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Impact of Land-use Change on Vertical Soil Bacterial Communities in Sabah

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Abstract Decline in forest productivity due to forest conversion is defining the Bornean landscape. Responses of bacterial communities due to land-use changes are vital and could define our understanding of ecosystem functions. This study reports the changes in bacterial community structure in organic soil (0–5 cm; O-Horizon) and organic-mineral soil (5–15 cm; A-Horizon) across Maliau Basin Conservation Area old growth forest (MBOG), Fragment E logged forest (FELF) located in Kalabakan Forest Reserve to Benta Wawasan oil palm plantation (BWOP) using two-step PCR amplicon analysis of bacteria DNA on Illumina Miseq next generation sequencing. A total of 30 soil samples yielded 893,752-OTU reads at $\geq 97\%$ similarity from 5,446,512 good quality sequences. Soil from BWOP plantation showed highest unshared OTUs for organic (49.2%) and organic-mineral (50.9%) soil. MBOG soil showed a drop in unshared OTUs between organic (48.6%) and organic-mineral (33.9%). At

phylum level, *Proteobacteria* dominated MBOG but shifted to *Actinobacteria* in logged and plantation soil. Present findings also indicated that only FELF exhibited change in bacterial communities along the soil depth, moving from the organic to the organic-mineral layer. Both layers of BWOP plantation soils deviated from other forests' soil in β -diversity analysis. To our knowledge, this is the first report on transitions of bacterial community structures with different soil horizons in the tropical rainforest including Borneo, Sabah. Borneo tropical soils form a large reservoir for soil bacteria and future exploration is needed for fully understanding the diversity structure and their bacterial functional properties.

Keywords Soil microbiome · Oil palm plantation · Logged forest · Borneo · Tropical rain forest

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Introduction

Tropical rainforests regulate regional and global climate, provide a wide range of ecosystem services, and support close to 50% of described species. Borneo, the third largest island in the world, has an average aboveground forest biomass that is 60% higher than the Amazonian average [1]. Based on IUCN information, Borneo harbours an estimated 14,423 plant and 1640 vertebrate species, of which 28% are endemic and 534 species threatened with extinction. However, tropical rainforests are fast declining, particularly in Borneo, by 16.8×10^6 ha from 1973 to 2010 due to logging, agricultural activities, and ENSO-induced wildfires [2]. Rapid rates of forest conversion and degradation have prompted intergovernmental agreements between Indonesia, Malaysia, and Brunei Darussalam to protect and sustainably use the forests that remain in Borneo, via Heart of Borneo Initiative.

To date, 5.8 million ha of tropical forest in Borneo has been converted for agriculture, especially for oil palm (*Elaeis guineensis*) plantation because of the increasing global demand for cheaper sources of oil for food and biofuel [3, 4]. The total area for oil palm cultivation in Southeast Asia has increased in excess of 87% over 2000–2015. Malaysia and Indonesia are the biggest global exporters of palm oil and their economies have become more reliant on this industry since the reduction in timber yields. Timber extraction resulted in conversion of habitat from primary forest to secondary forest, which was then further degraded-fragmented for agricultural purposes, primarily for the monocultures of oil palm [5].

Land-use change significantly affects the balance and stability of biodiversity and ecosystem processes. It causes large-scale shifts in species distributions and extinctions, and the resultant altered predator-prey interactions are the primary drivers for changes in key biogeochemical processes [3]. Lately, there has been an increase in effort to better understand the changes in microbial communities, particularly bacterial communities that play an important role across this land-use change gradient [4]. Data of bacterial communities will facilitate our understanding of how human-driven changes in biodiversity alter biogeochemical processes and forest productivity.

Limited information of bacterial communities across the land change gradient substantially restricts our ability to model and predict the response of tropical ecosystems to current and future environmental change [6, 7]. Tropical forest ecosystems have gained recognition as biodiversity hot spots due to their rich fauna, flora, and microflora and the complex relationships among them. Such relationships define the very existence of the forest types and dictate the physiochemical properties of these ecosystems.

Any effort to evaluate the impact of land-use and changes to the natural forest ecosystem warrants an in-depth investigation across a gradient of forest types, such as primary forest, secondary forest/logged forest, and oil palm plantation. Approximately, 80–90% of soil processes such as soil structure maintenance, organic matter decomposition, nitrogen fixation, as well as inorganic transformation are mediated by microorganisms [8]. Microbes are also regarded as the catalysts of these ecosystem processes and different microbes could play different roles. Variations in soil microbial diversity and community structures seriously affect soil organic matter turnover and thus affect ecosystem function of a given ecosystem [9]. Bacteria community structure of pristine forest, logged forest, and oil palm plantation has been studied [7, 10, 11] but has only focused on topsoil bacterial community structure at the phylum level. Therefore, a better understanding of the dynamics of bacterial communities on a vertical gradient of soil at species level is needed. This study reports on the dynamics of vertical gradients in bacterial community in the top organic soil layer (0–5 cm) (O-Horizon)

and the organic-mineral soil layer (5–15 cm) (A-Horizon) across land-use gradients at species level [12].

