Impacts of tropical forest modification on soil microbial communities, function and resilience

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Declaration

I declare that this thesis has not been submitted in support of an application for another degree at this or any other university. Collaboration with other researchers is specifically acknowledged throughout the document. Many of the ideas in this thesis were the product of discussion with my supervisors Professor Nick Ostle (Lancaster University) and Professor Niall McNamara (UK Centre for Ecology & Hydrology).

This thesis word length is 45,781 and therefore does not exceed the permitted maximum

Excerpts of this thesis have been published in the following academic publications:

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Statement of Authorship

This thesis is prepared in the alternative format as a series of four papers, one of which is published in a peer reviewed journal and is presented as the final copy before journal editing. The rest are intended for submission to peer reviewed journals. All papers have several authors. Their contribution to each paper are detailed below and have been approved by my supervisors. Chapters 1 and 6, the thesis introduction and general discussion respectively are not intended for submission.

Chapter 2 is intended for publication as:

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DMOE designed the field sampling approach, conducted field soil sampling, analysed samples in the lab, conducted all data analysis and prepared the manuscript. SB provided plant trait datasets to the manuscript and gave advice on the field sampling approach. TG conducted microbial sequencing analyses. SR assisted with sample collection. TR provided plant productivity datasets to the manuscript. NML conducted soil chemistry analyses and supported research permit applications. NJO, NPM and DJ gave advice on sampling design and data analysis. DFRPB, YM, RIG, DJ, NJO and NPM acquired funding which supported the work and all co-authors contributed to manuscript revisions.

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DMOE conducted field sampling, DNA extraction and sequencing, data analysis and prepared the manuscript. HG, LA, CLP and PE designed, implemented and maintained the field invertebrate manipulation plots. TG provided training and supervision of laboratory DNA sequencing. SR assisted with field sampling and contributed hyphal abundance data. NML carried out soil chemistry analyses. NPM and NJO gave advice on sampling design and data analysis. CLP, PE, RIG, NPM and NJO acquired funding which supported the work.

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DMOE collected and processed the samples, designed and set up the experiment, performed soil laboratory analyses, analysed the data and prepared the manuscript. SR assisted with sample collection and processing. SB conducted litter chemical analyses. TG extracted and sequenced DNA from soil samples. NML supported research permit applications and provided field logistical support. NJO and NPM provided advice on

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DMOE collected the samples, designed and set up the experiment, performed soil laboratory analyses, analysed the data and prepared the manuscript. SR provided advice on the field sampling and assisted with sample collection. TG extracted and sequenced DNA from soil samples. NML supported research permit applications and provided field logistical support. NJO and NPM provided advice on experimental design and acquired funding which supported the work.

I hereby agree with the above statements:

Prof. Nicholas J. Ostle

Prof. Niall P McNamara

Abstract

Tropical forests are hotspots of biodiversity and have global significance to the terrestrial carbon cycle. However, forest disturbance, clearance for plantation agriculture and future climate change are threatening their ability to sustain crucial ecosystem services. Ecosystem processes in tropical forests are underpinned by soil microbial activity, but knowledge of the principal drivers of microbial community dynamics and relationship to ecosystem functions is lacking. An improved understanding is therefore essential to better predict the response of tropical forests to a changing environment. The overarching aim of this thesis was to determine environmental drivers of soil microbial communities in tropical forest and explore the effects of forest modification (degradation and conversion) on soil microbial community composition, functioning and resilience to climate perturbations. Using a combination of field survey, *in situ* ecological manipulations and controlled laboratory experiments I found that fungal communities had stronger local covariance with standing tree communities and were thus more strongly influenced by tropical forest disturbance than bacterial communities. Moreover, the relative abundance of ectomycorrhizal fungi was strongly associated with the standing biomass of dipterocarp trees. In old growth forest, ants were found to modulate fungal growth rates and termites influenced the abundance and distribution of wood degrading taxa. Suppressed ant and termite activity also restructured microbial networks with properties associated with reduced resilience to climate extremes. As logging alters the functional diversity of ants and strongly reduces termite abundance in tropical forest, these findings indicate that invertebrate – microbial interactions may control the fungal contribution to soil C storage, rates of wood decomposition, and the

resilience of soil microbial decomposers to future climate extremes across OG and SL tropical forests. Microbial communities in SL forest did have lower resilience to experimental drought – rewetting relative to those in OG forest and oil palm plantations whilst communities in old growth tropical forest had broader functional abilities, degrading both forest and oil palm litters faster than communities from logged forest and oil palm plantations. Taken together, these findings suggest that logging of tropical forests reduces the function and resilience of soil microbial communities, by modifying tree community composition and invertebrate activity. This may influence the size and stability of soil C stocks under future climate change.

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It has been an immense privilege to work in the Bornean tropical rainforest during this PhD. I have learnt so much during my time spent in this amazing ecosystem and will always remember the incredible biodiversity, humbling animal encounters, falling asleep to the soundtrack of the forest and all the people that I met and worked with along the way. I am hugely grateful to all the SAFE research assistants who helped me in the field, without which this project would not have been possible. You taught me how to navigate through the forest, identify plants and animals, and introduced me to local cultures and language. Terima Kasih!

I reserve particular thanks for Sam Robinson whose friendship, field assistance, advice and sense of humour was invaluable during the course of this PhD. I will always remember our adventures in Sabah. We make a great team and am looking forward to working together again soon!

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1 Introduction

1.1 The global importance of tropical forests for the provision of ecosystem services

Biodiversity describes the variety of living organisms on earth and supports a myriad of ecosystem services, essential for human life and wellbeing. Ecosystem services can be classified as provisional (e.g. provision of Fibre, Food, Freshwater, Fuel and other essential resources), regulative (e.g. climate regulation, disease control and suppression of pathogens, water purification and regulation), supportive (nutrient cycling, primary production, soil formation) or cultural (Reid et al., 2005) with estimates valuing the services provided by global biodiversity at $125 trillion dollars annually (Costanza et al., 2014).

