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Effects of Land Use on Soil Microbial Communities in Tropical Montane Forests of Malaysian Borneo

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Effects of Land Use on Soil Microbial Communities in Tropical Montane Forests of Malaysian Borneo

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ABSTRACT

Land use, such as logging and forest conversion to agriculture, can modify soil physicochemical and biological properties, and affect soil health. To understand how land use change can impact soil properties and canopy structure, we used a land use gradient in Malaysian Borneo consisting of six sites, including old growth forests, mixed forests, and agriculture fields. Specifically, we aimed to answer the following questions: (1) How do soil physicochemical properties vary across land use types? (2) Does bacterial diversity and composition vary across different land use types? (3) Does fungal diversity and composition vary across different land use types?

We measured soil (top 5 cm) physicochemical properties (such as texture, temperature, water content, pH, organic matter, C and N content, and elements) and microbial properties (using next-generation amplicon sequencing). We also characterized understory and overstory canopy properties, including percent ground cover, canopy structure, and canopy closure. Our results indicate that old growth forests had the greatest forest cover and canopy closure, accumulated the highest soil organic matter, had a greater soil carbon and nitrogen ratio, were less acidic, and harbored greater bacterial and fungal diversity compared to mixed forests and agricultural fields.

Old growth forests had a higher abundance of slow-growing specialist bacterial and fungal phyla, while agriculture fields had a greater abundance of rapidly growing opportunistic, generalist, and disturbance-resistant bacterial and fungal phyla. Our findings suggest that land use not only affects the aboveground surrounding forest cover and canopy closure, which has compounding effects with affected soil physical and chemical properties on soil microbial diversity, but also affects the microbial community composition and phylum function.

CONTENTS

1. Introduction

Tropical rainforests are one of the most biodiverse biomes on Earth and provide vital ecosystem services, such as storing 25% of terrestrial carbon, influencing climate cycles and weather patterns, prevent erosion, and affecting the quality, storage, and delivery of freshwater, etc. (Brandon 2014, Smith et al. 2023). In tropical ecosystems, an estimated 38% of organic carbon is stored in soils and the remaining 62% of organic C is stored in tropical vegetation (Blais et al. 2005). Logging and forest conversion, especially agriculture, continue to threaten these ecosystems throughout the tropics (Curtis et al. 2018, Vancutsem et al. 2021, Pendrill et al. 2022). Deforestation has significant impacts on soil physical, chemical, and biological properties (Bore and Bedadi 2015), resulting in a decrease in soil pH, soil organic matter (SOM), soil C and N, exchangeable bases (Ca, Mg, K, Na) (Waldrop et al. 2000, Bore and Bedadi 2015), and significant shifts in soil bacterial (Rodrigues et al. 2013, Lee-Cruz et al. 2013) and fungal community (McGuire et al. 2015) composition, which can ultimately affect function of soil microbial phyla.

The soil microbiome plays a crucial role in nutrient cycling (de Graaff et al. 2015), regulating macronutrients, such as carbon (C) and nitrogen (N) through processes including N fixation, denitrification, N mineralization (Barrett and Burke 2000), and soil organic matter decomposition and stabilization (Gougoulias et al. 2014). While prior research has highlighted the effects of land use, particularly forest logging and conversion of old growth forests undisturbed for over 100 years, on soil microbial diversity (Sniegocki et al 2022), less is known about changes in soil microbial compositions resulting from land use change in high elevation tropical ecosystems. Sniegocki et al. (2022) found that land use recovery time, soil pH, surrounding percent forest cover, and SOM were the top predictors of soil bacterial diversity,

while land use recovery time, soil pH, surrounding percent forest cover, and soil aluminum were the strongest determinants for soil fungal diversity (Sniegocki et al. 2022).

With the essential ecosystem services (i.e., nutrient cycling and C sequestration) provided by the soil microbiome (Wagg et al. 2014, de Graaff et al. 2015, Jiao et al. 2019), it is important to understand how land use change could affect the soil microbial community composition and their function. Some studies have explored the relationship between land use conversion effects on soil microbial community shifts, yielding interesting findings. Many previous studies have already found an effect of land use conversion on soil microbial communities. For instance, soil pH was found to be the most significant determinant of soil bacterial community structure (Tripathi et al. 2012), while land use had the greatest impact on soil fungal community structure (Brinkmann et al. 2019). However, there is still a lack of information on community functional changes that occur with changing land use.

With an overarching goal of understanding the effects of land cover and land use on soil physicochemical and biological properties, we asked: (1) How do soil physicochemical properties change across a gradient of land use types? Previous studies have shown that tropical forest conversion for crop cultivation caused a decrease in soil pH, C, N, P, and water storing capacity (Waldrop et al. 2000, Singh et al. 2010, Ahirwal et al. 2021). We hypothesize that forest conversion will increase soil pH but decrease soil gravimetric water content (GWC), C, and N, (2) Does bacterial diversity and composition change across different land use types? (3) Does fungal diversity and composition change across different land use types? Forest conversion to agroforestry and agricultural sites often results in shifts in soil microbial community composition, which are driven by soil pH and environmental heterogeneity (Lan et al. 2021). We hypothesize that soil microbial community composition will shift along the land use gradient

from specific to generalist bacterial and fungal phyla that are adapted for disturbed ecosystems and recalcitrant material degradation (Rodrigues et al. 2013, Mueller et al. 2016, van der Plas et al. 2016).

2. Materials and methods

2.1 Study site

Data were collected from a total of six sites across a land use gradient in the Tambunan District of the state of Sabah, Malaysia (5.71750°, 116.40055°) (Fig. 1). The elevation ranges between 870 to 1150 m above sea level (asl) with 1968 mm average annual precipitation and 24.3 °C mean annual temperature across all sites. Study sites were chosen based on land use categorized into old growth forest, modified forest, and agriculture field. The old growth forest land use type comprises Angelo's Forest (AnF) and Mahua Falls Forest (MaF), while the modified forest land use type consists of Malungung Forest (MuF) and Abandoned Rubber Plantation (ARP), and lastly the agriculture field land use type containing Abandoned Agriculture Field (AAF) and Agriculture Field (AF). MaF and MuF are located within the federally protected land of Crocker Range Park which encompasses 139,919 ha. The MaF and MuF sites were logged ~100 years ago and logged ~70 years ago respectively (Table 1). The three remaining sites are located on private property. The Angelo's Forest (AnF) is an old growth forest that has been unlogged for more than 150 years. ARP was established 41 years ago after being cleared, terraced, and planted and has been abandoned for 15 years and untapped at the time of sampling. AAF was cultivated with chili then cleared in 2014 and abandoned 4 years before sampling and AF grew rambutan, mango, and soursop fruit trees from the year 1920 to 1985, then switched to sweet potatoes, chive, turmeric, and banana. We sorted the sites along a

land use gradient of old growth forest (OGF: AnF and MaF), modified forest (MF: MuF and ARP), and agriculture field (AF: AF and AAF). Soils in the area are classified as orthic acrisols, with low base saturation and high clay content in the B Horizon and equivalent to Ultisols in USDA soil taxonomy (Sakurai 1999, Chesworth 2007).

