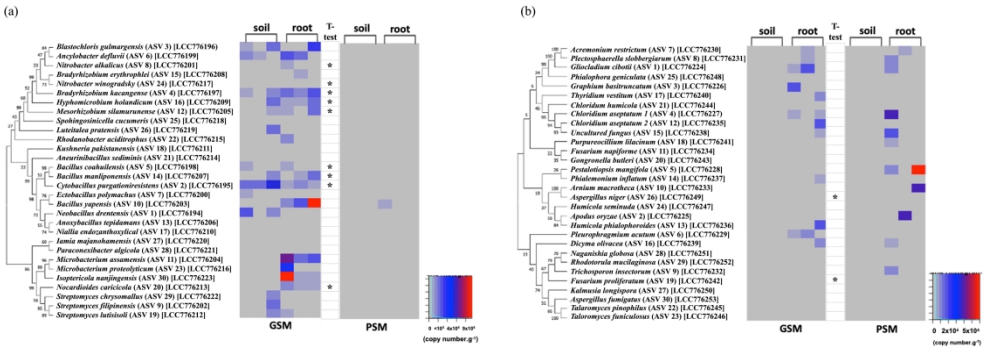

Figure 3. Top 30 bacterial heatmap (a) and fungal heatmap (b) based on the copy number in each sample and each site. The asterisk (*) shows significant difference of the bacterial and fungal ASV between GSM and PSM sites ($p<0.05$ by independent-samples T test)

839x311mm (132 x 132 DPI)

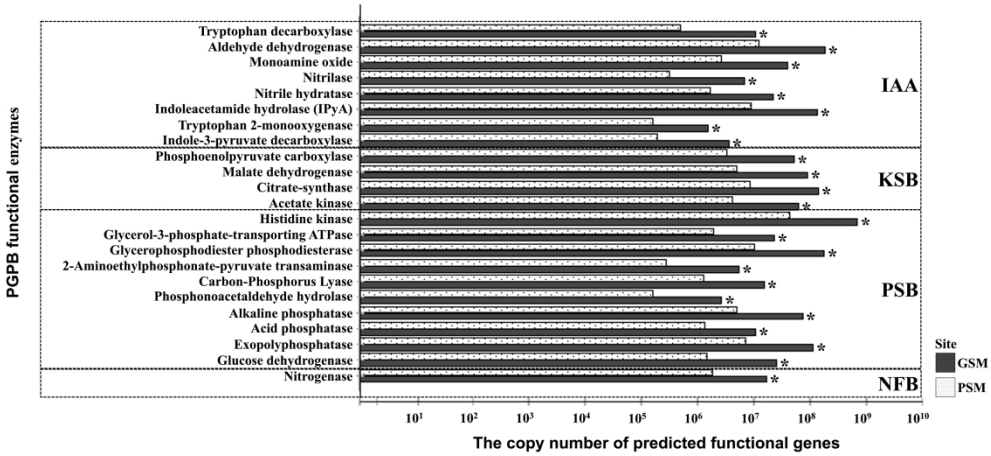

Figure 4. The abundance of plant growth-promoting bacteria (PGPB) functional enzymes comparison between Good Soil Management (GSM) and Poor Soil Management (PSM). NFB: nitrogen fixing bacteria; PSB: phosphate-solubilizing bacteria; KSB: potassium-solubilizing bacteria; IAA: indole acetic acid. The single asterisk (*) shows a significantly different of each PGPB functional enzymes in GSM plots compared to PSM plots ($p<0.05$ by independent-samples T test)

841x395mm (132 x 132 DPI)

Table S1: The number of reads, filtered reads, relative coverage after filtration, and copy number among the samples.

Site	Sub-sites	Raw		Filtered		Good Coverage		Copy number. g^{-1}	
		Bacterial	Fungal	Bacterial	Fungal	Bacterial	Fungal	Bacterial	Fungal
GSM	Soil	229,074	17,217	149,719	2,644	0.999	1.000	$6.97 \times \times 10^{7}$	4.44×10^{3}
GSM	Soil	11,941	14,406	6,084	4,590	0.998	0.994	2.63×10^{7}	8.84×10^{2}
GSM	Soil	15,161	16,318	5,245	5,717	1.000	0.991	6.25×10^{7}	1.43×10^{3}
GSM	Root	12,764	55,629	9,642	41,951	0.992	0.988	2.00×10^{8}	8.08×10^{4}
GSM	Root	28,721	26,217	18,265	20,421	0.978	0.988	1.35×10^{8}	7.40×10^{4}
GSM	Root	9,866	32,703	4,217	23,052	1.000	0.991	1.05×10^{8}	1.25×10^{5}
PSM	Soil	11,297	20,728	4,210	5,706	1.000	0.997	3.08×10^{5}	7.20×10^{3}
PSM	Soil	20,340	22,925	16,734	9,340	0.970	0.988	5.85×10^{5}	1.02×10^{4}
PSM	Soil	14,540	7,316	4,407	2,029	1.000	1.000	2.77×10^{4}	5.34×10^{3}
PSM	Root	30,860	32,643	8,548	24,258	0.998	0.986	2.40×10^{7}	2.66×10^{5}
PSM	Root	71,601	35,508	30,587	28,461	0.977	0.982	1.56×10^{7}	1.01×10^{5}
PSM	Root	21,543	28,930	11,540	22,406	0.998	0.990	4.90×10^{6}	2.53×10^{5}