Humid tropical forests play a disproportionate role in the provision of ecosystem services relative to other terrestrial biomes (Daily, 1997) as they are the most biologically rich and diverse ecosystems on Earth (Laurance, 2007; Pimm and Raven, 2000). Globally, tropical forests cover ~1.8 billion hectares (45 % of total global forest area) between the tropics of Cancer and Capricorn (FAO, 2020b), with the largest intact forests located within the Amazon basin, Congo basin and Indonesia (Hansen et al., 2013; Potapov et al., 2017). A majority (~60 %) of all known terrestrial

plant and animal species are found in tropical forests which cover just 5 % of global land area (Dirzo and Raven, 2003; Laurance, 1999) and provide multiple ecosystem services of global importance (Brandon, 2014; Foley et al., 2005). Intact tropical forests represent the world's largest terrestrial carbon (C) sink sequestering on average 1.4 ± 0.2 petagrams of C per year (Pg C yr^{-1}) between 1990 to 2007 (approximately half of the total global C sink in established forests) (Pan et al., 2011). Tropical forests also regulate global climate through their effects on water transpiration, cloud formation and atmospheric circulation (Devaraju et al., 2015; Lawrence and Vandecar, 2015; Spracklen et al., 2012). By moderating local air temperatures and enhancing regional rainfall (by returning up to 90 % of received rainfall to the atmosphere through evapotranspiration), tropical forests strongly influence regional weather patterns (Ellison et al., 2012; Kume et al., 2011; Lawrence and Vandecar, 2015). Due to high water infiltration rates and low rates of surface runoff (Ilstedt et al., 2007; Roa-Garcia et al., 2011), tropical forests can also stabilise soils and protect against soil erosion (Labrière et al., 2015). This in turn may prevent the sedimentation of freshwater courses and offer protection against landslides (Sidle et al., 2006). They also provide valuable resources of wild food, timber and non-timber forest products for rural communities (Guariguata et al., 2010). It is estimated that some 1.2-1.5 billion people rely directly upon the ecosystem services provided by tropical forests (Vira et al., 2015). No other terrestrial biome has such a profound influence on weather patterns, freshwater provision, biodiversity, food and human health.

1.2 Anthropogenic pressures on tropical forests

Over the last several decades, human activities have led to a large reduction in the global extent of tropical forests with a decline of 195 million hectares (from 1966 to 1770 million hectares) between 1990 and 2015 (Keenan et al., 2015). Although the

annual rate of global forest loss has declined from a peak in the 1980's (FAO, 2020b), primary tropical forest continues to be cleared at an alarming rate across the Amazon and Congo basins and Indonesia (Potapov et al., 2017; Turubanova et al., 2018). The majority of remaining tropical forests are degraded by human activities, even if many disturbed forests retain high levels of tree cover (Jacobson et al., 2019; Philipson et al., 2020). Despite regional variation, the dominant driver of global tropical forest loss is commercial and subsistence agricultural expansion (Geist and Lambin, 2002; Gibbs et al., 2010; Hansen et al., 2013; Hosonuma et al., 2012; Houghton, 2012). Between 1980-2000, ~55 % of new agricultural land came from the conversion of intact tropical forest and a further 28 % from degraded forests (Gibbs et al., 2010). Tropical deforestation is also driven by mining, infrastructure development and urban expansion whilst forest degradation is primarily driven by timber extraction via selective logging, fuelwood collection and charcoal production (Hosonuma et al., 2012).

The pervasive degradation and clearance of intact tropical forests has resulted in a patchwork mosaic of human modified landscapes across the tropics (Arroyo-Rodriguez et al., 2017; Gardner et al., 2009). This represents an ongoing catastrophe for biodiversity as large, intact, old-growth tropical forests are irreplaceable for sustaining species diversity (Barlow et al., 2007; Gibson et al., 2011; Watson et al., 2018). Although regenerating forests may rapidly recover structurally, biotic recovery may take centuries to millennia (DeWalt et al., 2003; Liebsch et al., 2008). Intact tropical forests store more C than degraded forests both above and below ground (Houghton, 2012; Pearson et al., 2017; Riutta et al., 2018; Roopsind et al., 2018). As C losses from deforestation and forest degradation outweigh C gains from intact forest and forest regrowth, tropical forests may now have transitioned from a net global C

sink to a net C source (Baccini et al., 2017; Mitchard, 2018). Moreover, degraded tropical forests are often subject to a number of secondary impacts due to fragmentation and associated edge effects. For example, forest fragments in Amazonia are subject to altered microclimates, have enhanced tree mortality and store less C than intact forest (Laurance et al., 2011), whilst fragmented forests may also be more vulnerable to climate change and wildfires (Malhi and Phillips, 2004). This further impacts the ability of tropical forests to provide crucial ecosystem functions, threatening human wellbeing (Bradshaw et al., 2009; Ferraz et al., 2014; Watson et al., 2018).

Tropical deforestation for agriculture results in even more severe impacts on the provision of ecosystem services. For example, conversion of Indonesian tropical forest for oil palm reduced freshwater quality available to rural farming communities by increasing sediment load, water temperature and biological oxygen demand (Carlson et al., 2014). Ongoing tropical deforestation also threatens global health, security and economic growth as the risk of emerging infectious zoonotic diseases is substantially elevated in high biodiversity forested tropical regions which are experiencing land use change (Allen et al., 2017).

The outlook for tropical forests is uncertain (Estoque et al., 2019). ~1 billion people live within 5 km of a tropical forest and this is likely to increase as the world’s population is growing rapidly across developing countries in the tropics (Newton et al., 2020). As most tropical deforestation is commodity driven (Curtis et al., 2018), increased population demand for agricultural products is likely to drive continued deforestation, degradation and fragmentation. Future climate change is also predicted to amplify tree mortality due to climatic extremes of drought and increased heat

(Allen et al., 2010; Rifai et al., 2019) and this may interact with land-use change due to vegetation-atmosphere feedbacks (Zemp et al., 2017).

1.3 Borneo – A threatened biodiversity hotspot

South East Asia covers only 4 % of the world's land area but is home to ~15 % of the world's tropical forests (Stibig et al., 2014). These forests are mostly distributed across three biogeographic sub-regions; Indochina (Cambodia, Laos, Vietnam), Sundaland (Sumatra, Java, Borneo) and the Philippines and are a global hotspot of mammal species richness (Catullo et al., 2008; Rondinini et al., 2011) and plant diversity (Barthlott et al., 2005; Myers et al., 2000). The region is so biodiverse that 20-25 % of all known animal and plant species on Earth are found here (Woodruff, 2010). The rich regional biodiversity results from the region's unique geography, its position in the humid tropics, its history of changes in land area, and its habitat fragmentation (Sodhi et al., 2004; Woodruff, 2010).

Borneo is situated at the heart of the exceptionally diverse Sundaland sub-region and has special biodiversity significance to SE Asia (Myers et al., 2000). Due to a unique evolutionary history, it has the highest terrestrial mammalian and vascular plant species richness in SE Asia (Barthlott et al., 2005; de Bruyn et al., 2014; Raes et al., 2009). Estimates suggest that Borneo has almost 15,000 plant species and close to 1700 vertebrate species, with 28 % of these being endemic (Mittermeier et al., 2004; Runting et al., 2015). Borneo also has over 3000 species of trees including 267 species of the Dipterocarpaceae family, of which 155 (58 %) are endemic (Mittermeier et al., 2004). Dipterocarp trees are highly productive (Banin et al., 2014) and dominate most mature forests in Borneo and across SE Asia; comprising over 20 % of all standing trees (Ashton and Kettle, 2012; Slik et al., 2003) and the majority of large canopy

dominant and emergent trees (Ashton, 1988; Brearley et al., 2016). Dipterocarps are also amongst the tallest trees in the tropics (Banin et al., 2012) and can reach in excess of 100 m in height (Shenkin et al., 2019). The dominance of dipterocarp tree species across the humid tropical forests of SE Asia is thought to explain an average aboveground biomass, which is 60 % higher than that found in Amazonian forests (Paoli et al., 2008; Slik et al., 2010). This highlights the disproportionate contribution of dipterocarp forests to the global terrestrial C balance (Qie et al., 2017).