Materials and Methods

Study Area The study was based in the Belian Plot of the Maliau Basin Conservation Area (4° 44' N, 116° 58' E), which is old growth forest dominated numerically by large Dipterocarpaceae and has never been logged (referred to as Maliau Basin old growth forest). Fragment E (FELF) was located in the SAFE project area, Kalabakan Forest Reserve (4° 41' N, 117° 35' E). The oil palm plantation plot (BWOP), finally, was in Benta Wawasan Oil Palm Estate (10-year-old plantation), Luasong, Kalabakan (4° 38' N, 117° 27' E), Sabah, Malaysia. Fragment E has undergone two rounds of selective logging since 1978 and presents a heterogeneous landscape with open canopy, a ground layer with gingers, vines, scrub, and abundant small trees (referred to as logged forest). The oil palm plantation that we sampled was on land cleared and terraced approximately 12 years ago and planted with young oil palm at the time. The palm trees are matured fruiting palms (10 years old), planted at 100 trees per hectare with a partially closed canopy (referred to as oil palm plantation). Algae and bryophyte covers can be observed in the plantation both on the ground and trunk of the oil palm trees. The plantations are intensively managed with periodic application of large amounts of chemicals and fertilizers. However, detailed information on quantities applied could not be obtained. All sites were placed to minimise variation in elevation, with mean elevation of all sample sites 450 m on slope type topography [13]. Physiochemical properties of soil collected are summarized in Supplementary Table 1.

Field Sampling Fieldwork was conducted from May to June 2015. A total of 45 soil cores were collected from old growth forest (15 soil cores), logged forest (15 soil cores), and oil palm plantation (15 soil cores). Soil cores were collected along a 100-m transect, with 20-m distance apart (total five sampling points). Three soil cores are collected from a sampling point. Soil in each core is separated into organic layer (normally darker in colour and loose in texture—O-Horizon) and organic-mineral layer (bottom later which is normally light brown in colour and usually compact and hard—A-Horizon); all three samples from the same sampling point were pooled together and homogenized before sieved through a 1-mm metal sieve [12].

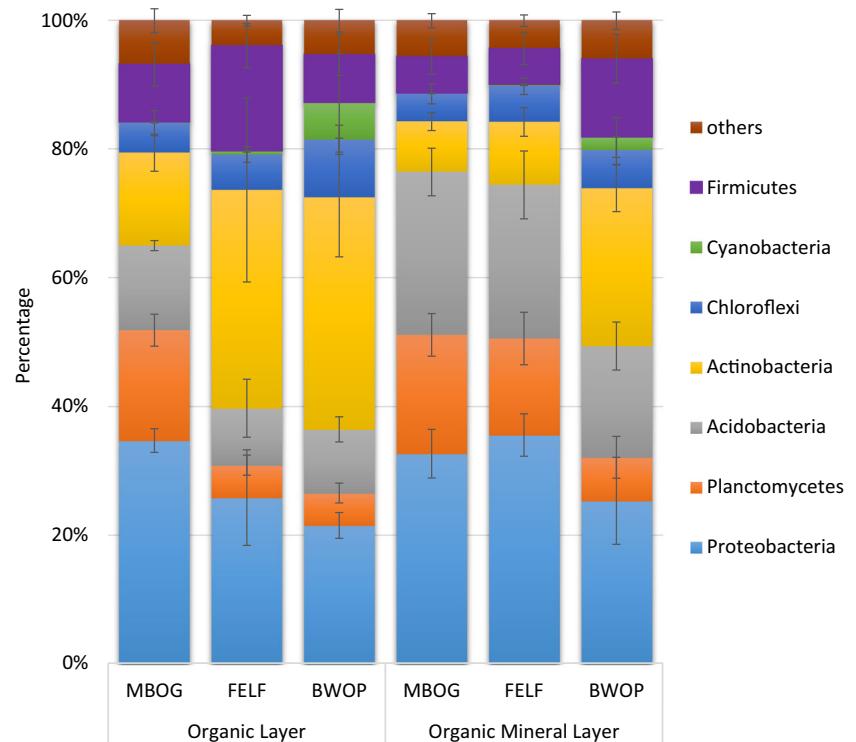
DNA Extraction, PCR Amplification, and Sequencing

Total soil DNA was extracted from 0.5 g from each of the collected soil samples using the PowerSoil DNA extraction kit (MoBio Laboratories, Carlsbad, CA) as directed by the manufacturer's instructions. Two-step PCR amplification

was performed according to Illumina 16S Metagenomic Sequencing Library preparation guide (Illumina) with slight modification, targeting the V4 region of the bacterial 16S rRNA gene with index sequences and adapter. First PCR amplification used primer 515f and 806r. Polymerase chain reactions were carried out on HiFi HotStart ReadyMix (Biosystem, USA) under the following conditions: initial denaturation at 95 °C for 3 min, followed by 20 cycles of denaturation at 98 °C for 30 s, annealing at 55 °C for 30 s, elongation at 72 °C for 90 s, and then by the final elongation for 5 min. The first PCR amplicons were purified using ISOSPIN for PCR Products (Nippon Gene, Japan) according to the manufacturer's protocol. Purified first PCR amplicons were then used in a second PCR amplification on HiFi HotStart ReadyMix (Biosystem, USA) under the same conditions as in first PCR amplification but with only 8 cycles. The second PCR amplicons were purified. Paired-end sequencing was performed using MiSeq sequencing system (Illumina) according to manufacturer's instructions.