2.2 Soil Sampling for Analysis

Soil samples were collected up to a depth of five centimeters at intervals of five meters along a 45 m transect on a slope gradient (Table 1) on each of the six sites. A soil core (corer diameter = 6.35 cm) was used to collect two to five soil cores within 1 m of each plot center to capture maximum onsite variability, which were composited and stored in plastic bags. In total, 10 plots were sampled for each of the six sites (sample size = 10 plots x 6 sites = 60) with each plot represented by a composite soil sample of two to five soil cores. The rocky terrain AnF, prevented the use of the 6.35 cm diameter soil auger and required the use of a 2.54 cm diameter soil core instead. Roots, rocks, and litter were removed from the samples. The composite samples were homogenized by mixing in the plastic bag. Soil temperature was measured up to a depth of five centimeters with a soil thermometer probe (digital soil thermometer probe, HANNA Instruments). A total of ten grams per site were collected through one-gram subsamples that were preserved in RNALater stabilization solution (ThermoFisher Scientific) and sent to the Molecular Research Laboratory (MR DNA, Shallowater, TX, USA) for microbial analysis. The remaining soil samples were cleared of visible rocks, roots, and decayed litter. After that, the soil was sieved with a two-millimeter sieve to separate out the soil fraction. The soil was then shipped to Texas Tech University's soil laboratory for soil physical and chemical analysis for soil elemental characterization (aluminum, sulfur, potassium, manganese, iron, nickel, copper, zinc, lead) using portable x-ray fluorescence (pXRF) (Goff et al. 2020), pH, texture, total C and N, and

percent soil organic matter. Samples for soil gravimetric water content were also collected and stored in air-tight containers. The soil gravimetric water content was analyzed by drying in an oven at 60 ℃ until all the water had evaporated. The soil gravimetric water content is calculated by dividing water mass with dried soil mass. Soil pH was measured with a pH electrode and meter using the saturated soil paste method (*Agriculture Handbook* 1954). The loss-on-ignition-method (Schulte n.d.) was used to determine soil organic matter concentration (loss of soil mass after incineration in a furnace at 360 °C for two hours), soil texture fraction (sand, silt, clay) was measured with a hydrometer (152H Hydrometer) after mixing at 30 seconds and 1 minute, then at intervals of 3, 10, 30, 60, 90, 120, and 1440 minutes using the hydrometer particle size analysis method (Gee and Bauder 1986).

2.3 Soil Microbial Analysis

Final operational taxonomic units (OTUs) were assigned based on 97% similarity and followed the proprietary MR DNA analysis pipeline (Dowd et al. 2008). The bacterial 16S rRNA gene and fungal ITS1 region were amplified. Polymerase chain reaction (PCR) primers 515, ITS1, ITS2, and HotStarTaq Master Mix Kit (Qiagen, USA) were used for 30 PCR cycles in the order of 94 °C for 3 minutes, 30 cycles of 94 °C for 30 seconds, 53 °C for 40 seconds, 72 °C for 1 minute, and a final elongation step at 72 °C for 5 minutes. DNA fragments are then sorted by molecular weight and concentration using 2% agarose gel after amplification. The sorted DNA fragments were then purified with AmpureXP beads and checked with an Agilent High Sensitivity (HS) Chip on Bioanalyzer 2100 and quantified on fluorimeter by Qubit dsDNA HS Assay kit (Brand from MR DNA). This library was then loaded onto the Illumina Platform for clustering and sequencing. Paired-End sequencing allows for template fragments to be sequenced in both forward and reverse directions. Sequencing was completed on an illumina MiSeq

following the manufacturer's protocols and data was analyzed with the proprietary MR DNA analysis pipeline (Dowd et al. 2008). Sequences with less than 150 bp or with ambiguous base calls were removed. To summarize, sequences were denoised, operational taxonomic units (OTUs) were assigned based on 97% similarity, and chimeras were removed. Archaea and mitochondrial or chloroplast OTUs were removed from the 16S data and non-fungal OTUs from ITS1 data. A total of 31,261 bacterial and 0 fungal chimeric were removed from further downstream analysis. The final OTUs were assigned using BLASTn with cloned sequences searched against a database derived from RDP-II and NCBI (www.ncvi.nlm.nih.gov, http://rdp.cme.msu.edu).

Soil bacterial and fungal diversity across all samples (alpha diversity) was calculated using the Chao1 diversity index at the OTU level, which was chosen as it is weighted by rare taxa. Chao1 bacterial and fungal diversity was calculated for each of the 10 replicate soil sample using the "SpadeR" package (Chao et al. 2016) in R (R Core Team 2022). Soil bacterial and fungal phylum abundances were calculated as the sum of each detected phylum OTUs and was standardized to a scale of zero to one using the 10 replicate sample values where the average phylum abundance (x) is subtracted by the minimum abundance value (*min*) and divided by the maximum phylum abundance (*max*) subtracted by the minimum phylum abundance (*min*) value using the formula: $scaled\ abundance = \frac{x-min}{min-max}$

2.4 Land Cover Analysis:

High-resolution SENTINEL-2 satellite imagery was obtained from the Copernicus Open Access Hub (https://scihub.copernicus.eu/). SENTINEL-2 products were chosen because of their

superior spatial resolution (10 m) and availability in our study area. Much of the imagery was littered with cloud cover in our specific study area due to the study area's tropical nature; however, imagery from March 2, 2019, was obtained which had no cloud cover in our specific study sites. Both the true color imagery (pre-processed) and the multispectral bands were obtained. Using the multispectral bands, false color composite imagery was created. The accuracy of land cover classification of each true and false color composite imagery was compared prior to model selection.

The coordinates of the six study sites were turned into a vector point layer and added to raster imagery in ArcMap 10.6.1. The projected coordinate system, Asia South Albers Equal Area Conic, was used to accurately represent the study area located near the equator in Southeast Asia. Next, a 100-m radius (approximately 7.8 acre) buffer around each of the points was created to capture the area of influence around each point (Brown et al. 2005). This area was represented by approximately 317-10 x10 m^2 pixels.

We used maximum likelihood classification to classify the land cover classes on both the true and false color composite imagery. Maximum likelihood classification is a tool that combines user input (supervision), pixel color, and pattern recognition to designate land classes on a raster layer. The user supplies a training sample or signature file to guide the program through the land cover designations (Parece et al. 2010). Because I worked extensively at the six sites in June - August 2018, familiarity with the study area allowed a more accurate training sample. The signature file identified five prominent land cover classes: forest, herbaceous/shrub, bare/non-vegetated, water, and no data. The first three land cover classes are defined based on the density and height of vegetation (or lack thereof), water includes any inland or marine body of water large enough to distinguish with 10-m resolution, and no data include clouds and clouds

shadows as well as any additional undefined pixels (Table 1). After comparing the output classification rasters of both the true and false color composite input rasters, the true color composite classification was selected for use in the analysis due to its greater accuracy in distinguishing forest and herbaceous/shrub, particularly at the study sites.

Next, the “Extract by Mask” tool within ArcMap 10.6.1. selected newly classified raster only data within each of the six site buffers. After doing this, the statistical analysis tools analyzed only the areas of interest. Because of interest in each of the six separate sites, each of the six site buffers were turned into their own separate layer file. Next, two data fields were added to each of the attribute tables: “Percent” and “Acres”. Using the pixel count for each land cover class, we then used the Field Calculator to compute the percent coverage and the total acreage of each land cover class. Vertical bar graphs visually displayed the data alongside the maps.

2.5 Statistical Analysis:

The statistical analysis was performed using a one-way analysis of variance to detect significant differences between means of soil properties, bacterial and fungal richness, diversity, and abundance using 20 replicates among each land use type (n = 10 plots x 2 study sites per land use type = 20). The analysis was conducted in R using the “stats” base package (R Core Team 2022). Subsequently, a post hoc Fisher’s least significant difference test was employed to compare the significantly different means of soil properties, bacterial and fungal richness, diversity, and abundance using the “agricolae” package (Mendiburu 2021) in R (R Core Team 2022). The Fisher’s least significant difference test was chosen as it does correct for multiple comparisons which results in a greater statistical power compared to other post-hoc methods

(i.e., honestly significant difference test or Tukey test). Finally, we generated heatmaps using the "pheatmap" package (Kolde 2019) and constructed a co-occurrence network model based on bacterial and fungal standardized abundance data.