The rich terrestrial and freshwater biodiversity of Borneo is under sustained threat from overexploitation of natural resources (Logging of valuable timbers, hunting, fishing, trade of plant and animal tissues) (Nijman, 2010; Peh, 2010; Reynolds et al., 2011), deforestation and habitat conversion for agriculture (Koh and Wilcove, 2008; Wilcove and Koh, 2010), human population growth (DeFries et al., 2010; McDonald et al., 2008) and climate change (Chapman et al., 2020; Siegert et al., 2001). Borneo has some of the highest rates of deforestation in the world (Miettinen et al., 2011) and has lost forest cover almost twice as fast as the rest of the world's humid tropical forests over the last three decades (Achard et al., 2002; Gaveau et al., 2014) (Figure 1.1). The most recent estimates suggest that current forest cover on Borneo stands at around 50 % of total land area (Gaveau et al., 2014; Hughes, 2017) (Down from 73 % in 1973). However, 70 % of this remaining forest cover is degraded (Gaveau et al., 2014), particularly in lowland areas.

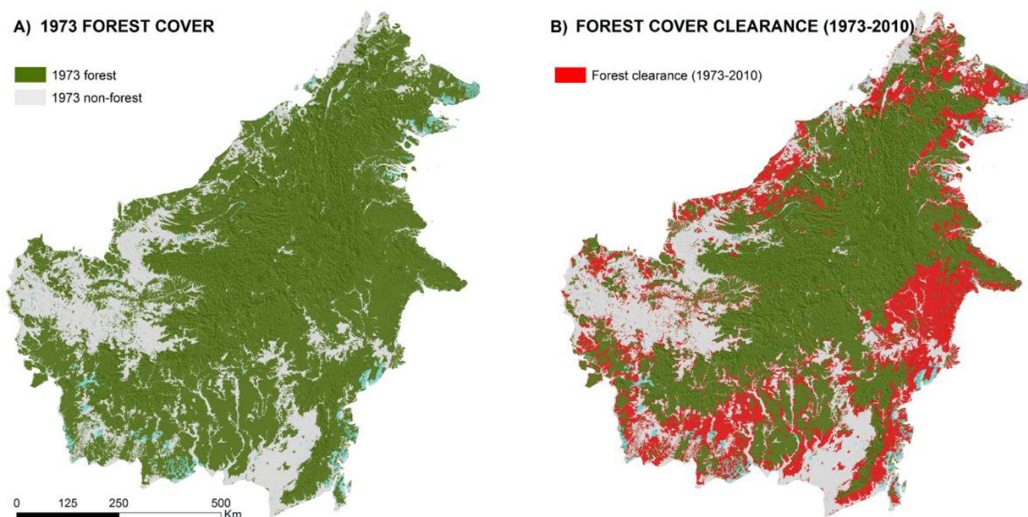

Figure 1.1 *- Panel A showing land area of Borneo covered in forest (dark green) and non-forest (white) in year 1973 (Residual clouds are shown in cyan). Panel B showing areas of forest loss during period 1973–2010 (red). Modified from Gaveau et al. (2014). Forest cover in 1973 was derived from LANDSAT MSS Imagery. Forest loss (1973-2010) was derived from comparison between LANDSAT imagery and the 2010 SARVISION forest cover map (Hoekman et al., 2011).*

Across Borneo, 16 % of land area is covered by old growth (OG) intact forest in protected areas (Scriven et al., 2015) (Figure 1.2). However, the Malaysian states of Sabah and Sarawak have only 8 % and 3 % of intact forest remaining within protected areas respectively, with over 80 % of land either cleared or impacted by high intensity logging (Bryan et al., 2013). Protected areas are relatively small in scale and mostly isolated within a matrix of human modified landscapes comprising remnant forest fragments, degraded logged forest and monoculture plantations (Marsh and Greer, 1992; Reynolds et al., 2011; Scriven et al., 2015) (Figure 1.2).

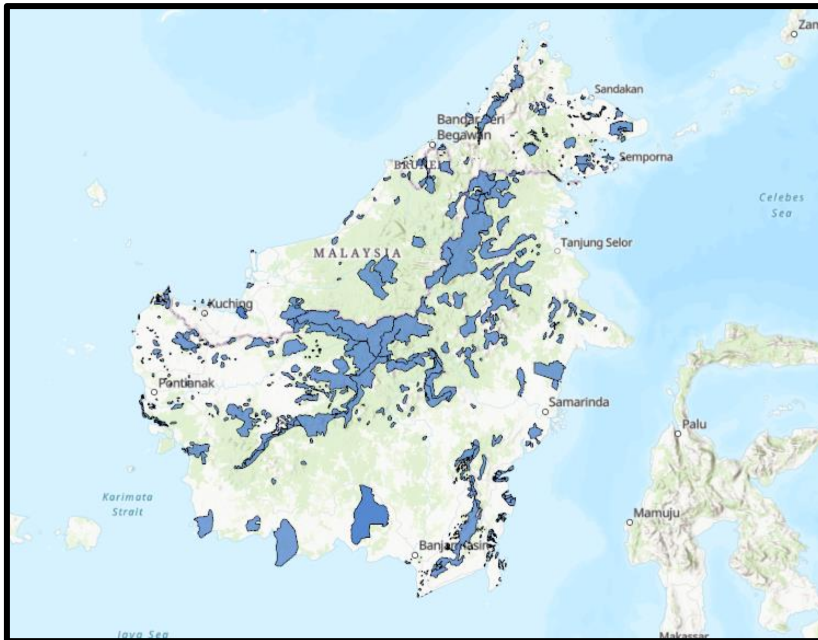

Figure 1.2 *- Land area of Borneo covered by intact OG tropical forest within legally protected areas (Blue shaded polygons). Protected areas can be designated as national parks, nature, wildlife sanctuaries and game reserves, recreational parks, virgin jungle reserves, and protection forests. For Kalimantan (Indonesian Borneo), protected area boundaries were obtained from provincial and national spatial plans. For the Malaysian province of Sabah, protected area boundaries were obtained from Sabah's Forestry Department. For the Malaysia province of Sarawak and for Brunei, protected area boundaries were obtained from the World Database of Protected Areas. Downloaded from and freely available at* ***https://services.arcgis.com/P8Cok4qAP1sTVE59/arcgis/rest/services/Protected_Area_of_Borneo/FeatureServer****. Accessed on 01/11/2020.*

Selective logging of commercial timber species typically precedes land clearance and conversion (Abdul Aziz et al., 2010; Giam et al., 2011). This involves the selective removal of large commercially valuable trees, which in Borneo and across SE Asia are primarily dipterocarps (Edwards et al., 2011; Sist et al., 2003). Selective logging activities modify forest carbon cycling by modifying forest structure, dynamics (Riutta et al., 2018; Sist and Nguyen-Thé, 2002), understorey plant (Döbert et al., 2017) and tree species composition (Verburg and van Eijk-Bos, 2003). Canopy gaps are created where large individual trees are felled (Muscolo et al., 2014). This influences tree seedling recruitment (Curran et al., 1999; Dupuy and Chazdon, 2008) and alters forest floor microclimates (Blonder et al., 2018; Hardwick et al., 2015).