Table S2: Linear correlation between the PGPB functional enzyme and soil nutrient content in GSM and PSM plots

Functional genes	Correlation coefficient (r-value)
Nitrogen fixation	
Nitrogenase	0.768*
Phosphate solubilization	
Glucose dehydrogenase	0.560*
Exopolyphosphatase	0.461
Acid phosphatase	0.429
Alkaline phosphatase	0.554*
Phosphonoacetaldehyde hydrolase	0.180
Carbon-phosphorus lyase	0.469
2-Aminoethylphosphonate-pyruvate transaminase	0.753*
Glycerophosphodiester phosphodiesterase	0.513*
Glycerol 3-phosphate-transporting ATPase	0.502*
Histidine kinase	0.506*
Potassium solubilization	
Acetate kinase	0.596*
Citrate synthase	0.601*
Malate dehydrogenase	0.709*
Phosphoenolpyruvate carboxylase	0.567*

Notes: * significant correlation (p<0.05) by Pearson correlation between the abundance of genes encode PGPB functional enzyme (nitrogen fixation; phosphate solubilization; potassium solubilization) and soil nutrient content (total nitrogen, available phosphate, and available potassium)

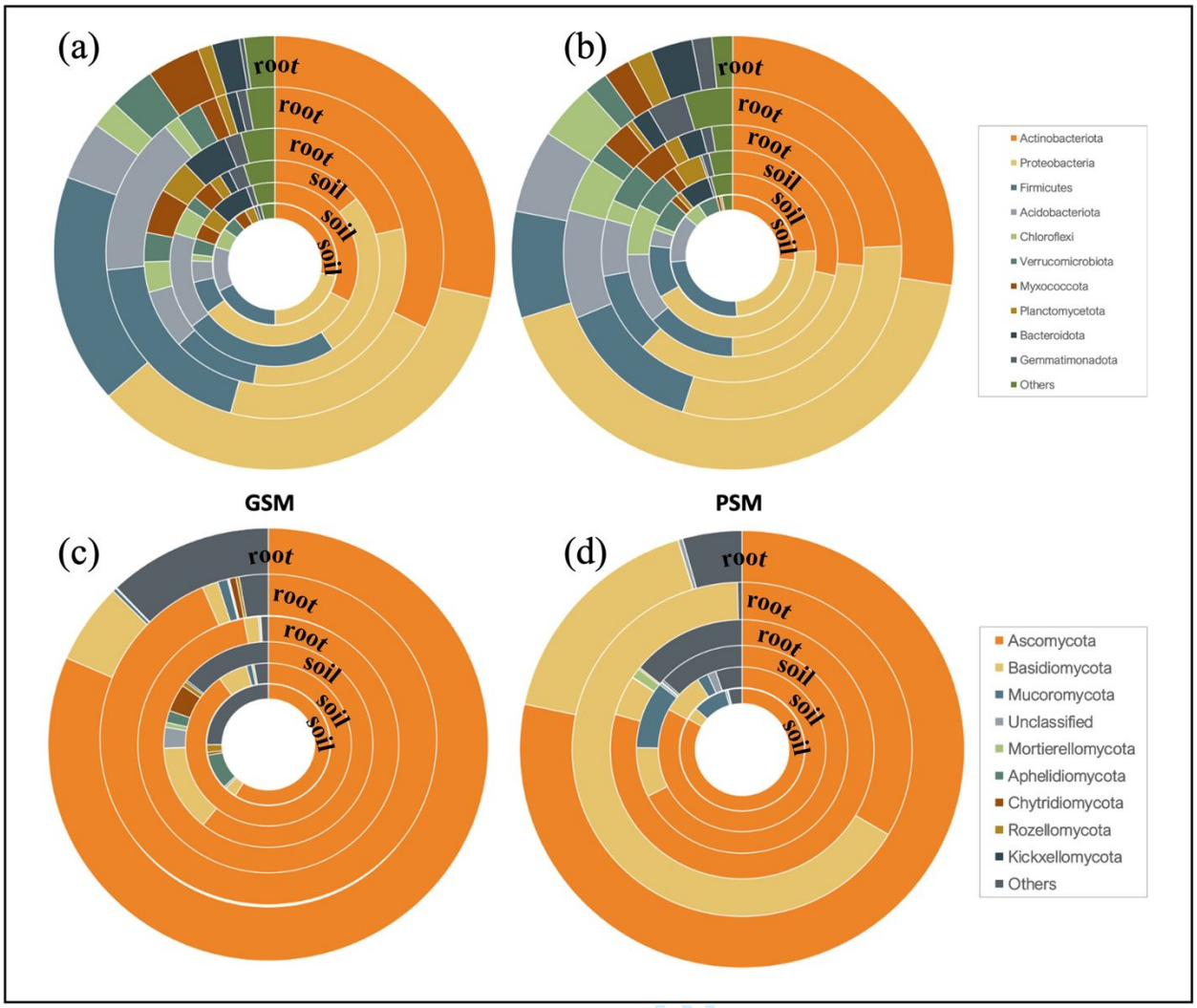

Figure S1: Comparison of bacterial and fungal community structure at phylum level in soil and root of oil palm plantations in GSM and PSM plots. Top 10 bacterial phyla in GSM (a) and PSM (b); Top 10 fungal phyla in GSM (c) and PSM (d)