3. Results

3.1 Effects of Land Use on Soil Physicochemical Properties and Surrounding Land Cover

Soil temperature ranges were significantly different across all three land use types with the highest mean soil temperature of 22.54 °C in AF sites (Table 2, Figure 3). Soil temperature increased from 20.51 °C to 22.54 °C at OGF and AF sites respectively. All land use types had an acidic soil pH, ranging from 3.67 to 5.07, with OGF sites having the highest average soil pH of 5.07 and AF sites having the lowest average soil pH of 3.67 (Table 2). We observed a significant decrease in soil GWC following OGF (0.74 g/g) conversion to MF (0.48 g/g) and AF (0.47 g/g), with both land use types having similar soil GWC values (Table 2, Figure 3). The OGF sites had the highest soil water with a GWC of 0.74 g/g, while AF sites had the lowest soil water content (Table 2, Figure 3). The soil carbon and nitrogen ratio values of OGF and MF were not different but are significantly greater than AF sites, corresponding to the higher SOM and C content in OGF.

The surrounding land cover of OGF sites was predominantly forests, covering 94.21% of the area, while MF and AF sites had a mixed landscape with a combination of forests (69.75%, 51.38%), shrubs and herbaceous vegetation (16.08%, 30.82%), and bare ground (14.17%, 17.79%) (Table 2, Figure 2).

3.2 Effects of Land Use on Soil Bacteria Diversity and Community Composition

In terms of bacterial chao1 diversity, we observed that OGF sites had the highest diversity compared to MF and AF sites (Figure 3). Among the 31 total detected bacterial phyla, the most detected bacterial phylum in all three land use sites was Proteobacteria (Table 3). Among land use types, the OGF had the highest abundance of several bacterial phyla, including Synergistetes, Thermotogae, Planctomycetes, Nitrospirae, Cyanobacteria, Synergistetes, Deinococcus thermus, Bacteroidetes, Thermodesulfobacteria, Chlorobi, and Gemmatimonadetes. On the other hand, MF sites showed the greatest abundance of Tenericutes, Actinobacteria, Nitrospinae, Deferribacteres, Armatimonadetes, Bacteroidetes, Chlamydiae, Cloacimonetes, Elusimicrobia, Acidobacteria, Chloroflexi, Nitrospinae, Chrysiogenetes, Proteobacteria, Aquificae, and Fusobacteria bacterial phyla. Additionally, AF had the highest abundance of Fibrobacteres, Firmicutes, Ignavibacteriae, Spirochaetes, Chloroflexi, Candidatus Saccharibacteria, and Verrucomicrobia bacterial phyla. The bacteria phyla Fibrobacteres, Gemmatimonadetes, Actinobacteria, Nitrospinae, Planctomycetes, Chlamydiae, Synergistetes, Deinococcus - Thermus, Nitrospirae, Firmicutes, Bacteroidetes, Chlorobi, Acidobacteria, Ignavibacteriae, Chrysiogenetes, Fusobacteria, and Verrucomicrobia was statistically different among land use types (Table 3, Figure 4).

3.3 Effects of Land Use on Soil Fungi Diversity and Community Composition

In terms of fungal diversity, we observed that OGF sites had the highest chao1 diversity compared to MF and AF sites (Figure 3). The most common fungal phylum in all land use types was Ascomycota (Table 3). The OGF had the highest abundance of Entomophthoromycota fungal phylum. Compared to other land use types, MF sites showed an increased abundance of

Monoblepharidomycota, Blastocladiomycota, Chytridiomycota, Neocallimastigomycota, and Ascomycota fungal phyla. Finally, AF had a higher abundance of Glomeromycota, Basidiomycota, and Cryptomycota fungal phyla. There were statistical differences among land use types for Glomeromycota and Basidiomycota fungal phyla (Table 3, Figure 4).

4. Discussion

4.1 Effect of Land Use on Soil Physicochemical Properties

Land use changes in tropical regions, specifically logging and forest conversion, have lasting impacts on soil physical and chemical properties. Consistent with previous research, our study found changes in soil properties along a land use gradient (Table 2, Figure 2 and 3). This finding aligns with previous studies that have reported an increase in soil temperature after logging and clearing of ground vegetation (Yashiro et al. 2008, Bai et al. 2020). The reduction of overstory and ground vegetation cover in AF sites could explain the observed increase in soil temperature.

The lower soil GWC levels in disturbed sites may be due to loss of SOM, which has been found to have a positive relationship with soil water holding capacity (Gregory et al. 2016). However, a meta-analysis study suggested a modest effect of adding SOM on soil water holding capacity (Minasny and McBratney 2018). Alternatively, greater GWC could be attributed to the shade provided by overstory cover (Figure 2). Our findings align with previous research indicating that land use changes in tropical regions have lasting impacts on soil physical and chemical properties (Table 2, Figure 2 and 3), and highlight the potential consequences of disturbances on soil moisture and carbon dynamics.

Our study found that soil pH decreased with land use change from 5.07 in OGF to 3.67 in AF sites (Table 2, Figure 3), which corresponds to acidification of soil after clearing of vegetation other studies in the tropics and other regions (Ribeiro Filho et al. 2013). The decrease in soil pH in MF and AF sites could be explained by leaching of soil base cations into the soil profile.

Moreover, we observed that soil nutrient sources and contents (i.e., SOM, total C and N, and C:N ratio) decreased with increasing intensity of land use change and management, which is consistent with numerous studies (Singh and Singh 1996, Gong et al. 2006, Yu et al. 2012). Forest conversion may have caused the decrease in soil nutrient sources and concentrations due to the removal of aboveground plant biomass. The loss of soil C could also be attributed to the increase in soil temperature and respiration rates in soil (Nottingham et al. 2020).

4.2 Changes in Soil Bacterial Alpha Diversity and Community Composition

This study, along with several previous studies (da C Jesus et al. 2009, Rodrigues et al. 2013, Lee-Cruz et al. 2013, Paula et al. 2014, McGuire et al. 2015, 2015, Brinkmann et al. 2019), confirms that land use changes in tropical ecosystems have significant effects on soil microbial diversity and community composition. Specifically, forest conversion from OGF to MF and AF significantly decreased bacterial alpha diversity (Table 3, Figure 3). These results are consistent with findings in similar climates, where increased anthropogenic disturbance resulted in decreased bacterial alpha diversity (Berkelmann et al. 2020). However, some studies have reported either no reduction in alpha diversity (da C Jesus et al. 2009) or an increase in alpha diversity (Rodrigues et al. 2013, de Carvalho et al. 2016).

The ability to utilize amino acids as an energy source from the greater turnover of microbial biomass may explain the increase of abundance of Synergistetes in OGF sites (Geng et al. 2022). Most members of Thermotogae can use simple and complex carbohydrates (starch, glycogen, cellulose, and keratin) to grow, which may assist in decomposing these types of carbohydrates present in OGF sites that are nutrient poor and have quick nutrient turnovers (Lanzilli et al. 2021). The members of the phylum Planctomycetes are widespread and found in most terrestrial and aquatic environments and play a role in the global carbon and nitrogen cycle (Buckley et al. 2006, Wiegand et al. 2018). Nitrospirae are known nitrite oxidizers and had the highest abundance in OGF sites that had the greatest total nitrogen content; while in contrast, results found by another study showed that Nitrospirae had a negative relationship with total nitrogen content (Xue et al. 2016). The ability for members in Chlorobi phylum to fix carbon through anoxygenic photosynthesis and their increased presence in OGF may be because of the greater concentration of total carbon (Ward and Shih 2022). Members from the Deinococcus thermus phylum are extremophiles and resist radiation and extreme temperatures, but there is still a lack of understanding pertaining the ecosystem functions of this phylum (Theodorakopoulos et al. 2013, Ho et al. 2016). The understudied phylum Gemmatimonadetes can be found commonly in terrestrial and aquatic environments, but only one strain is known for nitrite reduction to nitrogen gas (Park et al. 2017, Chee-Sanford et al. 2019). However, there is a lack of information on factors that affect the distribution of Planctomycetes and Gemmatimonadetes, but the increased abundance could be related to greater nitrogen content and the formation anaerobic conditions due to the high soil moisture content during precipitation events in OGF soils (Meng et al. 2013).