Logging operations also cause damage to residual forest which increases the volume of dead wood (Keller et al., 2004; Palace et al., 2007) and the creation of skid trails and haul roads causes soil damage through compaction and erosion (DeArmond et al., 2019; Pinard et al., 2000) (See Figure 1.3 for an example of OG and logged forest in Sabah, Malaysia).

Selective logging affects forest biodiversity with negative impacts on invertebrates (Edwards et al., 2014; Ewers et al., 2015; Luke et al., 2014), freshwater fish (Wilkinson et al., 2018), amphibians (Konopik et al., 2015), mammals (Brodie et al., 2015; de Almeida-Rocha et al., 2017; Wells et al., 2007) and birds (Cleary et al., 2007; Edwards et al., 2013; Hamer et al., 2015). However, the severity of logging impacts on biodiversity tends to relate to the intensity of logging and period of recovery (Burivalova et al., 2014; Mahayani et al., 2020). The intensity of logging across Borneo is exceptional by global standards as between 1980-2000, the volume of timber exported from Borneo alone (Kalimantan, Sarawak, and Sabah) was higher than all tropical wood exports from tropical Africa and Latin America combined (Curran et al., 2004). The dipterocarps account for 80 % of timber exports from SE Asia and ~25 % of global consumption of tropical hardwoods (Kettle, 2010). Although, reduced impact logging guidelines have been proposed (Pinard et al., 1995; Putz et al., 2008), the vast majority of timber is still harvested unsustainably (Ellis et al., 2019). However, selectively logged forests across SE Asia still retain many forest species and have a high conservation value (Berry et al., 2010; Edwards et al., 2011; Woodcock et al., 2011).

A.

B.

Figure 1.3 *– A. Old growth intact forest dominated by canopy forming trees of the Dipterocarpaceae family. B. Heavily degraded and fragmented selectively logged forest dissected by logging roads. Photographs were taken by the author in Sabah, Malaysia at Maliau Basin Conservation Area (A.) and the Kalabakan Forest Reserve (B.).*

The expansion of plantation agriculture is recognized as arguably the greatest immediate threat to regional biodiversity in Borneo (Wilcove and Koh, 2010) as land use economics drive the rapid clearance of selectively logged (SL) forests to oil palm or softwood timber plantations (acacia, rubber) plantations, where short term financial returns are high (Fisher et al., 2011a; Koh and Wilcove, 2008). From 1990–2005, 55–59 % of oil palm expansion in Malaysia, and at least 56 % of that in Indonesia occurred at the expense of forests (Koh and Wilcove, 2008). From 1973-2015 plantation area (softwood timber and oil palm) across Borneo increased by ~9.2 Mha (Figure 1.4), with half of these plantations (4.8 Mha) established between 2005 and 2015 (Gaveau et al., 2016). ~3 Mha of OG forest were cleared to make way for this expansion (Gaveau et al., 2019) (Figure 1.4).

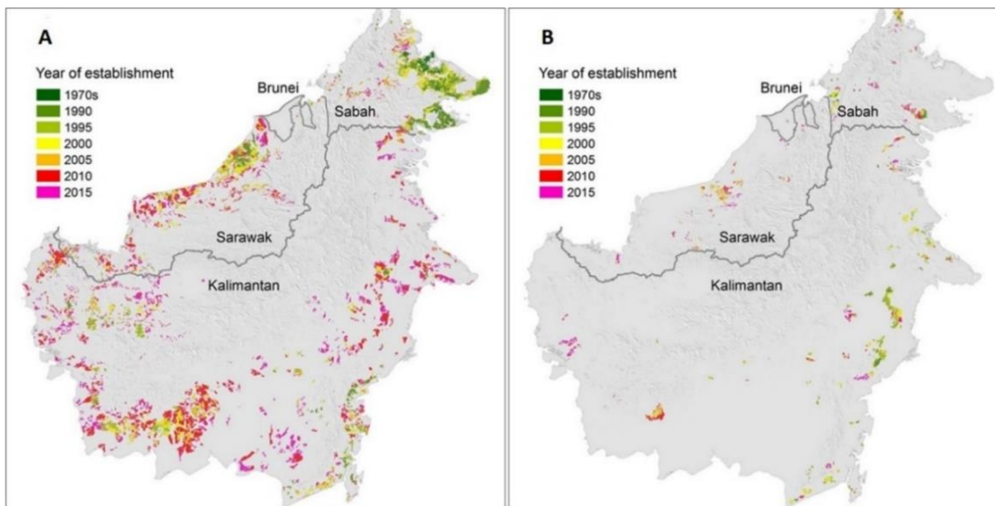

Figure 1.4 *- Panel A showing the expansion of industrial oil-palm plantations from 1973-2015 (7.8 Mha). Panel B showing the expansion of industrial pulpwood plantations from 1973-2015 (1.3 Mha). The expansion of plantation areas was mapped using time-series LANDSAT satellite imagery. Adapted from Gaveau et al. (2016).*

Oil palm (*Elaeis guineensis*), a palm species native to tropical Africa, is highly productive per unit of land area, has low operational costs and is robust to many pests and diseases, making it not only an incredibly profitable cash crop but also the most economically efficient oil producing crop globally (Wahid et al., 2005). As a result, oil palm is now one of the world's most rapidly expanding crops and is grown throughout the humid lowland tropics (FAO, 2020a). However, plantations are heavily concentrated in Indonesia and Malaysia which alone account for ~85 % of global crude palm oil production (FAO, 2020a). Approximately half (9.2 Mha) of global palm oil plantations (~18 Mha) are concentrated on the island of Borneo covering approximately 10 % of the total land area (Gaveau et al., 2014) (See Figure 1.5 for the development of an oil palm plantation on deforested land).

Whilst oil palm cultivation can deliver significant socio-economic benefits to rural communities, it comes at a significant cost to biodiversity and the ecosystem functions they provide (Sharma et al., 2019). Almost all organisms studied have lower species richness in oil palm plantations than in forests (Dislich et al., 2017). Not only is species richness lower, the species present are more likely to be common, generalist species (Fitzherbert et al., 2008). A meta-analysis revealed that 11 out of the 14 ecosystem functions considered in the study showed a net decrease in the level of function provided when comparing oil palm to native tropical forest ecosystems (Dislich et al., 2017). Conversion from tropical forest to oil palm leads to a strong decline in climate regulation functions (emissions of greenhouse gases and volatile organic compounds, C sequestration and storage).

A.

B.

C.