Sequence Processing Illumina sequencing data were pair-assembled using Basespace (Illumina). The Mothur pipeline was used to align, filter, trim, and remove chimeras of sequencing reads. Each operational taxonomic unit (OTU), defined at a 97% cut-off of sequence similarity, was classified based on the RDP database [14]. All statistical analyses were performed on a subsample of OTUs at 10,185 reads per sample. Relative abundance, richness, diversity indices, and dissimilarity matrices were estimated using QIIME [15].

Fig. 1 Relative abundance of dominant bacteria taxa in Maliau Basin old growth forest (MBOG), Fragment E logged forest (FELF), and Benta Wawasan oil palm plantation (BWOP) on organic (O-Horizon) and organic-mineral (A-Horizon). Low abundance bacteria taxa have been grouped under "others." Error bars represent the standard deviation ($n = 5$)

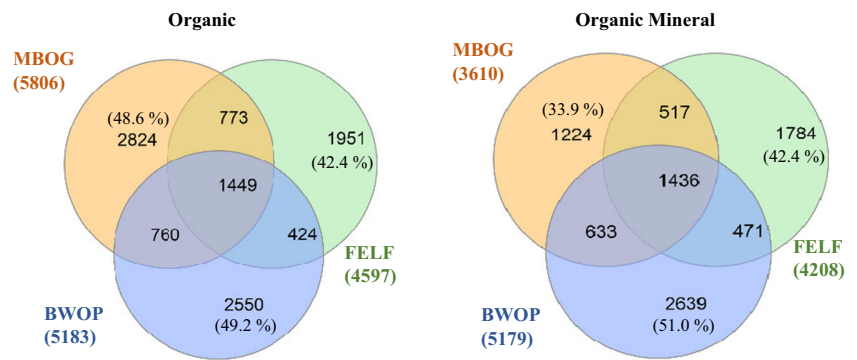


Results

A total of 30 samples yielded 893,752-OTU reads at $\geq 97\%$ similarity from 5,446,512 good quality sequences. The average number of OTUs per sample was 29,792, ranging from 10,185 to 71,594. Organic layer soils from Maliau Basin old growth forest (MBOG) are dominated by *Proteobacteria* (30.3%) while *Actinobacteria* dominate in Fragment E logged forest (FELF) and Benta Wawasan oil palm plantation (BWOP), with 30.5 and 29.3%, respectively (Fig. 1). Other dominant phyla include *Planctomycetes* (15.0%) in MBOG, *Proteobacteria* (23.1%), and *Firmicutes* (14.7%) in FELF as well as *Proteobacteria* (17.4%) in BWOP plantation soil. Meanwhile, the organic-mineral layer soil exhibits higher *Acidobacteria* and *Planctomycetes* but lower *Actinobacteria*, as compared to organic soil. High abundance of *Cyanobacteria* was observed in both organic and organic-mineral soils in BWOP plantation.

Figure 2 describes the independent and shared bacterial OTUs between sampling sites. Highest percentage of unshared OTUs could be seen in both organic and organic-mineral soil layers on BWOP plantation soil, 49.2 and 50.9%, respectively. MBOG showed a decrease in vertical unshared OTUs between organic and organic-mineral soil layers (48.6 to 33.9%), while there were no significant vertical differences in unshared OTUs in oil palm plantation soil of BWOP plantation (49.2 and 50.9%). OTUs shared by all three (3) forest types for both organic and organic-mineral soils were relatively similar, at 1449 and 1436 OTUs, respectively.

Fig. 2 Venn Euler diagram in comparison of bacteria OTUs between the two soil types (organic (O-Horizon) and organic-mineral layer (A-Horizon)) of Maliau Basin old growth forest (MBOG), Fragment E logged forest (FELF), and Benta Wawasan oil palm plantation (BWOP)



A total of 40 OTUs were selected with relatively high abundances in the respective soils at organic and organic-mineral layers for the forest types and affiliated to the cultured bacteria at species level (Fig. 3). Two OTUs related to *Pseudolabrys taiwanensis* (homology percentage 96.4%) and *Stella vacuolata* (92.9%) were predominant in both organic and organic-mineral layers at MBOG and FELF. Meanwhile, 4 OTUs related to *Sinosporangium fuscum* (93.7%), *Actinomadura alba* (95.3%), *Marmoricola aquaticus* (92.1%), and *Actinoallomurus spadix* (94.1%) were

detected with high abundances in the organic layer of FELF and followed in organic layer by BWOP plantation. In the organic layer of the BWOP plantation, OTUs related to *Conexibacter woesei* (96.1–96.8%) were abundant. In particular, an OTU distantly related to *Gemmata obscuriglobus* (77.5%) was distinctly predominant in the organic-mineral layer of all types of forests.