The MF sites, on the other hand, showed an increased abundance of Actinobacteria, Nitrospinae, Cloacimonates, Tenericutes, Acidobacteria, and Fusobacteria bacterial phyla (Table 3, Figure 4). This study shared similar results of secondary mixed forests holding the majority of Actinobacteria abundance, which could be explained by its generalist ecological function of decomposing different carbohydrates, amino acids, lipids, and lignin (da C Jesus et al. 2009, Eisenlord and Zak 2010). Nitrospinae is commonly found in marine environments as nitrite oxidizing bacteria, but their ecological role in soil remains unclear (Lücker et al. 2013, Pachiadaki et al. 2017). Commonly found in biogas reactors, Cloacimonetes are methanogens that conduct acidogenic fermentation (Saha et al. 2019, Klang et al. 2019). Tenericutes members are pathogenic and form commensal or virulent relationships with their hosts, including plants, animals, arthropods, and humans (Gupta et al. 2018). In highly disturbed forests, the reduction of poor hosts species due to biodiversity loss may increase transmission of pathogens, which could explain the increased relative abundance of Tenericutes (Keesing et al. 2010). Results matched a similar report that Acidobacteria were the dominant phylum in rubber due as it is a oligotrophic bacteria found in highly acidic environments (Zhang et al. 2019). Fusobacteria may ferment carbohydrates to produce organic acids, but there are few to no reports on detection of Fusobacteria in mixed forests and rubber plantations (Shah et al. 2009).

Finally, AF had the highest abundance of Verrucomicrobia bacterial phyla, and Glomeromycota, Basidiomycota fungal phyla (Table 3, Figure 4). Although Verrucomicrobia make up a relatively smaller proportion of soil microbial abundance, they are reported as responsible for contributing to the majority of polysaccharides decomposition in systems and their resistance to environmental perturbations may explain their greater abundance in AF sites (Martinez-Garcia et al. 2012, Nixon et al. 2019).

Interestingly, OGF and AF sites shared some similar abundance of cellulose-decomposing (Fibrobacteres, Ignavibacteriae, and Bacteroidetes), SOM decomposing bacteria (Firmicutes). Fibrobacteres, originally thought to only occupy guts of herbivores, are actually widely distributed in the environment and serve as potent decomposers of lignocellulosic material (Ransom-Jones et al. 2012, 2014). Members of the Ignavibacteriae phylum are facultative anaerobes that are able to decompose cellulose and xylan and are commonly found in paddy fields, a possible explanation for their presence in OGF and AF sites may be due to the highly varying aerobic and anaerobic conditions in tropical soils and readily available supply of organic material from litterfall (Lin et al. 2010, Podosokorskaya et al. 2013, Meng et al. 2013, Bei et al. 2021). Bacteroidetes and endospore forming Firmicutes are fast-growing, opportunistic bacteria that are able to exploit available organic substrates, which may explain their increased abundance in OGF and AF sites (Trivedi et al. 2013, Liu et al. 2018).

Understanding the drivers of shifts in soil microbial communities is crucial for gaining insights into the direct and indirect effects of land use. Consistent with previous reports, I detected Acidobacteria, Proteobacteria, Verrucomicrobia, and Chloroflexi as the most common bacterial phyla across all land use sites (Kerfahi et al. 2016). Results indicate an increase in the abundance of Acidobacteria and Actinobacteria, but a decrease in Proteobacteria following forest conversions, which aligns with Berkelmann et al. (2020) which showed that these abundances were mainly driven by soil pH, C:N ratio, C and N content. The decrease in phylum function redundancy of certain nutrient cycling processes observed in this study might be indicative of biotic homogenization (Rodrigues et al. 2013, van der Plas et al. 2016). In the long term, changes in plant species abundance and diversity were found to be the most significant factors in soil microbial community dynamics (Chernov and Zhelezova 2020), while soil pH mediated the

effect of land use intensity on soil bacterial community composition (de Carvalho et al. 2016), which may explain the observed changes in soil microbial community in our study.

4.3 Changes in Soil Fungal Alpha Diversity and Community Composition

This study revealed that more intense human disturbances led to a decrease in soil fungal alpha diversity (Figure 3), consistent with another study (McGuire et al. 2015), while other studies reported no difference (Lan et al. 2020) or increased fungal alpha diversity (Berkelmann et al. 2020, Lan et al. 2021).

The AF had the highest abundance of Glomeromycota and Basidiomycota fungal phyla (Table 3, Figure 4). Glomeromycota are known plant symbionts that form arbuscular mycorrhizal relationships with plant roots and its abundance in AF sites may be due to inoculation of roots in colonizing plant species (Schüβler et al. 2001). The increased abundance of Basidiomycota in agricultural sites could be attributed to its ability to decompose recalcitrant substrates, which remain in agriculture sites (Kerfahi et al. 2014).

Ascomycota increased abundance in tropical forests converted to mixed rubber plantations, consistent with previous studies, but results were opposite with observed lower abundance of Basidiomycota in rubber plantations (Lan et al. 2020). Ascomycota and Basidiomycota were the most common fungal phyla, in line with prior research in tropical climates and globally (Tedersoo et al. 2014, Mueller et al. 2016, Lan et al. 2020). In the long term, soil fungal community dynamics shared similar significant factors with soil bacterial community dynamics of changes in plant species abundance and diversity. (Chernov and Zhelezova 2020), potentially explaining the observed changes in soil microbial community in our study.

5. Conclusions

This study shows the significant and effects of converting old growth forests that have been undisturbed for over 100 years on surrounding vegetation, soil physical and chemical properties, and soil microbial diversity and community composition. Forest conversion to agriculture caused a shift in community composition from specialist taxa to disturbance adapted generalist taxa. It is important to recognize the magnitude of these impacts and the need for further research to understand how they affect ecosystem function and processes. Such research could inform conservation and management strategies aimed at mitigating the negative consequences of land use change on tropical ecosystems.

6. Declaration of Conflict

Authors declare no conflict of interests.

7. Author Contribution

Kusum Naithani and Jessica B. Moon designed the study; KN, Renee Sniegocki, JBM, and Abby Rutrough conducted field work; Yang Kai Tang, RS, AR, JBM, Jaya Seelan Sathiya Seelan and KN analyzed the data. YKT and KN made figures and wrote the first draft of the manuscript. All authors discussed, edited, revised and approved the final version of the manuscript.

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10. Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below:

1. https://doi.org/10.5061/dryad.0vt4b8h1t.

2. Data for composition

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12. Tables

Table 1: List of study sites describing geolocation (decimal degrees), altitude (m ± SE) , slope (% ± SE), slope aspect, vegetation type, and land use sorted on a land use gradient of OGF (Angelo's Forest (AnF), Mahua Falls Forest (MaF)), MF (Malungung Forest (MuF), Abandoned Rubber Plantation (ARP)), and AF (Abandoned Agriculture Field (AAF), and Agriculture Field (AF)).

Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)	Altitude (m) ± SE	Slope (%) ± SE	Slope Aspect	Land Use History
Old Growth Forests (OGF): Mixed Dipterocarp Forest						
Angelo's Forest (AnF)	5.713	116.335	900 ± 5	44 ± 19	WNW	Not clear-cut for > 150 years, currently forested.
Mahua Falls Forest (MaF)	5.797	116.406	1140 ± 2	78 ± 0	NNE	Clear-cut ~ 100 years ago, selectively logged until ~ 1983, currently forested.
Mixed Forests (MF): Mixed Dipterocarp Forest (MuF); Rubber Trees and Roadside Fern (ARP)						
Malungung Forest (MuF)	5.661	116.251	862 ± 2	26 ± 4	WNW	Clear-cut ~ 70 years ago, selectively logged until ~1993, currently forested.
Abandoned Rubber Plantation (ARP)	5.765	116.469	879 ± 2	26 ± 4	SSE	Terraced and planted with rubber trees in 1977, currently abandoned and trees are untapped.
Agriculture Field (AF): Bamboo, mostly cleared (AAF) and Mixed Home Garden (AF)						
Abandoned Agriculture Field (AAF)	5.766	116.470	891 ± 1	56 ± 11	SSW	Previously cultivated for chili, cleared in 2014 and currently abandoned.