Figure 1.5 *– The progression from land clearance to oil palm plantation in Sabah, Borneo. A. – Deforested land cleared for oil palm cultivation. B. – Terraced hillsides planted with oil palm seedlings. C. – A mature oil palm plantation. All photographs were taken by the author in Sabah, Malaysia on Benta Wawasan Sdn. Bdh. oil palm estates.*

For example, the conversion of forest to oil palm plantation on mineral soil results in ecosystem carbon losses (702 ± 183 (S.D.) Mg CO_2 ha^{-1} over 30 years) (Fargione et al., 2008) and persistent declines in soil organic C stocks over a decade following conversion (Guillaume et al., 2018). Oil palm plantations are major emitters of volatile organic compounds (VOC's) (i.e. Isoprene) which can reduce regional air quality (Fowler et al., 2011) and have significantly warmer understorey microclimates relative to forests (Hardwick et al., 2015). Oil palm plantations also store less water than forests, primarily due to peatland drainage and reduced water infiltration (Evers et al., 2017; Merten et al., 2016) and are associated with reduced water quality (Carlson et al., 2014; Comte et al., 2012). The risks of flooding, drought, landslides, and wildfires are also higher in landscapes dominated by plantations (Dislich et al., 2017) and rates of surface soil erosion increase following conversion from tropical forest (Guillaume et al., 2015; van Straaten et al., 2015). Because of the pervasive logging and land clearance for plantation agriculture, the concept of a 'natural ecosystem' is fast disappearing across Borneo. Intact OG forest is limited to isolated protected areas (Figure 1.2) interspersed within a human modified mosaic landscape of plantations and regrowth forest vegetation.

1.4 The importance of soil microbial communities to the maintenance of ecosystem functions in tropical forests

Microorganisms are probably the most abundant (Whitman et al., 1998) and diverse organisms on earth (Torsvik et al., 2002). However, they go largely unnoticed, despite their fundamental importance to the biosphere as drivers of biogeochemical cycles, thus supporting crucial ecosystem functions, services and sustaining all life on Earth (Crowther et al., 2019; Pace, 1997). The advent of culture independent techniques such as ribosomal DNA analysis (Muyzer et al., 1993) and next generation high-

throughput sequencing (Caporaso et al., 2012; Caporaso et al., 2011) has revolutionised microbial ecology and allowed for the characterisation of the full extent of microbial community diversity from a wide array of environments at large spatial scales (Dupont et al., 2016; Fierer and Jackson, 2006; Rappe and Giovannoni, 2003; Shearer et al., 2007; Sunagawa et al., 2015; Talbot et al., 2014; Tedersoo et al., 2014). This has revealed that microorganisms are far more diverse than previously assumed (Gibbons and Gilbert, 2015) although many identified taxa are still, as yet unclassified (Delgado-Baquerizo, 2019).

Soils contain members from all three domains of life (Archaea, Bacteria, Eukarya) but harbour particularly diverse prokaryotic communities (Bacteria and Archaea) (Bates et al., 2011; Lozupone and Knight, 2007); with an estimated 10^9 individual bacterial cells and ≈10^4 to 10^5 unique individuals per gram of soil (Torsvik et al., 2002). Soils also harbour a tremendous abundance and diversity of eukaryotic microorganisms such as protists (Bates et al., 2012; Geisen et al., 2018), hold the majority of known fungal diversity (Peay et al., 2016) and have highly diverse viral communities (Kimura et al., 2008; Paez-Espino et al., 2016). Taken together, the biomass of the “soil microbiome” is thought to be equivalent to the total aboveground biomass of plants or animals, exceeding >1000 kg microbial biomass C per hectare (Fierer et al., 2009; Serna-Chavez et al., 2013).

The soil microbiome has both direct and indirect effects on many ecosystem level processes (Figure 1.6). Soil microbes directly regulate soil carbon dynamics by balancing the relative storage and release of organic C through decomposition of soil and plant organic matter (Gleixner, 2013; Schimel and Schaeffer, 2012). Microbes are also central to the cycling of nutrients through the soil profile (e.g. N, P, S), thus

determining soil fertility (Fierer, 2017; Kuypers et al., 2018) and regulate the production and consumption of atmospheric greenhouse and trace gases (CO_2, CH_4, N_2O, volatile organic compounds, H_2) (Conrad, 1996; Insam and Seewald, 2010; Smith et al., 2003) (Figure 1.6). Soil microbes can also modulate soil water availability (Morales et al., 2010), control rates of soil aggregation (Rillig and Mummey, 2006) and degrade an array of xenobiotic compounds (Eyers et al., 2004).

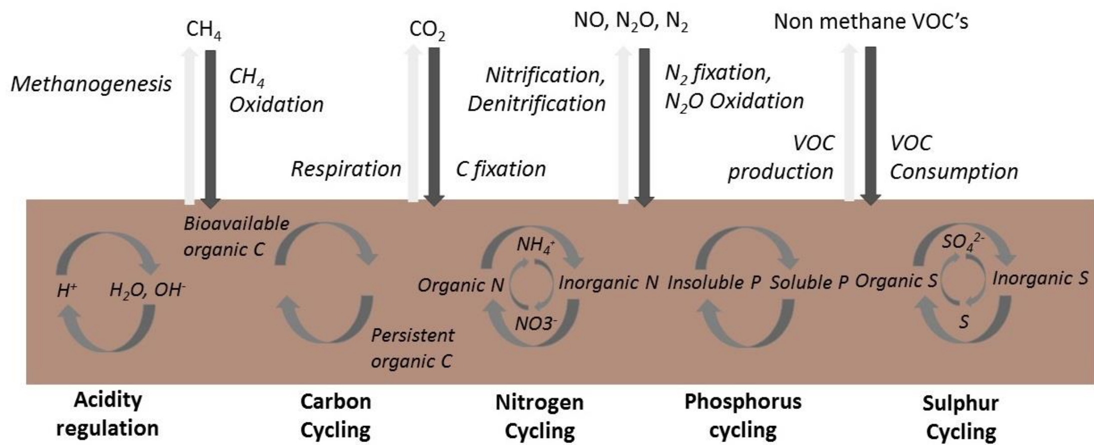

Figure 1.6 *- Diagram describing a subset of important soil biogeochemical processes that are mediated by soil microorganisms. Vertical arrows indicate gas exchange between the soil and atmosphere whilst curved arrows represent microbial processes that occur with the soil matrix. VOC's = volatile organic compounds. This represents only a subset of the microbially mediated processes and does not include interactions between processes. Redrawn and adapted from Fierer (2017).*

Soil microorganisms also exert controls on ecosystem level processes through antagonistic or symbiotic interactions with aboveground plant communities (Figure 1.7) (Van Der Heijden et al., 2008).