In the organic soil layer in general, *Proteobacteria* dominate the MBOG while FELF contains mainly *Acidobacteria* as specific bacteria (Table 1). A large amount of *Chloroflexi*

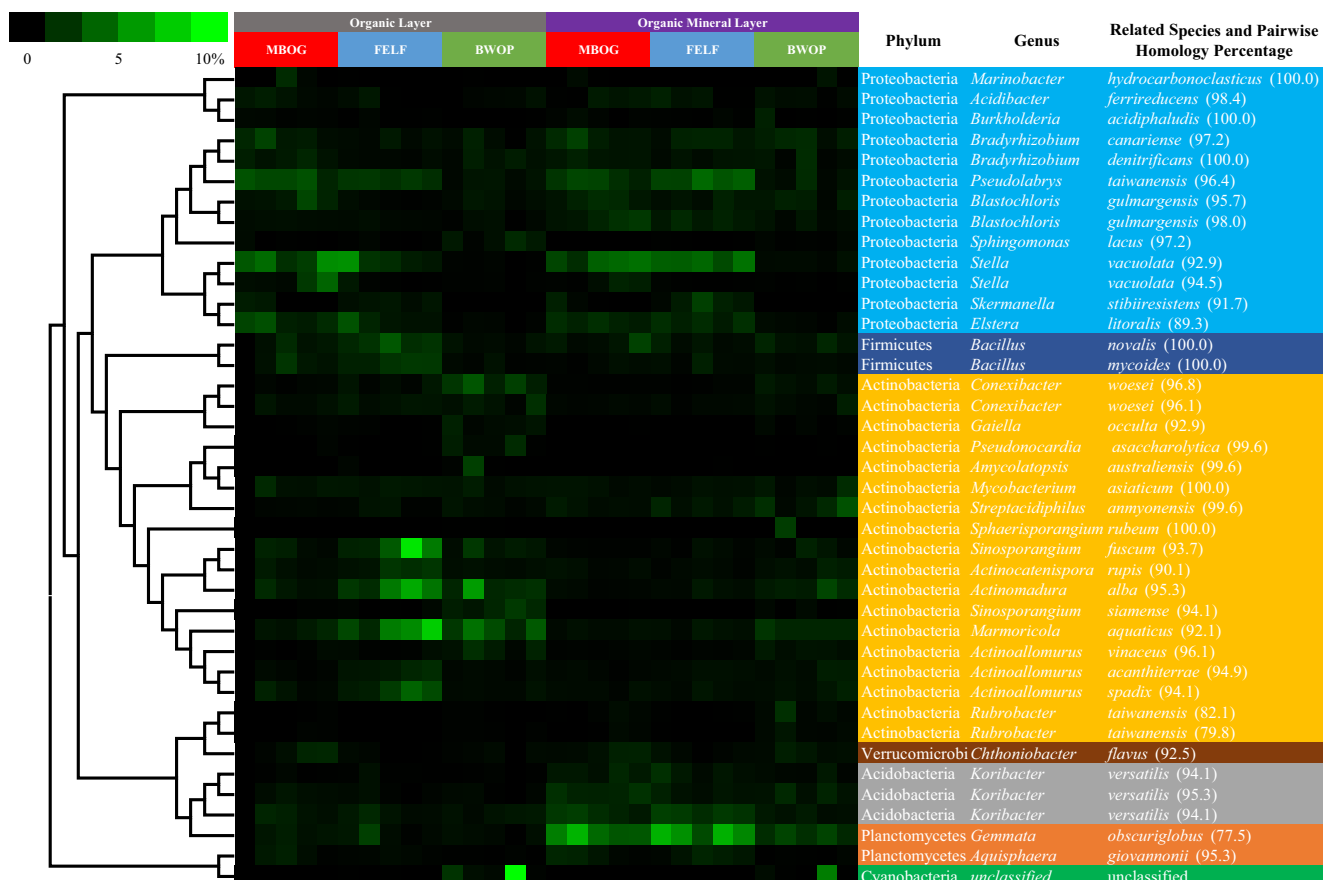


Fig. 3 Heatmap of 40 bacterial OTUs based on average relative abundance (green/black) across different soils of Maliau Basin old growth forest (MBOG), Fragment E logged forest (FELF), and Benta

Wawasan oil palm plantation (BWOP) and related species with pairwise homology percentage. Darker colour indicates lower relative abundance

Table 1 Specific OTUs of Maliau Basin old growth forest (MBOG), Fragment E logged forest (FELF), and Benta Wawasan oil palm plantation (BWOP) in both organic and organic-mineral soil layers with related species and their percentages of pairwise homology