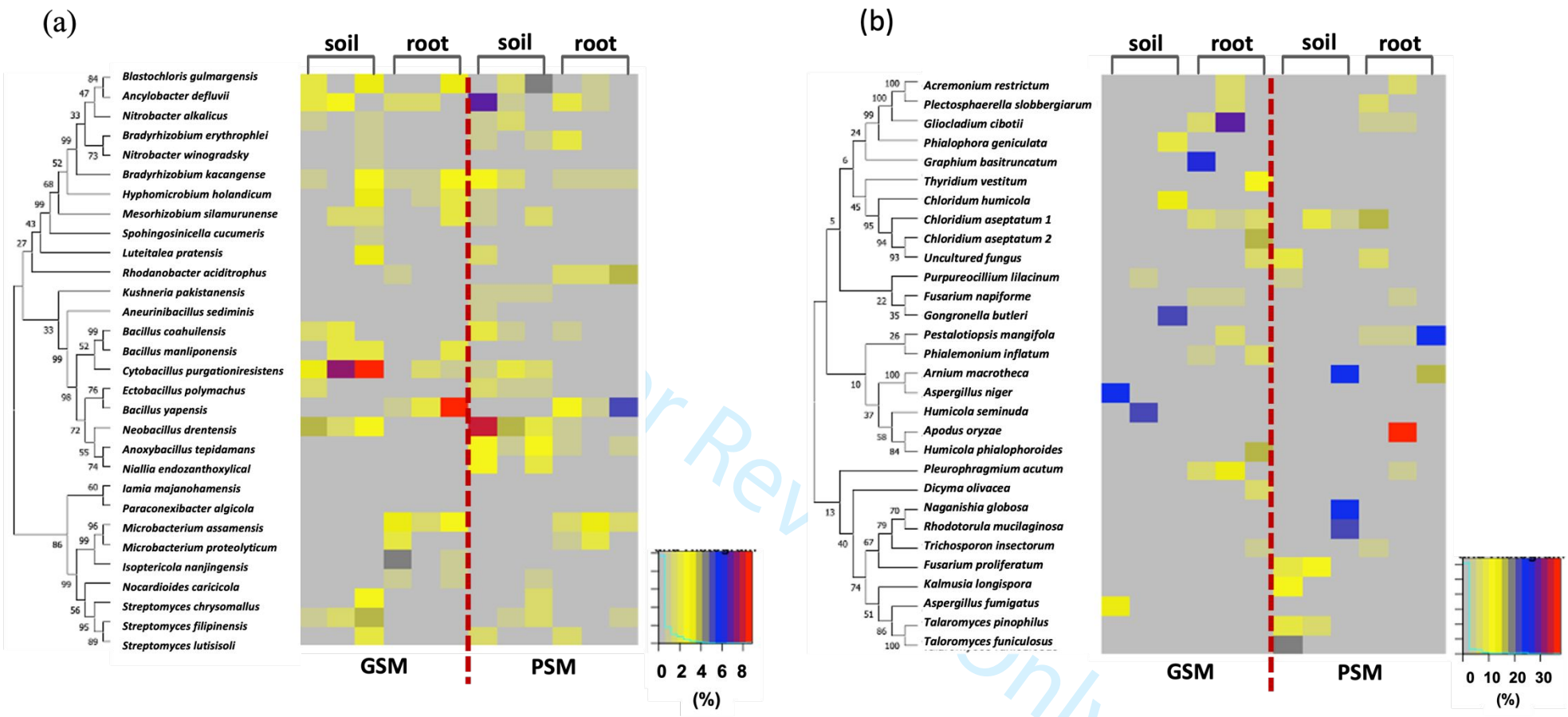

Figure S2: Top 30 bacterial (A) and fungal (B) heatmap based on the relative abundance.

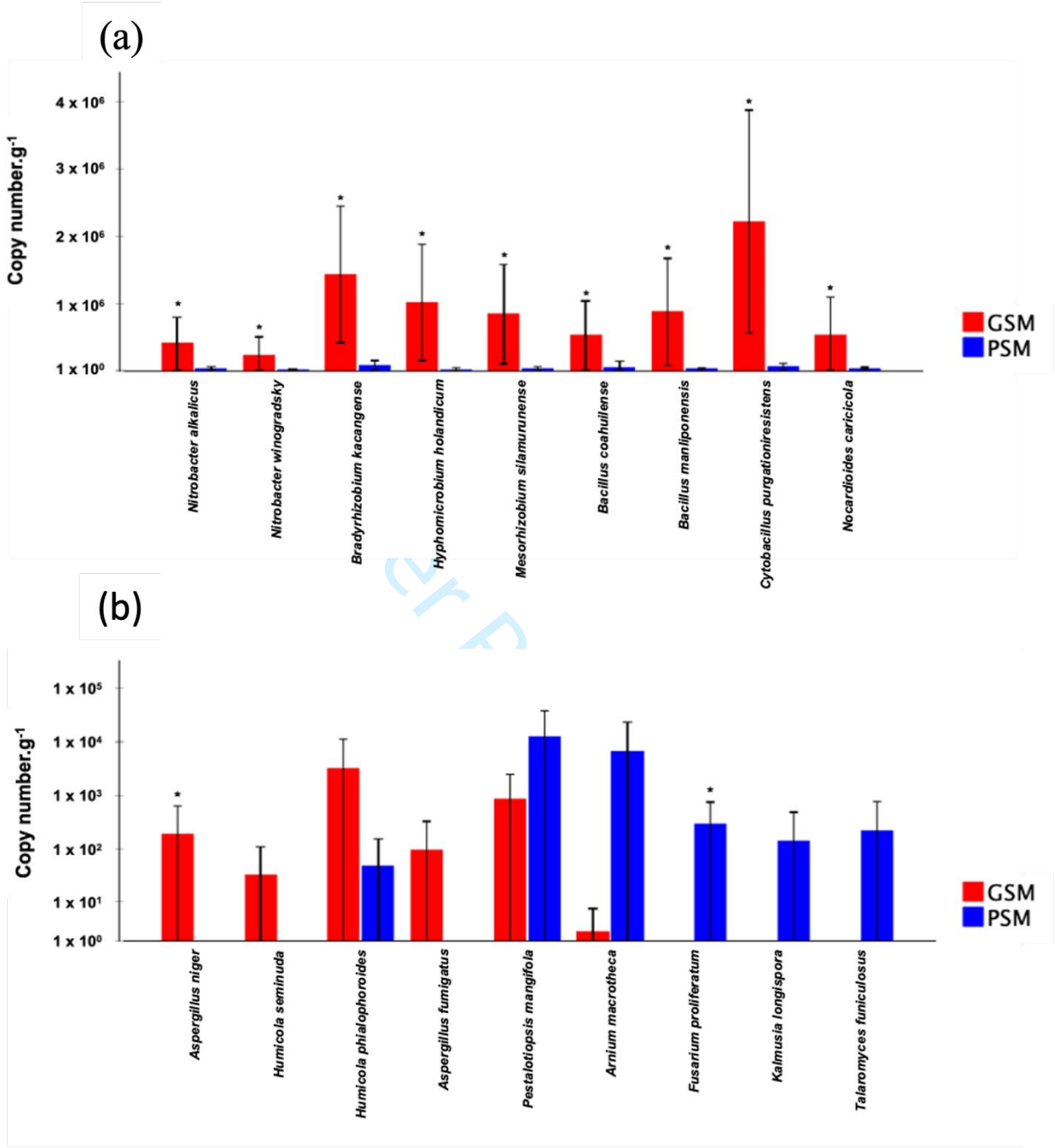

Figure S3: The most significant bacteria (A) and specific fungi (B) in each sites according to the copy number (*: $p<0.05$ by independent-samples T test)