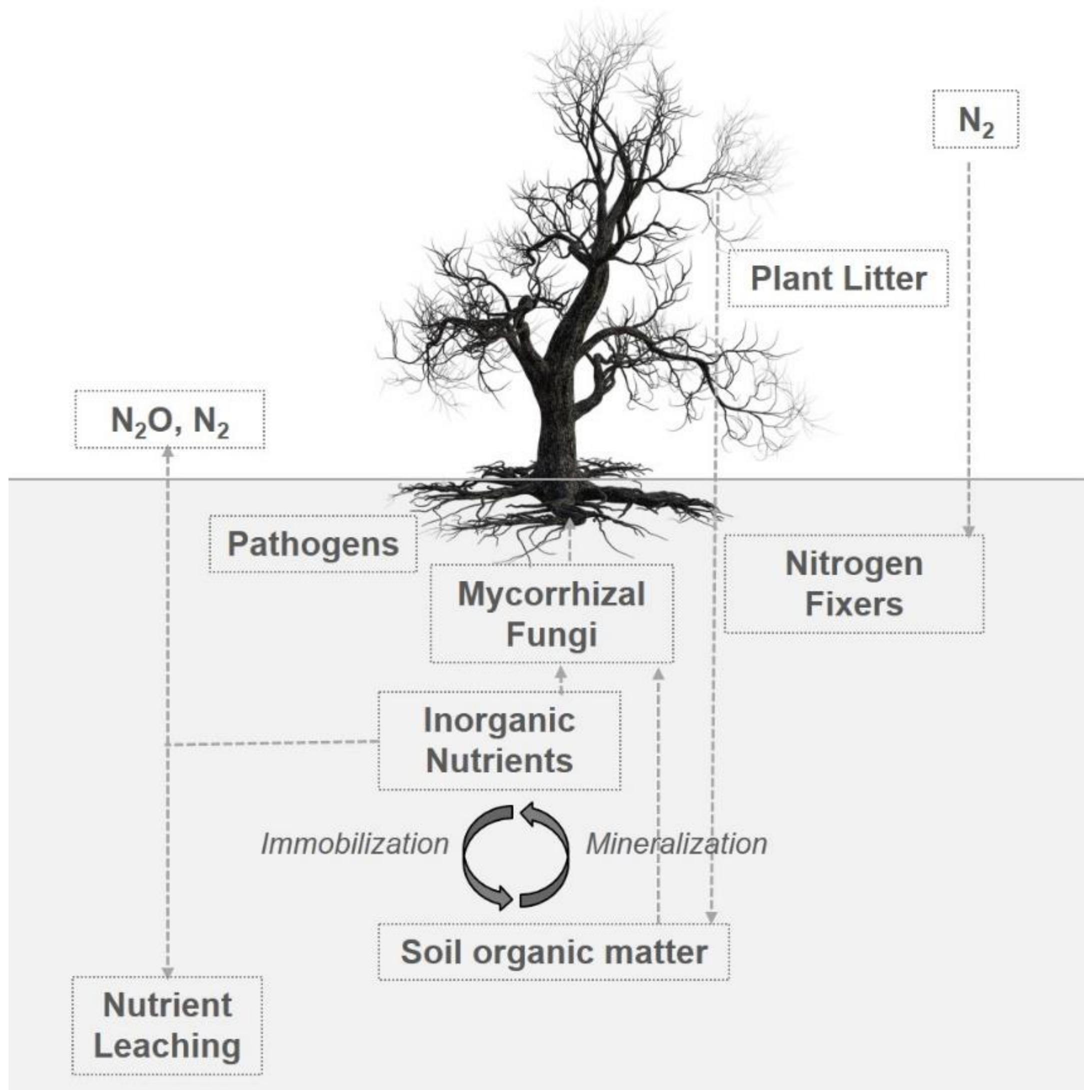

Figure 1.7 *- A schematic diagram showing how soil microbial communities influence soil nutrient availability, plant nutrient acquisition and plant productivity. A wide array of free-living soil microbes are responsible for the turnover (immobilization and mineralization) of fresh plant litter and existing soil organic matter. Mineralization liberates organic nutrients for plant uptake via mycorrhizal fungi although some mycorrhizae may also access organic nutrients directly. Some nutrients may be lost to the atmosphere or leached by the activities of denitrifying and nitrifying bacteria. Nitrogen fixers transform dinitrogen into ammonium which can boost plant productivity whilst pathogens can negatively impact plant productivity Redrawn and modified from Van Der Heijden et al. (2008).*

In tropical forests, suppression of dominant tree species by soil pathogens may be an important mechanism contributing to the maintenance of extremely high tree species diversity (Bachelot et al., 2017; Bell et al., 2006; Mangan et al., 2010) whilst in N limited ecosystems, plant symbiosis with nitrogen (N) fixing bacteria may confer a competitive advantage by supplying ammonium to plant hosts in exchange for C derived from photosynthesis (Hayat et al., 2010). Mycorrhizal fungi are some of the most important soil microorganisms and associate symbiotically with most (>80 %) terrestrial plants (Smith and Read, 2008b). In exchange for sugars derived from photosynthesis, mycorrhizal fungi acquire organic and inorganic soil nutrients via extensive hyphal networks and supply this to the plant host (Parniske, 2008). They may also enhance plant tolerance to environmental stressors (Auge, 2001; Evelin et al., 2009), alter soil carbon cycling (Averill et al., 2014; Clemmensen et al., 2013; Rillig and Mummey, 2006), reduce nutrient leaching (Bender et al., 2015; van der Heijden, 2010) and influence tree seedling recruitment and survival (Van Der Heijden and Horton, 2009). Several distinct types of mycorrhizal associations exist which include arbuscular, ericoid, orchid and ectomycorrhizal (Brundrett, 2009; van der Heijden et al., 2015). Arbuscular mycorrhizal (AM) fungi are the predominant and ancestral type of mycorrhiza in vascular land plants and are found across the majority of terrestrial habitats globally (Wang and Qiu, 2006). AM fungal symbioses play a crucial role in plant phosphorus (P) acquisition as they are capable of effectively scavenging P from large volumes of soil (Powell and Rillig, 2018; Smith et al., 2011). They are therefore of great significance to the maintenance of tropical forests, which are thought to be primarily P limited (Camenzind et al., 2018; Camenzind et al., 2019). Ectomycorrhizal (EcM) fungi are a highly diverse group of fungal species (circa 20,000 species) (van der Heijden et al., 2015) and form associations with the

roots of primarily woody perennial plant species (Smith and Read, 2008a; Taylor and Alexander, 2005). Unlike AM fungi, EcM fungi may also scavenge nutrients from soil organic matter via oxidative or enzymatic processes (Corrales et al., 2016; Frey, 2019; Lindahl and Tunlid, 2015; Pellitier and Zak, 2018; Read and Perez-Moreno, 2003; Shah et al., 2016). Although the majority of tropical trees are AM associating (McGuire et al., 2008), all members of the Dipterocarpaceae family (>500 spp.) associate exclusively with EcM fungi (Taylor and Alexander, 2005). Dipterocarps account for 80 % of canopy and 40 % of understorey trees in lowland SE Asian tropical forests (Taylor and Alexander, 2005). Therefore EcM fungi have significant ecological importance to the forest ecology of SE Asia (Brearley, 2012; Brearley et al., 2016).