Organic soil layer					
Plot	Phylum	Class	Related species	Percentage of homology	Percentage of relative abundance
MBOG	<i>Acidobacteria</i>	<i>Acidobacteria</i>	<i>Candidatus Koribacter versatilis</i>	93.68	0.03
MBOG	<i>Proteobacteria</i>	<i>Deltaproteobacteria</i>	<i>Pyxidococcus fallax</i>	90.91	0.01
MBOG	<i>Proteobacteria</i>	<i>Gammaproteobacteria</i>	<i>Idiomarina piscisalsi</i>	100.00	0.18
MBOG	<i>Proteobacteria</i>	<i>Gammaproteobacteria</i>	<i>Halomonas alimentaria</i>	100.00	0.13
FELF	<i>Acidobacteria</i>	<i>Acidobacteria</i>	<i>Candidatus Koribacter versatilis</i>	84.98	0.01
FELF	<i>Acidobacteria</i>	<i>Acidobacteria</i>	<i>Candidatus Koribacter versatilis</i>	87.35	0.01
FELF	<i>Acidobacteria</i>	<i>Acidobacteria</i>	<i>Candidatus Koribacter versatilis</i>	84.19	0.01
BWOP	<i>Acidobacteria</i>	<i>Solibacteres</i>	<i>candidatus solibacter usistatus</i>	91.70	0.12
BWOP	<i>Actinobacteria</i>	<i>Actinobacteria</i>	<i>Sinomonas humi</i>	100.00	0.18
BWOP	<i>Chloroflexi</i>	<i>Anaerolineae</i>	<i>Ornatilinea apprima</i>	83.00	0.11
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Ktedonobacter racemifer</i>	87.35	0.18
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Ktedonobacter racemifer</i>	83.40	0.17
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Ktedonobacter racemifer</i>	86.96	0.10
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Thermogemmatisspora foliorum</i>	83.00	0.34
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Thermogemmatisspora foliorum</i>	83.40	0.11
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Thermogemmatisspora foliorum</i>	84.58	0.10
BWOP	<i>Chloroflexi</i>	<i>Thermomicrobiota</i>	<i>Shaerobacter thermophilus</i>	79.05	0.14
BWOP	<i>Cyanobacteria</i>	<i>Chroobacteria</i>	<i>Microcoleus paludosus</i>	95.26	0.09
BWOP	<i>Firmicutes</i>	<i>Bacilli</i>	<i>Paenibacillus ehimensis</i>	95.24	0.05
BWOP	<i>Firmicutes</i>	<i>Bacilli</i>	<i>Paenibacillus ehimensis</i>	77.38	0.14
Organic-mineral soil layer					
Plot	Phylum	Class	Species	Percentage of homology	Percentage of relative abundance
MBOG	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Thermosporothrix hazakensis</i>	87.35	0.02
MBOG	<i>Firmicutes</i>	<i>Clostridia</i>	<i>Anaerobacterium chartisolvens</i>	95.65	0.02
MBOG	<i>Planctomycetes</i>	<i>Planctomycetacia</i>	<i>Gemmata obscuriglobus</i>	92.09	0.02
FELF	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Ktedonobacter racemifer</i>	89.33	0.05
FELF	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Thermosporothrix hazakensis</i>	84.19	0.04
FELF	<i>Proteobacteria</i>	<i>Alphaproteobacteria</i>	<i>Skermanella xinjiangensis</i>	90.51	0.04
FELF	<i>Proteobacteria</i>	<i>Alphaproteobacteria</i>	<i>Stella vacuolata</i>	90.91	0.04
FELF	<i>Verrucomicrobiota</i>	<i>Verrucomicrobiae</i>	<i>Pedospaera parvula</i>	90.91	0.01
BWOP	<i>Actinobacteria</i>	<i>Actinobacteria</i>	<i>Sphaerisporangium rubeum</i>	100.00	0.57
BWOP	<i>Actinobacteria</i>	<i>Actinobacteria</i>	<i>Sinomonas humi</i>	100.00	0.26
BWOP	<i>Actinobacteria</i>	<i>Thermoleophillia</i>	<i>Solirubacter phytolaccae</i>	91.30	0.30
BWOP	<i>Chloroflexi</i>	<i>Ktedonobacteria</i>	<i>Ktedonobacter racemifer</i>	83.40	0.01

bacteria species such as *Thermogemmatisspora foliorum* (homology percentages 83.0%), *Ktedonobacter racemifer* (83.4–87.4%), *Shaerobacter thermophiles* (79.1%), *Cyanobacteria* species *Microcoleus paludosus* (95.3%), and *Firmicutes* species *Paenibacillus ehimensis* (77.4–95.3%) were specifically found in the BWOP plantation organic layer.

Higher bacterial species richness (Chao 1), species evenness (Shannon Index), and observed OTUs for bacterial communities were found in the organic layer of BWOP plantation soil, comparable to the organic soil in MBOG (Fig. 4). On the

other hand, α -diversity of organic-mineral soil of MBOG was found to be as low as those in FELF. A relatively low variation was observed on diversity indices from MBOG as compared to FELF and BWOP plantation. Medians for Good's coverage of all sampled soils are above 0.90 and once 5000 of sequences were sampled; Chao1 richness estimates began to reach an asymptote (Fig. S1 in the supplemental material) implicating completeness of sampling. Data obtained from this analysis give relative differences in bacterial OTUs between the land-use types. Based on the analysis, it is clear that