Agriculture Field (AF)	5.710	116.408	622 ± 1	1 ± 1	SSW	Planted with coffee in 1985 and rambutan in 2000, currently home garden (i.e., banana, sweet potatoes, other row crops).

Table 2: Mean (±SE) values of vegetation (surrounding land cover, canopy closure, ground cover (coarse woody debris (CWD))) and soil physicochemical properties (temperature, pH, gravimetric water content (GWC), sand content, soil organic matter (SOM), carbon (C), nitrogen (N), C:N ratio, Sulfur (S), Potassium (K), Manganese (Mn), and Aluminum (Al)) across a land use gradient including Old Growth Forests (OGF), Mixed Forests (MF), and Agriculture Fields (AF) (n = 20). Fisher's least significant difference results are denoted by lowercase alphabets.

Land Use Type	**OGF**	**MF**	**AF**
Vegetation Characteristics			
Surrounding Land Cover (%)			
Forest	94.2	69.8	51.4
Shrub/Herbaceous	5.8	16.1	30.8
Bare	0.0	14.2	17.8
On-site Ground Cover (%)			
Bare Ground	2.0^{a} (1.11)	0.0^{b} (0.00)	0.0^{b} (0.00)
Rocks	7.3a (2.96)	0.0^{b} (0.00)	0.0^{b} (0.00)
Litter	47.0^{a} (5.64)	56.3^{a} (6.91)	49.8^{a} (8.57)
CWD	3.3^{ab} (2.12)	0.8^{b} (0.55)	7.5^{a} (3.41)
Grasses	0.0^{b} (0.00)	3.3^{b} (2.03)	27.1^{a} (8.99)
Forbes	42.0^{a} (5.77)	40.3^{a} (6.18)	14.6^{b} (4.54)
Shrubs	0.0^{a} (0.00)	0.0^{a} (0.00)	1.0^{a} (1.00)
On-site Canopy Closure (%)	89.2^{a} (1.11)	82.4^{a} (2.56)	52.0^{b} (6.25)
Soil Physicochemical Properties			
Sand (%)	46.9^{a} (2.69)	40.7^{b} (1.06)	35.6^{c} (1.18)
GWC (g/g)	0.7^{a} (0.10)	0.5^{b} (0.02)	0.5^{b} (0.02)
Temperature (°C)	20.5^{c} (0.14)	21.4^{b} (0.06)	22.5^{a} (0.38)
pH	5.1^{a} (0.10)	4.5^{b} (0.03)	3.7^{c} (0.17)
SOM (%)	8.5^{a} (0.96)	5.0^{b} (0.45)	3.1^{c} (0.18)
C (%)	7.6^{a} (0.80)	4.8^{b} (0.68)	2.6^{c} (0.16)
N (%)	0.7^{a} (0.06)	0.4^{b} (0.04)	0.3^{b} (0.02)
C:N	10.5^{a} (0.67)	10.7^{a} (0.49)	8.0^{b} (0.19)
S (mg/g)	0.8^{a} (0.09)	0.5^{b} (0.07)	0.4^{b} (0.04)
K (mg/g)	9.7^{b} (0.78)	11.6^{a} (0.49)	12.6^{a} (0.58)
Mn (mg/g)	1.0^{a} (0.09)	0.2^{c} (0.05)	0.5^{b} (0.05)
Al (mg/g)	66.3^{b} (2.88)	84.9^{a} (2.25)	89.1^{a} (1.62)

Table 3: Mean (standard error) values of soil microbial diversity (chao1 diversity index for bacterial and fungal communities) and composition (abundance of bacterial and fungal phyla) across a land use gradient including Old Growth Forests (OGF), Mixed Forests (MF), and Agriculture Fields (AF). Fisher's least significant difference results are denoted by lowercase alphabets.

	Land Use Type		
	OGF	**MF**	**AF**
Fungal Diversity	3894.3^{a} (74.89)	3585.9^{a} (76.45)	3220.5^{b} (194.85)
Fungal Phyla			
Monoblepharidomycota	3.4^{a} (0.79)	6.5^{a} (3.87)	1.9^{a} (0.92)
Blastocladiomycota	2.8^{a} (1.28)	8.5^{a} (7.77)	2.9^{a} (1.50)
Glomeromycota	318.3^{b} (46.84)	473.2^{ab} (82.34)	574.0^{a} (106.89)
Basidiomycota	15779.9^{b} (2654.03)	27652.1^{ab} (5759.94)	38024.3^{a} (11576.56)
Chytridiomycota	472.7^{a} (107.18)	924.8^{a} (324.04)	738.1^{a} (181.39)
Neocallimastigomycota	7.1^{a} (1.66)	12.9^{a} (3.45)	10.5^{a} (5.45)
Ascomycota	47827.3^{a} (2079.1)	49504.0^{a} (3556.03)	33789.9^{b} (3159.95)
Entomophthoromycota	15.3^{a} (2.25)	8.6^{a} (2.05)	11.0^{a} (3.48)
Cryptomycota	9.5^{a} (1.44)	10.0^{a} (1.97)	10.1^{a} (2.27)
Bacterial Diversity	10822.1^{a} (237.29)	8294.0^{a} (202.68)	8815.1^{b} (333.06)
Bacterial Phyla			
Fibrobacteres	22.2^{a} (2.67)	6.4^{b} (1.95)	24.7^{a} (7.52)
Tenericutes	12.3^{b} (3.84)	22.3^{a} (3.93)	18.0^{ab} (2.00)
Gemmatimonadetes	1193.8^{a} (59.20)	272.4^{c} (33.22)	746.0^{b} (131.88)
Actinobacteria	5639.1^{c} (405.32)	9897.1^{a} (563.46)	7334.4^{b} (689.95)
Nitrospinae	38.1^{b} (5.43)	82.0^{a} (7.05)	54.5^{b} (10.15)
Deferribacteres	0.0^{a} (0.00)	0.4^{a} (0.35)	0.2^{a} (0.15)

Armatimonadetes	12.5[a] (2.08)	18.2[a] (6.87)	14.5[a] (1.81)
Planctomycetes	2340.2[a] (149.69)	1340.4[b] (59.01)	1632.4[b] (143.91)
Chlamydiae	176.8[b] (32.49)	485.3[a] (49.52)	136.5[b] (18.17)
Cyanobacteria	186.2[a] (21.81)	140.0[a] (22.82)	164.1[a] (23.55)
Synergistetes	2.0[a] (0.52)	0.1[b] (0.10)	0.8[b] (0.30)
Deinococcus thermus	159.7[a] (17.85)	15.3[c] (3.36)	73.5[b] (21.27)
Nitrospirae	954.5[a] (91.94)	105.0[c] (20.65)	397.4[b] (92.35)
Cloacimonetes	0.1[ab] (0.10)	0.4[a] (0.18)	0.0[b] (0.00)
Firmicutes	1454.0[a] (144.28)	966.0[b] (62.35)	1517.7[a] (178.31)
Bacteroidetes	4706.9[a] (319.77)	2510.6[b] (119.45)	4103.4[a] (629.85)
Elusimicrobia	71.4[a] (9.47)	94.2[a] (10.61)	72.9[a] (12.86)
Thermodesulfo-bacteria	0.2[a] (0.16)	0.0[a] (0.00)	0.1[a] (0.10)
Chlorobi	34.7[a] (5.56)	1.6[b] (0.40)	6.2[b] (2.02)
Acidobacteria	7285.7[b] (568.92)	11939.1[a] (530.82)	8579.36[b] (648.07)
Ignavibacteriae	52.4[a] (7.75)	22.4[b] (2.63)	73.5[a] (10.63)
Chrysiogenetes	0.1[b] (0.05)	3.5[a] (0.74)	0.4[b] (0.22)
Fusobacteria	153.5[b] (44.71)	365.1[a] (30.19)	225.7[b] (37.86)
Spirochaetes	37.3[a] (5.78)	23[a] (2.65)	41.5[a] (11.24)
Chloroflexi	1371.2[a] (106.28)	1374.8[a] (133.22)	1517.9[a] (111.56)
Candidatus saccharibacteria	0.2[a] (0.09)	0.4[a] (0.18)	0.4[a] (0.13)
Proteobacteria	27861.0[a] (1514.62)	28374.9[a] (1212.69)	25451.8[a] (1767.57)
Aquificae	0.2[a] (0.15)	0.6[a] (0.36)	0.0[a] (0.00)
Thermotogae	0.4[a] (0.22)	0.1[ab] (0.05)	0.0[b] (0.00)
Verrucomicrobia	3333.6[b] (325.90)	3008.6[b] (167.00)	4479.5[a] (358.75)