1.5 The impacts of selective logging and agricultural conversion on soil microbial community structure

Research to date on the biotic impacts of forest disturbance and land clearance from tropical forest to agriculture has focused primarily on aboveground plant and animal communities (Alroy, 2017; Barlow et al., 2007; Barlow et al., 2016), with far less attention paid to soil microbial communities and soil processes (Camenzind et al., 2018). It is likely that forest disturbance and conversion to oil palm also influences microbial community assemblages due to changes and interactions between abiotic, edaphic and aboveground biotic factors, all of which can structure soil microbial communities (Figure 1.8).

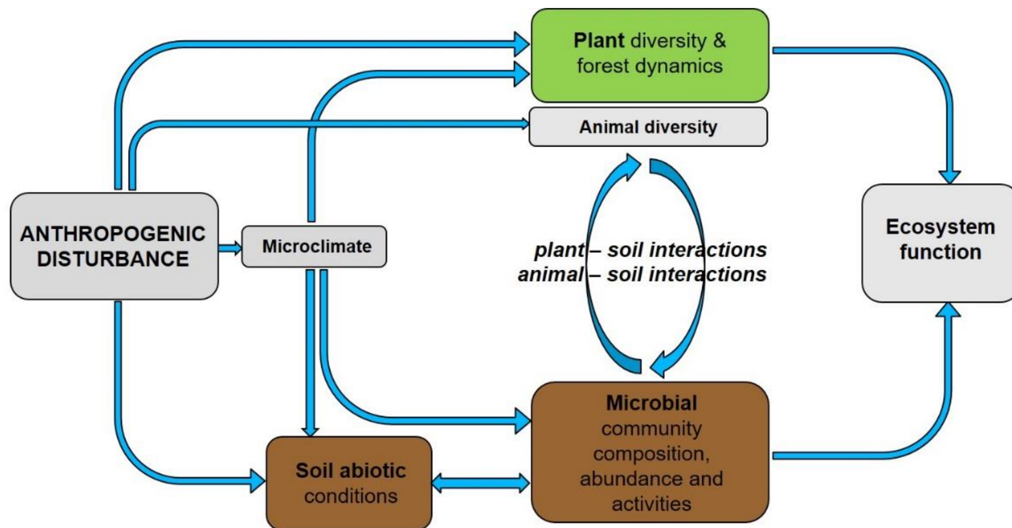

Figure 1.8 *- Simplified schematic diagram showing how anthropogenic disturbance may drive modification to ecosystem function through linkages between soil, plants, animals and microbial communities. Green shaded boxes = aboveground factors. Brown shaded boxes = belowground factors. Grey shaded boxes represent factors, which may operate both above and belowground. Some potential paths and interactions have been omitted for clarity.*

A handful of recent studies have showed that tropical forest clearance for agriculture has substantial but inconsistent effects on bacterial communities (Lee-Cruz et al., 2013; Merloti et al., 2019; Tripathi et al., 2016). Agricultural conversion of tropical forest appeared to increase local diversity (α diversity) of bacterial communities, regulated primarily by shifts in soil pH due to changes in vegetation cover and land management (de Carvalho et al., 2016; Mendes et al., 2015; Tripathi et al., 2012; Wood et al., 2017). However, the effects on community differentiation across space (β diversity) were context dependent (de Carvalho et al., 2016; Lee-Cruz et al., 2013; Rodrigues et al., 2013) and therefore what consequence this has for landscape scale biodiversity is unclear. Land clearance for agriculture strongly shifted soil fungal communities (Brinkmann et al., 2019; Kerfahi et al., 2014; Lan et al., 2020; McGuire et al., 2015; Mueller et al., 2016; Shi et al., 2019a; Song et al., 2019) with limited

evidence for declines in mycorrhizal fungal diversity in rubber and oil palm plantations (McGuire et al., 2015; Song et al., 2019). However, as a whole, the mycorrhizal diversity of tropical ecosystems is particularly understudied (Tedersoo and Smith, 2013; van der Heijden et al., 2015).

The effects of selective logging on soil bacterial and fungal communities appear subtle and variable, with studies showing similar community composition between OG and SL forest (Kerfahi et al., 2014; Lee-Cruz et al., 2013; McGuire et al., 2015; Rodrigues et al., 2013; Tripathi et al., 2016). However, a challenge to characterising soil microbial communities in selectively logged tropical forest is their sheer complexity as they comprise a highly heterogeneous mosaic of disturbed and remnant forest patches, and encompass a wide variation in logging management practices, intensities and recovery times (Blonder et al., 2018; Putz et al., 2019). Protists are an important component of the soil biota and occupy key roles in microbial food webs as consumers of bacteria, fungi and other small eukaryotes (Geisen et al., 2018). However, protists have received far less attention than other components of the soil microbiome and how communities respond to tropical ecosystem disturbance is almost unknown. The single study performed to date was restricted to OG tropical forest, rubber and oil palm plantations and suggest that protist communities may be sensitive to land use change (Schulz et al., 2019b).

1.6 Drivers of microbial communities across human modified tropical forests

Although soil microbial communities have recently been characterised across a number of tropical ecosystems, there is a need to better define the abiotic and biotic drivers of variation in soil microbial communities, particularly across complex, human modified tropical forest landscapes. Even the principal mechanisms controlling microbial community variation within the tropics are poorly understood (Pajares et al., 2016). This will not only allow for better predictions of microbial responses to future disturbances and environmental change, but may also inform strategies for effective future forest restoration.

At large spatial scales, climate and soil properties are the primary drivers structuring soil microbial communities (Bates et al., 2012; Fierer and Jackson, 2006; Tedersoo et al., 2014). However, complex plant-microbial interactions may also act as strong local controls on microbial community structure and function (Van Der Heijden et al., 2008; Wardle et al., 2004). Logging driven changes to tropical tree species composition may influence the diversity and activity of symbiotic rhizobia (Wurzburger and Hedin, 2016) and mycorrhizae (Peay et al., 2010). Tree species shifts may also indirectly influence soil microbial communities as tree species differ in traits that effect the local soil environment such as the composition and quantity of litter inputs, fine root biomass and root exudates (Russell et al., 2018). To date there is limited and conflicting evidence for whether there are linkages between the taxonomic and functional diversity of tree and microbial communities in tropical forests (Bachelot et al., 2016a; Barberán et al., 2015; McGuire et al., 2012; Schappe et al., 2017).