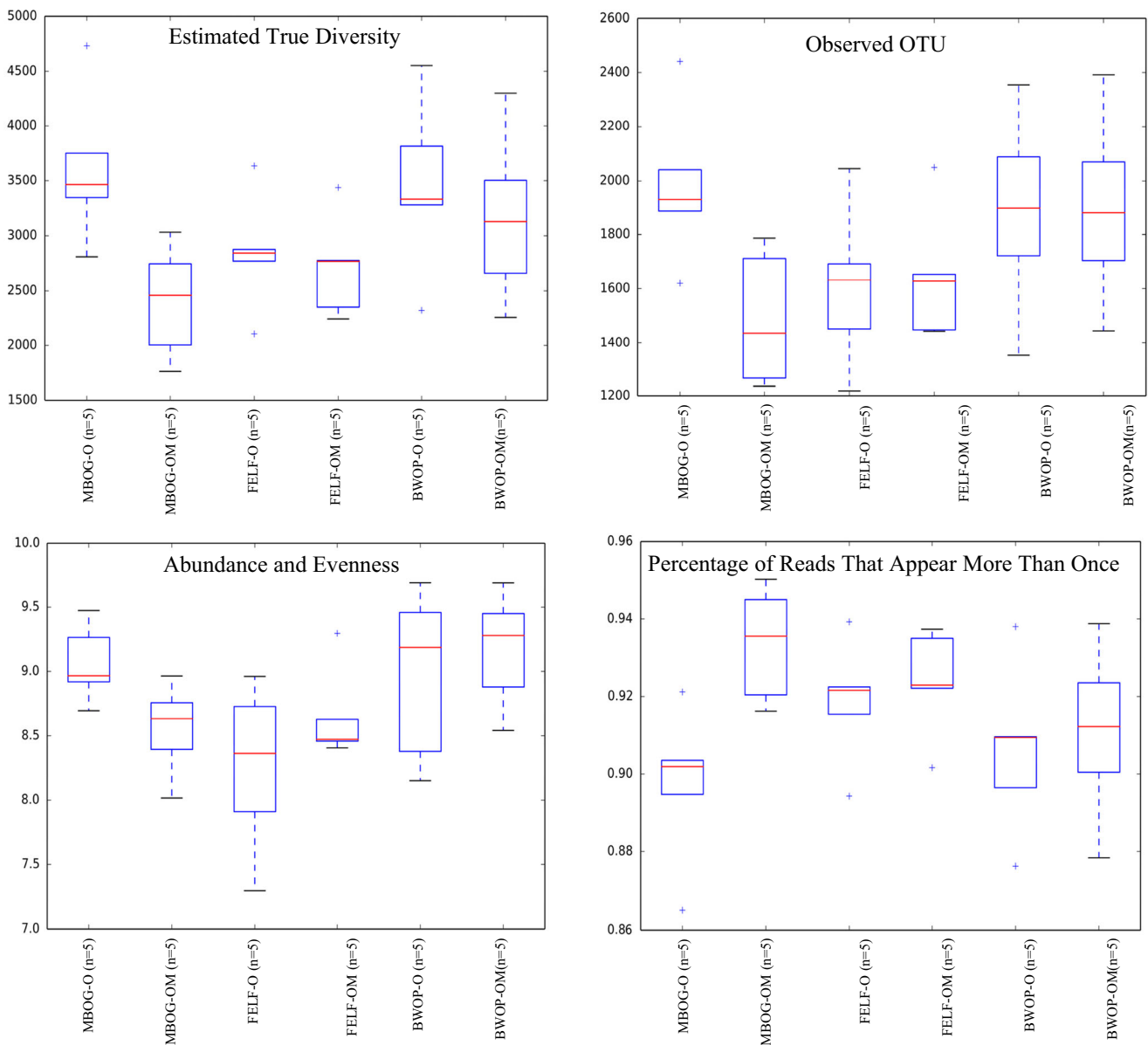


Fig. 4 α -Diversity analysis of bacteria OTUs across soil types of Maliau Basin old growth organic (*MBOG-O*), Maliau Basin old growth organic-mineral (*MBOG-OM*), Fragment E logged forest organic (*FELF-O*), Fragment E logged forest organic-mineral (*FELF-OM*), Benta Wawasan

oil palm organic (*BWOP-O*), and Benta Wawasan oil palm organic-mineral (*BWOP-OM*) layers based on 10,185-OTU read at 3% dissimilarity. Error bars represent the standard deviation ($n = 5$) and red line indicates the mean value

observed variability is high. However, the general trend is that the oil palm plantation soil does not seem to have a significantly reduced diversity.

In β -diversity estimation using weighted UniFrac, unweighted UniFrac distance matrices, and Bray-Curtis dissimilarity matrices displayed in principal coordinate analysis (PCoA) (Fig. 5) showed three clear clusters. The first cluster was formed by BWOP plantation soil, both organic and organic-mineral layers. The second cluster was for organic layer soil of FELF while the third cluster was for the bacterial community in organic and organic-mineral of MBOG and FELF organic-mineral soil.

Discussion

Conversion of primary forest to monoculture plantation, particularly oil palm plantation in South East Asian countries, is primary threats to ecosystem functions [16]. Diversity and community structure of soil bacteria in tropical rainforest ecosystems are poorly understood. In this study, we report on the bacterial community structure and identified the major bacterial species across the three-different land-use types: MBOG, FELF, and BWOP soils at different horizons. Our study revealed that *Proteobacteria* are generally dominant in MBOG while *Actinobacteria* are dominant in FELF and BWOP