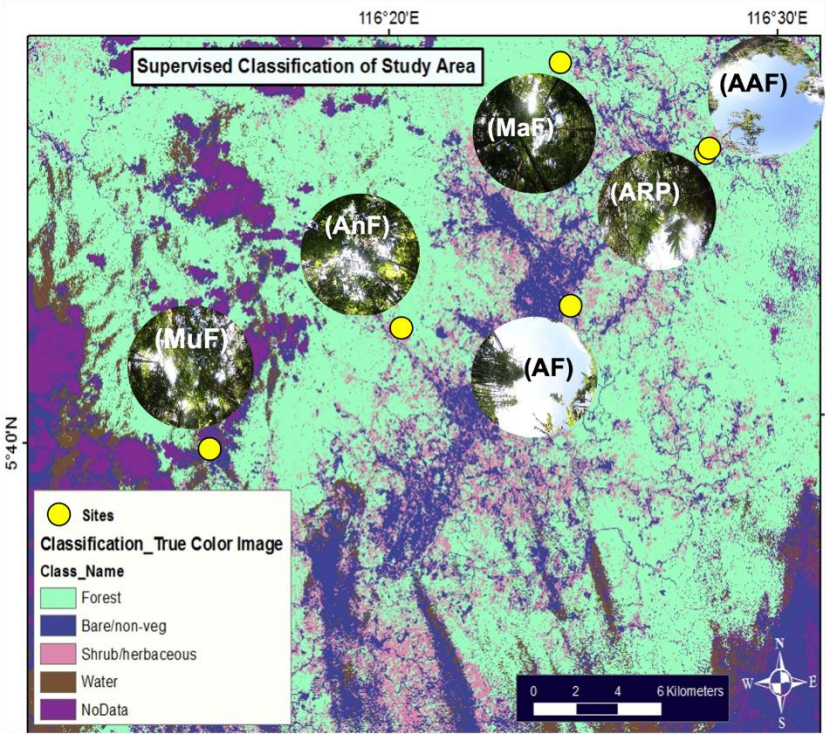

Figure 1: Supervised classification map of the study area showing the northern region of Sabah, Malaysian Borneo. Yellow circles indicate the location of each site and the fisheye lens images display the canopy of each sites: Angelo's Forest (AnF), Mahua Falls Forest (MaF), Malungung Forest (MuF), Abandoned Rubber Plantation (ARP), Abandoned Agriculture Field (AAF), and Agriculture Field (AF).

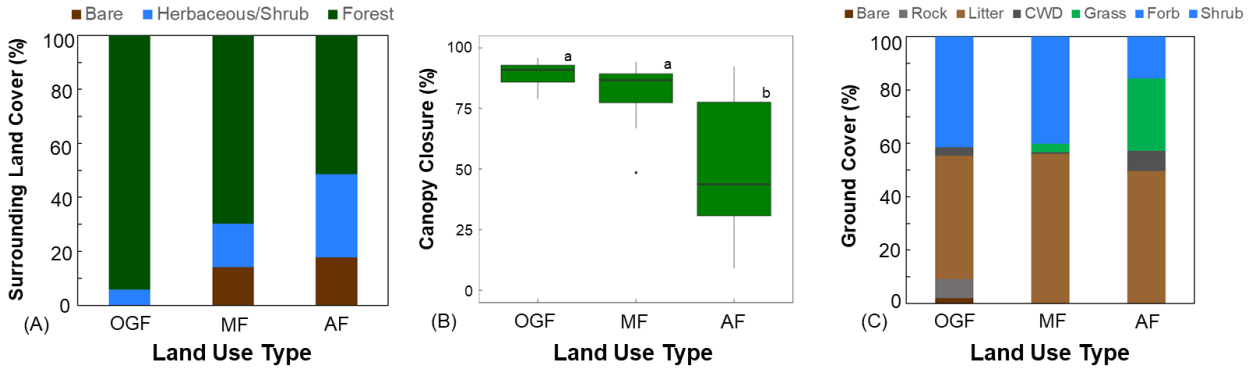

Figure 2: Percentages of (A) surrounding Land Cover (bare, herbaceous/shrub, forest), (B) canopy closure, and (C) ground cover (bare, rock, litter, coarse woody debris (CWD), grass, forb/shrub) of different land use types. Fisher's least significant difference results are denoted by lowercase alphabets on associated boxplots.