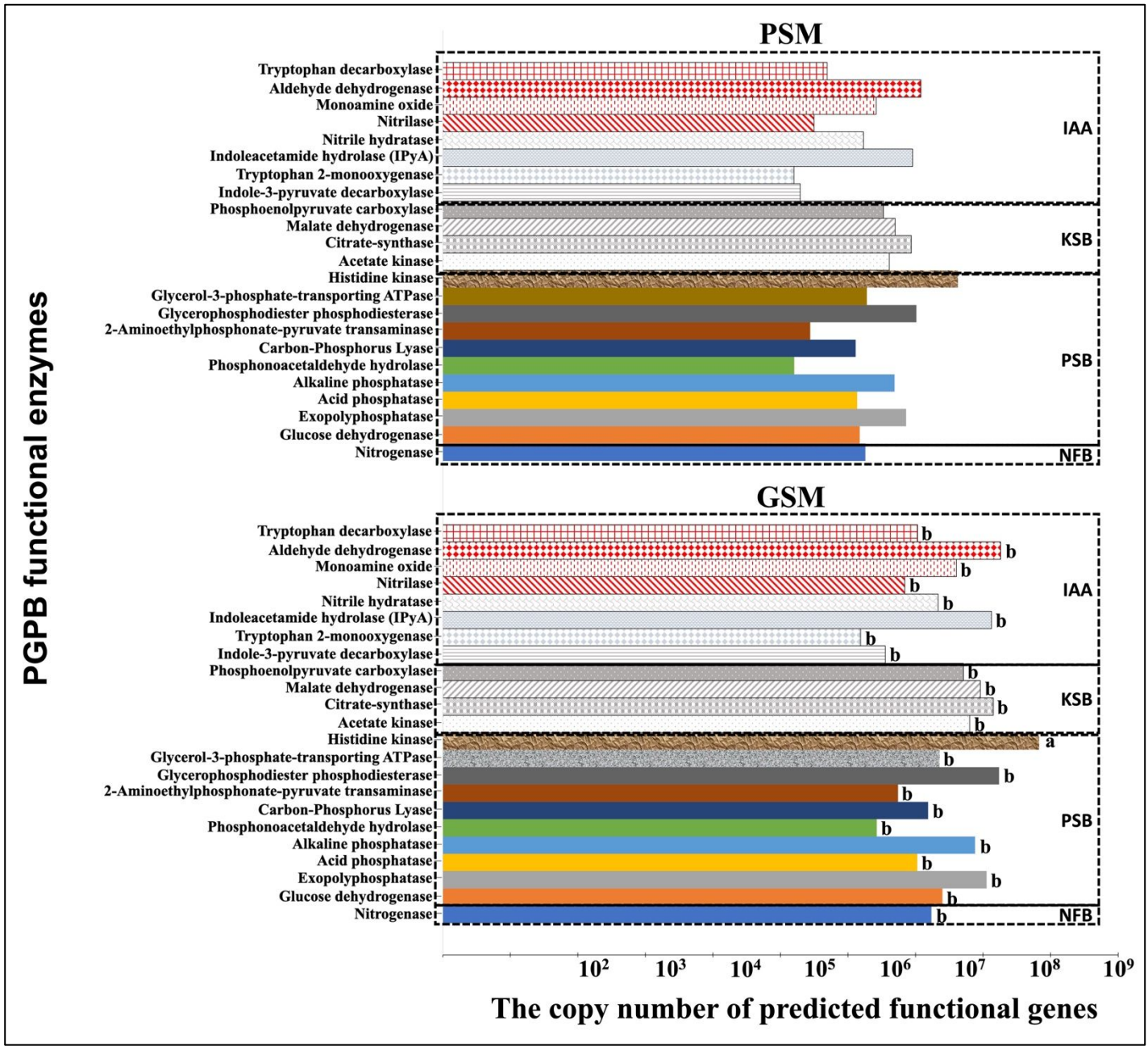

Figure S4: Comparison of the PGPB functional genes abundance in each site. NFB: nitrogen fixing bacteria; PSB: phosphate-solubilizing bacteria; KSB: potassium-solubilizing bacteria; IAA: indole acetic acid. The different letter beside bars in the GSM plot indicates significant difference ($p<0.05$ by Tukey HSD), while PSM site shows no significantly different among the functional enzymes ($p>0.05$ by Tukey HSD).