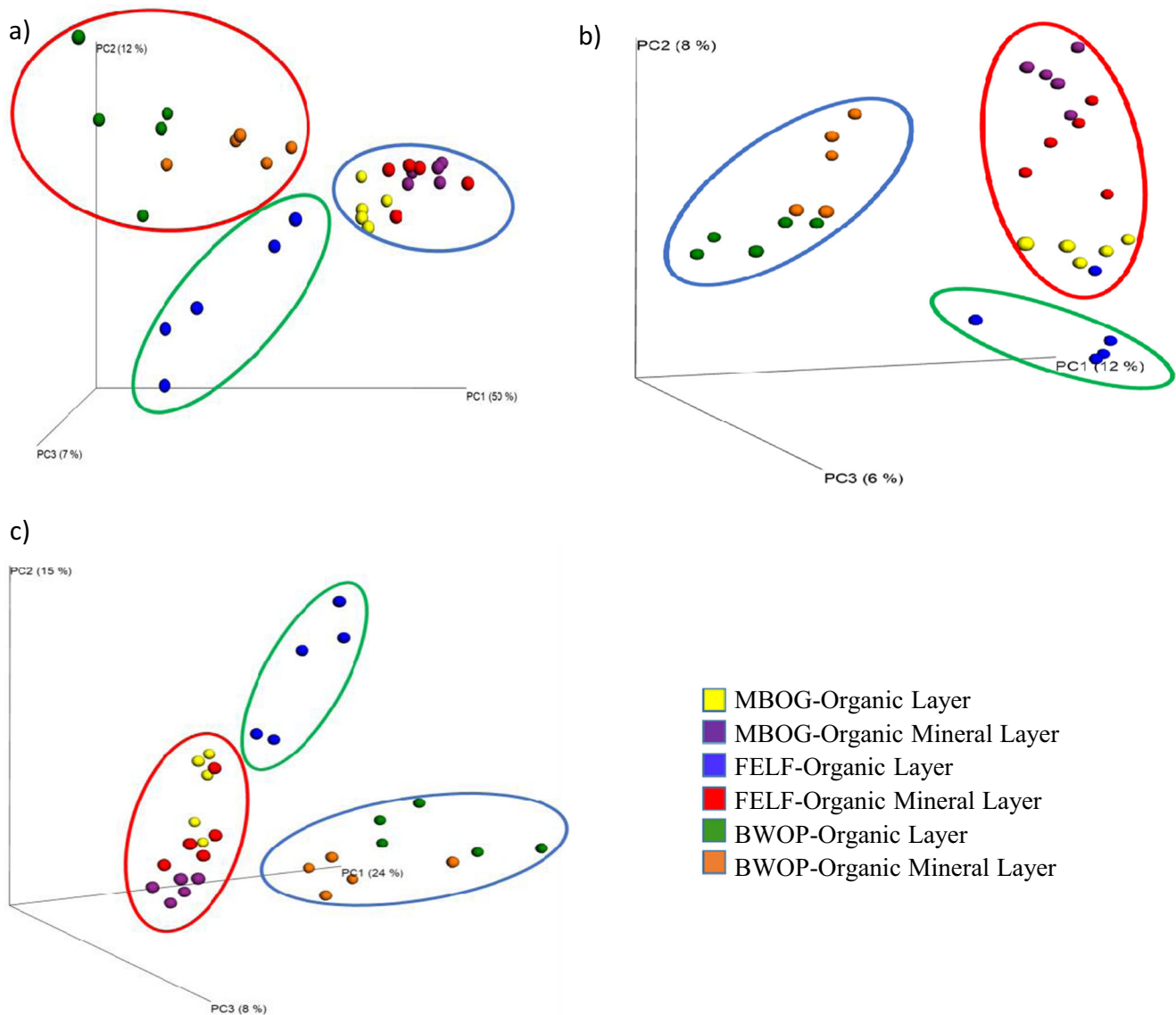


Fig. 5 Principal coordinate plots (*PCoA*) of soils using **a** weighted UniFrac, **b** unweighted UniFrac distance matrix, and **c** Bray-Curtis dissimilarity matrix β -diversity analysis of Maliau Basin old growth

forest (*MBOG*), Fragment E logged forest (*FELF*), and Benta Wawasan oil palm plantation (*BWOP*) soils

plantation in the organic layer soil (Fig. 1). Lee-Cruz et al. [7] and Tripathi et al. [9], who studied the top 5 cm of soil (i.e. organic layer) in Danum Valley, Sabah, found that *Acidobacteria* were dominant in unlogged pristine forest and once-logged forest, while twice-logged and oil palm plantation soils were dominated by *Firmicutes*. Even though the authors [7, 9] reported that oil palm plantation soil exhibits significantly higher numbers of *Actionobacteria* than both logged and unlogged forest, they only represented 10% of the overall bacterial population. Meanwhile, *Acidobacteria* and *Firmicutes* were found at relatively low abundance (<17%) taxa in current study. Both studies discussed above focused on the impact of land-use changes in bacterial communities only in Danum Valley, Sabah, while this study was conducted in the Maliau Basin Conservation Area and the

Kalabakan Area (Kalabakan Forest Reserve and oil palm plantation). The variation in observation of bacterial populations could be possibly due to the spatial, temporal, or locality effects since the study areas as well as sampling times are different. It is also important to note that although taxonomy and phylogeny of bacteria cannot predict the direct functional responses of microbial communities, data could suggest important bacteria responses to land change and ecosystem function [17].