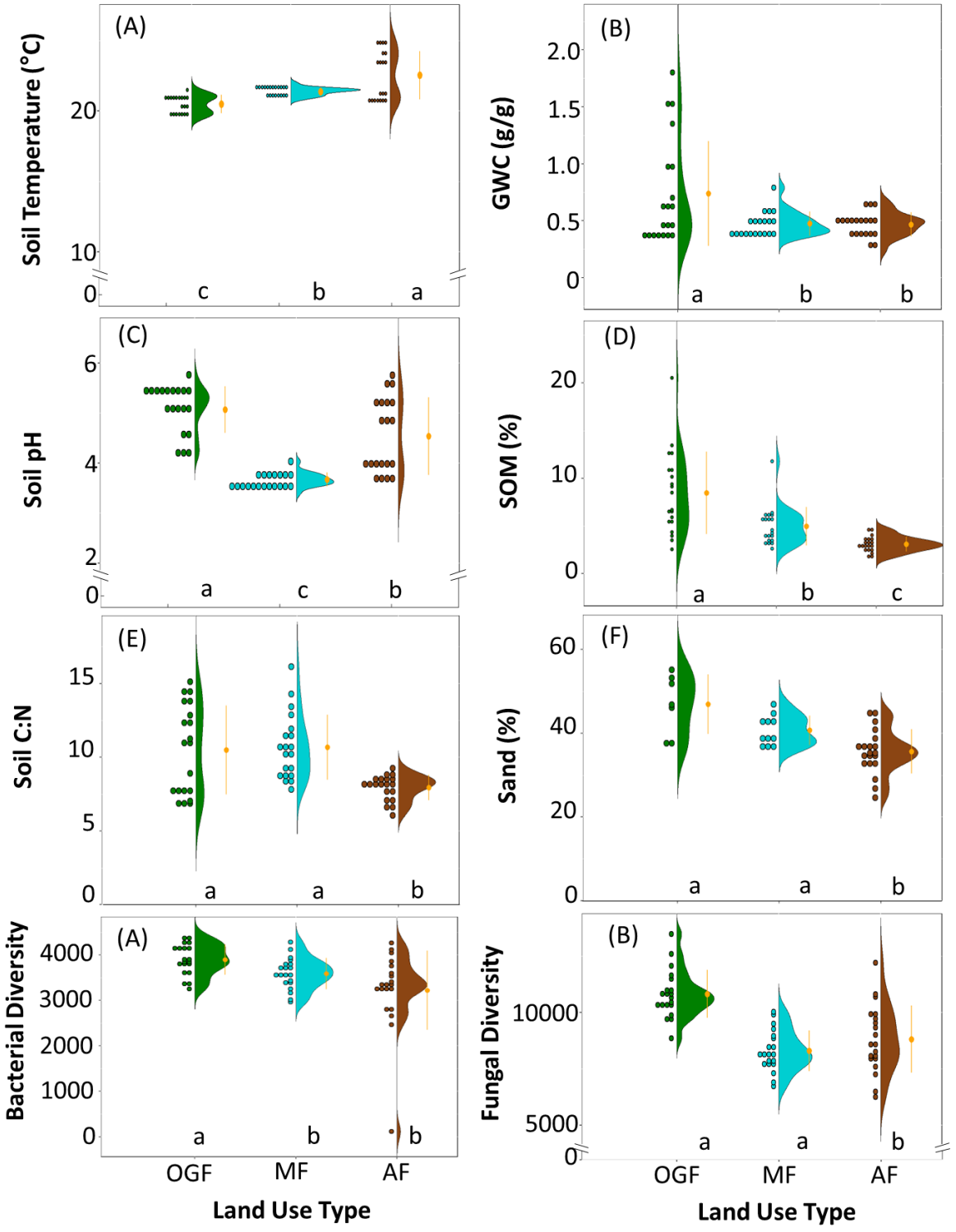

Figure 3: Soil physicochemical properties (soil temperature (A), gravimetric water content (GWC) (B), soil pH (C), percent SOM (D), soil carbon and nitrogen ratio (E), percent sand (SOM) (F), and Chao1 bacterial (G) and fungal diversity (H)) on violin plots showing sample points, distribution, average (yellow dots), and standard error bars (yellow lines) with Fisher's least significant difference results represented by lowercase alphabets (n = 20).

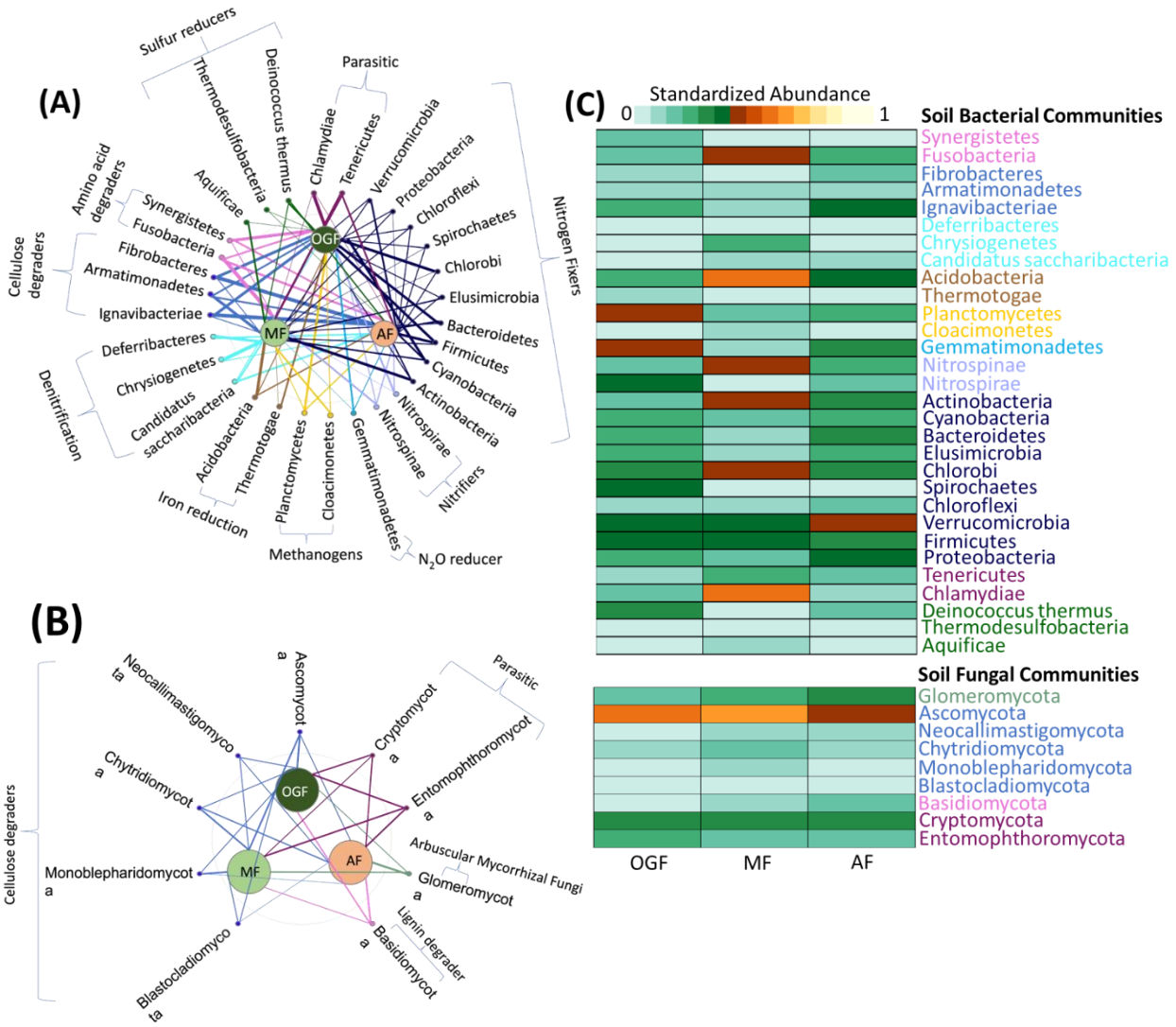

Figure 4: Co-occurrence abundance network for bacterial (A) and fungal phyla (B), and (C) heat map showing the differences in bacterial and fungal standardized abundance across land use types. Thicker lines in co-occurrence abundance networks represent greater abundance and matching font and line colors represent majority function within each phylum.