Changes of bacterial community structure in accordance with soil depths have been reported in non-tropical forested areas [18, 19]. Our result indicated that only *FELF* exhibited drastic changes of the phyla abundances from organic layer to organic-mineral layer, in particular, increasing *Acidobacteria*, *Proteobacteria*, and *Planctomycetes* and decreasing

Actinobacteria and *Firmicutes* (Fig. 1), which would result in different clusters of beta-diversities between each layer (Fig. 5). On the other hand, because soil surfaces including organic layer in forests are subjected to litter fall and nutrient input from animals, the diversities in the organic layer are generally higher than those in the organic-mineral layer due to the accessibility of nutrients, water content, as well as oxygen [16, 19]. In this study, α -diversity analysis indicated that findings were obtained in MBOG that are similar to those in the literature while stable diversities in FELF and BWOP plantation were observed between organic and organic-mineral layer (Fig. 4). To our knowledge, this is the first report on transition of bacterial community structures with different soil horizons from the tropical rainforest region, Sabah, Borneo.

Tripathi et al. [8] suggested that pHs ranging between 3 and 4.5 for organic layers in tropical soils in Malaysia exhibited significant correlations with abundances of *Proteobacteria* (negatively), *Acidobacteria* (positively), and *Actinobacteria* (negatively). Our results in both organic and organic-mineral layers appeared to contradict this. At MBOG (pH 4.24), *Proteobacteria* abundance (30.3%) was higher than the 23.1% at FELF (pH 3.67) and 17.4% at BWOP (pH 4.28) of organic layer of the soil. However, in the organic-mineral layers, *Proteobacteria* abundance at MBOG (pH 4.30) was at 28.4% similar with FELF (30.0%) at pH of 3.72, but it was much higher compared to soil from BWOP (20.8%, pH 4.21) (Fig. 1, Supplementary Table 1). Furthermore, obvious correlations of C/N ratios in soils with abundances of those phyla were not observed in either organic or organic-mineral layers. Additional studies are required to investigate the correlations of the other physicochemical properties in soil with bacterial community structure in Borneo forests.

To understand the functional ecology of each species of bacterium in an environment, information on their bacterial community structure has a great significance [20]. Therefore, we have presented the representative OTUs with specificities in each soil type (Table 1) and their abundances (Fig. 3) to the bacteria species. Because the homology values higher than approximately 97% have been considered as the threshold commonly used for single species [17], only 5 OTUs detected as specific bacteria in the respective soil layers showed higher homologies than the threshold, which were highly related to *Idiomarina piscisalsi* and *Halomonas alimentaria* in organic layer at MBOG, *Sinomonas humi* in both layers at BWOP plantation, and *Sphaerisporangium rubeum* in mineral organic layers at BWOP plantation (with 100% homology) (Table 1). Although basic characteristics for taxonomic classifications of these species and amyloytic ability by *Si. humi* were reported [21], the functions of these bacteria in their habitats are still unknown. Surprisingly, all 8 predominant OTUs described in the “Results” section did not show homologies higher than 97%, which strongly suggested that unisolated and novel bacteria contribute in an

important way to the soil ecosystems in Borneo. We are presently attempting to isolate and characterize those predominant bacteria.

Several previous reports from Malaysian forested regions indicated that land-use such as logging and oil plantation impacts on soil bacterial communities and soil properties in the organic layers [7–9]. Although the sample sizes in our study are insufficient, our results of bacterial community structure analysis (Figs. 1, 3, and 5) allow us to hypothesise the following scenario: soil bacterial community structures are relatively similar in both organic and organic-mineral layers in old growth forest. After logging, soil bacterial community structure shows changes in organic layer, but the organic-mineral soil layer in logged forest is still undisturbed, hence suggesting absence of agricultural activities. Land-use conversion into oil palm plantation further affects soil bacterial community structures of both layers to become quite different from old growth and logged forests. Organic-mineral clustering patterns observed in organic logged forest soil probably indicate the priming effects of litter cover due to logging activities. To test our hypothesis, further work is required to investigate more samples, temporal analysis, or overall analysis along a gradient from primary forest to plantation.

Conclusions

The experimental areas of the current study were limited to three sites in Borneo, one per forest type. Due to this limitation, we demonstrated different bacterial communities in Borneo tropical forest soil with different land-use types, which is affected by the depth of soil. Certain bacterial genera and species were found selectively distributed in vertical soil horizon which was reflected in their α - and β -diversity. Conversion of primary or logged forest into oil palm plantation may have resulted in higher bacterial species diversity as indicated in higher numbers of observed OTUs and α -diversity indices. In addition, β -diversity analysis of OTUs also indicated that changes in land-use have impact on the vertical bacterial community structure as shown in oil palm plantation organic (O-Horizon) and organic-mineral (A-Horizon) soils. Findings presented here are only snapshot in time and long term study is needed to enable an elucidation of whether the changes in soil bacteria across land-use conversion are a more permanent effect or simply temporary disturbance. However, additional research with continuous monitoring at a larger experimental area is needed to provide a better understanding on the relationship between the tropical soil properties and bacterial communities. Finally, we propose that the implementation of environmentally friendly practices by the oil palm industry may help to maintain the microbial diversity and ecosystem functions in natural habitats.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that there is no conflict of interest.

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