13. Supplementary Material

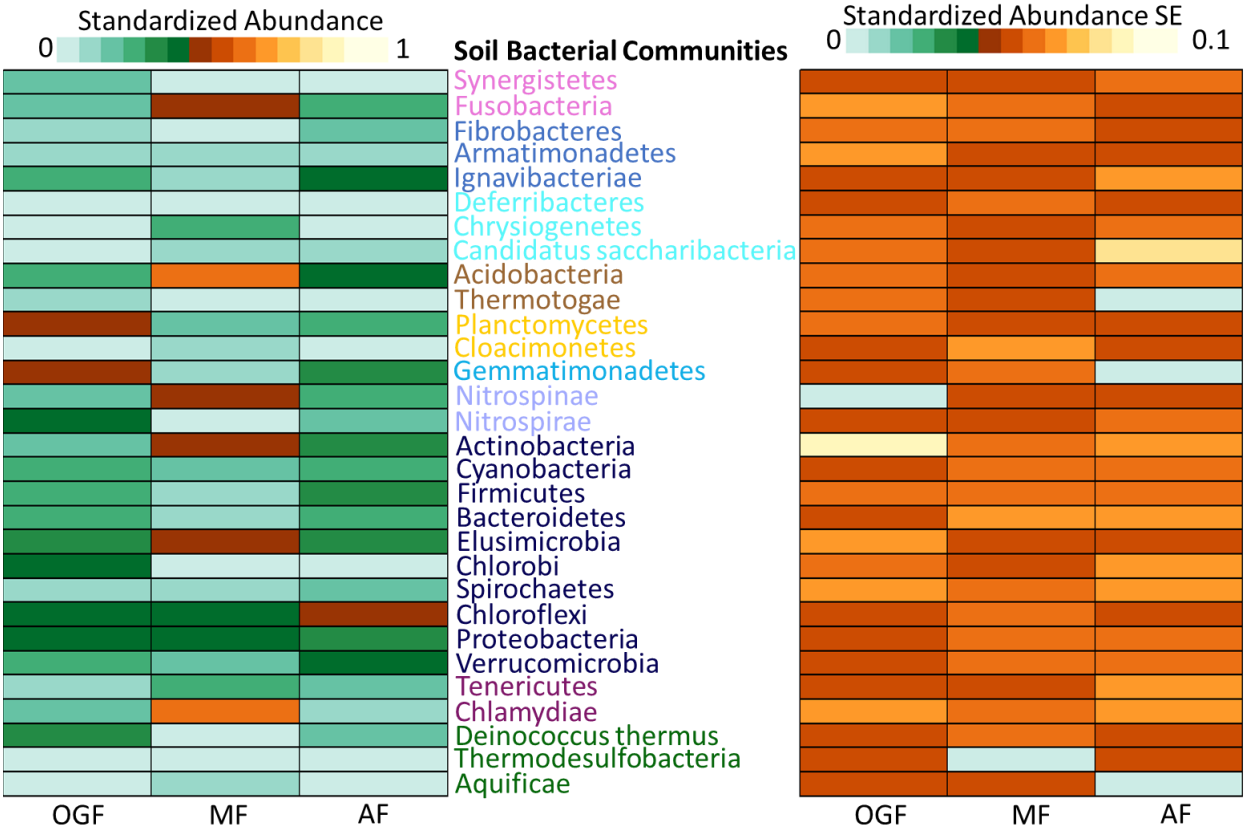

Figure S1: Heat map showing the differences in bacterial standardized abundance and standard error across land use types. Matching font and line colors represent majority function within each phylum.

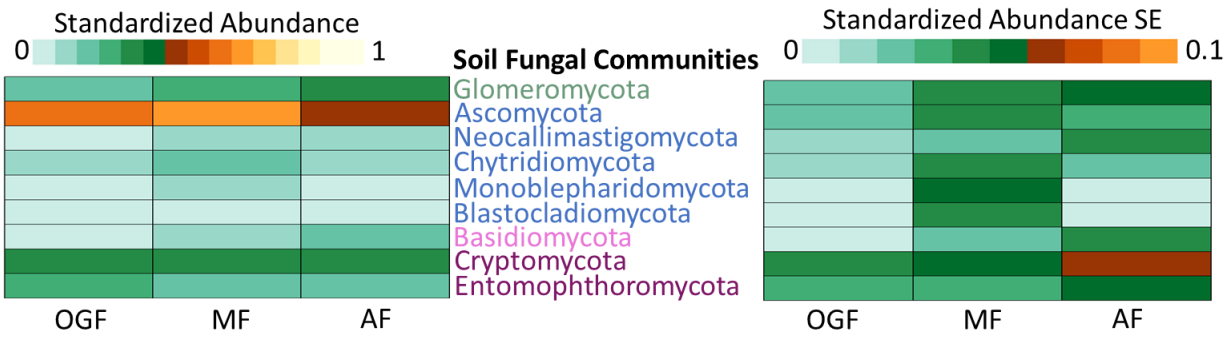

Figure S2: Heat map showing the differences in fungal standardized abundance and standard error across land use types. Matching font and line colors represent majority function within each phylum.

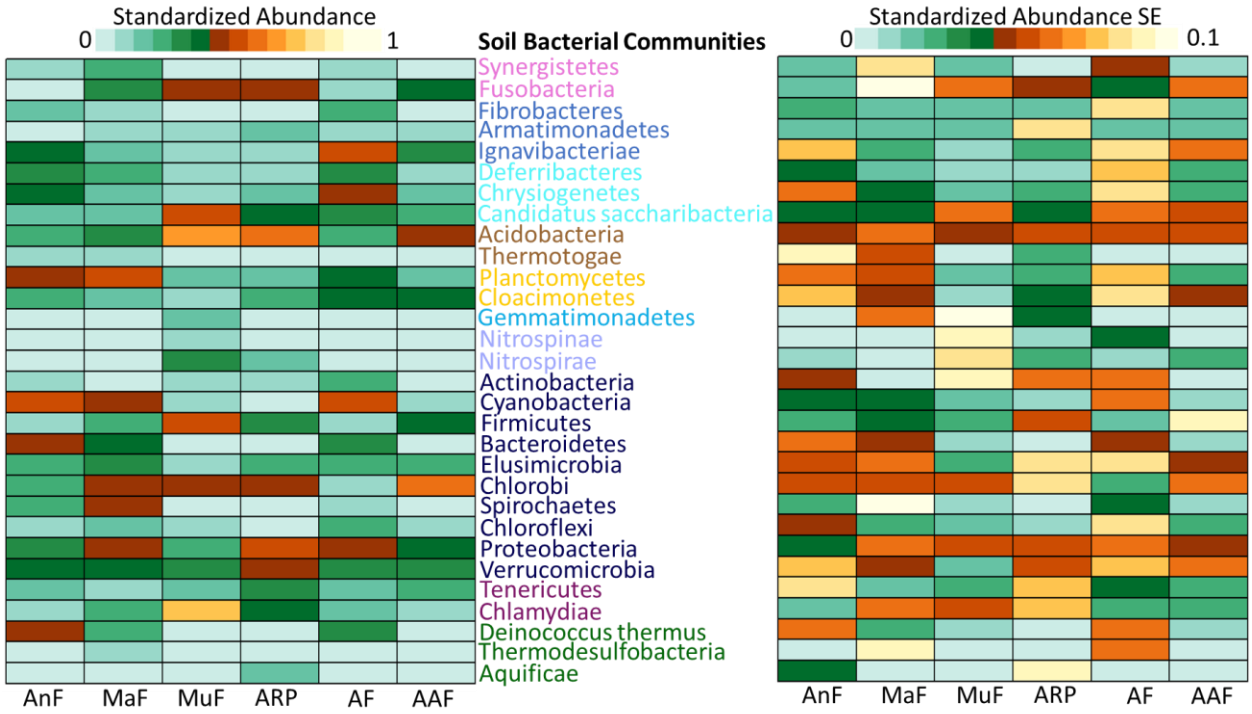

Figure S3: Heat map showing the differences in bacterial standardized abundance and standard error across each site with an increasing land use gradient from the left to right (Angelo's Forest, Mahua Falls Forest, Malungung Forest, Abandoned Rubber Plantation, Agriculture Field, and Agriculture Field). Matching font and line colors represent majority function within each phylum.

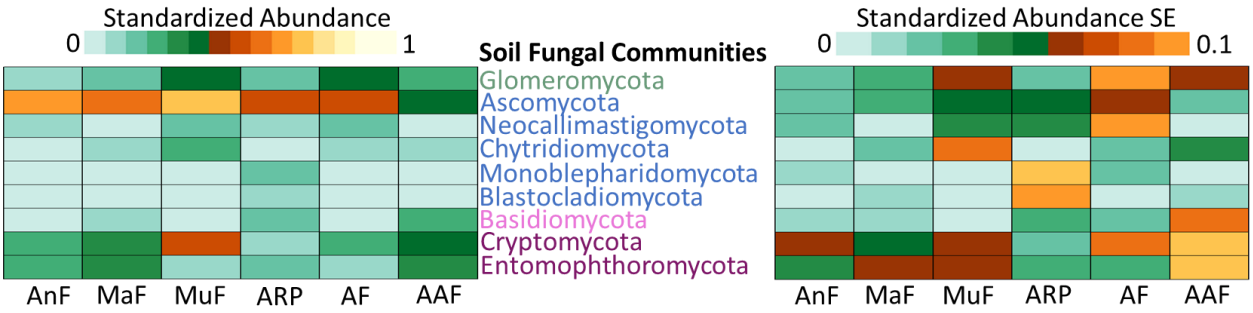

Figure S4: Heat map showing the differences in fungal standardized abundance and standard error across each site with an increasing land use gradient from the left to right (Angelo's Forest, Mahua Falls Forest, Malungung Forest, Abandoned Rubber Plantation, Agriculture Field, and Abandoned Agriculture Field). Matching font and line colors represent majority function within each phylum.