Soil fauna may also interact with microbial communities, influencing their distribution and function (Crowther et al., 2013; Grandy et al., 2016). In tropical forests, ants and termites occupy keystone positions as “ecosystem engineers”, exerting a disproportionate influence on ecosystem stability and functioning relative to their abundance (Folgarait, 1998; Jouquet et al., 2011). Both ants and termites play crucial roles in organic matter decomposition, nutrient redistribution and recycling (Griffiths et al., 2019; Griffiths et al., 2018). Through the removal of detritus from the forest floor and subsequent transport to nests, ants and termites may create localised soil nutrient hotspots and areas of depletion, potentially influencing fungal foraging behaviour and microbial decomposer assemblages (Ackerman et al., 2007; Griffiths et al., 2018). As omnivores, ants may also exert top down control on fungal communities by grazing on fungal hyphae or predating other fungal consumers such as collembola and mites (Wilson, 2005). Termites mechanically fragment plant material with their mandibles, thus increasing surface area available for microbial decomposers (Jouquet et al., 2011) and are also critical to the breakdown of woody necromass and coarse woody debris (Yamada et al., 2005). Termites chemically alter woody fibres (breakdown of lignocellulose) via endosymbionts and endogenous cellulases (Bignell, 2011), thus occupying a functional niche with strong potential impacts on saprotrophic microbial activity. Forest disturbance strongly influences both ants and termites with declines in species richness, abundance and altered distributions (Donovan et al., 2007; Ewers et al., 2015; Jones et al., 2003) but how disturbance driven shifts in tropical forest ant and termite assemblages may interact with and influence microbial community dynamics is completely unknown.

1.7 Functional implications of microbial community structure in tropical ecosystems and their resilience to future climate extremes

Given the crucial role of microbial communities in the provision of ecosystem functions, it is critically important to determine whether any shifts in soil microbial assemblages are consequential for ecosystem process rates. It has long been assumed that the inherently high diversity of soil biotic communities would confer functional redundancy (whereby metabolic functions can be performed by multiple coexisting and taxonomically distinct organisms) (Allison and Martiny, 2008; Louca et al., 2018; Nannipieri et al., 2003). However, recent studies from temperate ecosystems suggests that microbial compositional shifts can be associated with changes to ecosystem process rates (Allison et al., 2013; Delgado-Baquerizo et al., 2016a; Delgado-Baquerizo et al., 2016b; Wagg et al., 2014). Few studies have examined the functional implications of microbial community shifts in tropical ecosystems and addressed whether microbial communities are functionally dissimilar between undisturbed and disturbed forests (Kroeger et al., 2020; Lan et al.; Merloti et al., 2019; Tripathi et al., 2016; Waldrop et al., 2000). Recent studies have shown that conversion of Amazonian rainforest to agriculture altered the abundance of microbial N-cycling genes and stimulated methanogenesis (Kroeger et al., 2020; Merloti et al., 2019). However, linking soil microbial communities to ecosystem functions remains a grand challenge in ecology (Hallin and Bodelier, 2020; Stein and Nicol, 2011) and whether soil microbial community – ecosystem function relationships exist more generally across tropical ecosystems remains largely unresolved.

A further challenge to our understanding of the functional role of soil microbial communities in tropical ecosystems, is to determine whether the composition of

microbial communities across land uses influences their resistance (degree of insensitivity to disturbance), resilience (rate of recovery following disturbance towards a pre-disturbance state) or sensitivity (inverse of resistance – degree of transition to an alternative stable state following disturbance) to future climate extremes. This is important as climate change is driving increased spatio-temporal variability in global precipitation patterns, with more intense drought periods interspersed with heavy precipitation (Cai et al., 2014; Dai, 2013; Fischer and Knutti, 2016). This is likely to be further amplified in tropical regions, where reductions in tropical forest cover have already led to elevated air temperatures and reduced precipitation totals (Kumagai et al., 2013; McAlpine et al., 2018). Differences in land use driven environmental factors such as understorey microclimate and soil physico-chemical conditions may influence microbial resistance and resilience, by selecting for certain taxa with environmental preferences and life histories (Bardgett and Caruso, 2020; Bouskill et al., 2013). This may drive differential responses in ecosystem process to drought and rewetting events across tropical land uses. Although studies have shown microbial metabolic responses to drought in tropical forests (Bouskill et al., 2016; Waring and Hawkes, 2015) and effects on soil greenhouse gas (GHG) production (Davidson et al., 2004; van Haren et al., 2005), whether tropical microbial community responses to drought are influenced by drought intensity or diverge across tropical land uses is not known.

1.8 Thesis aims and objectives

This thesis aimed to explore knowledge gaps in our understanding of the abiotic and biotic drivers structuring soil microbial assemblages across human modified tropical forests, the nature of interactions between key invertebrates and soil microbes and how forest modification and land use change (degradation and conversion to oil palm

plantations) impacts upon on soil microbial community composition, function and resilience to climate extremes.

Specifically I aimed to address the following research questions:

1. Does selective logging influence soil microbial communities and what factors structure soil microbial communities across human modified tropical forests? (Chapter 2).
2. Do ants and termites regulate microbial community structure and function in OG tropical forest? (Chapter 3).
3. Are soil microbial communities functionally equivalent or dissimilar across a tropical land use gradient? (Chapter 4).
4. Does the resistance and resilience of soil microbial communities to climate extremes vary across a tropical land use gradient? (Chapter 5).

This thesis addressed the scientific questions using field surveys, existing *in situ* ecological manipulations and *ex situ* laboratory incubations and consisted of 4 research chapters with the following objectives:

1. To conduct a field soil survey across 8 OG and SL tropical forest plots for the characterisation of soil bacterial, protistan and fungal communities, quantification of microbial abundance and measurement of abiotic soil properties. These data were combined with existing tree species, trait and productivity census data collected during the Natural Environment Research Council funded *Biodiversity and Land Use Impacts on Tropical Ecosystem Function* (BALI) project.
2. To conduct high resolution soil sampling across *in situ* invertebrate exclusion and control treatment plots in OG forest for the characterisation of soil microbial communities and soil properties. Soil microbial communities were characterised using high throughput sequencing.
3. To collect soil and litter mixtures across a tropical land use disturbance gradient from OG forest to oil palm plantation and conduct an *ex situ* litter decomposition laboratory incubation experiment. Measurements of microbial decomposer communities were made using high throughput sequencing and phospholipid fatty acid biomarker techniques.
4. To collect intact soil cores from the 3 dominant tropical land uses (OG forest, SL forest and oil palm) and conduct an *ex situ* drought-rewetting laboratory incubation experiment. Measurements of soil greenhouse gas emissions (CO_2, CH_4, N_2O) were taken prior to and following rewetting to determine the resistance and resilience of microbial activity. These measurements were combined with soil properties and measures of nutrient availability to identify predictors of microbial responses to drought-rewetting across land uses.

2 Impacts of selective logging on tropical forest soil microbial communities

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2.1 Abstract

Understanding how the effects of land-use change on plant communities affect soil microbial communities remains a key challenge in ecology, especially in tropical forests where selective logging has strongly modified tree species distributions. We investigated the impact of selective logging on soil microbial assemblages in Malaysian Borneo and determined the relative influence of tree community characteristics, tree traits and soil properties as determinants of soil microbial community structure. Whilst bacterial communities were similar between old growth (OG) and selectively logged (SL) forest, protistan and fungal communities were distinct. Logging strongly reduced the relative abundance, diversity and heterogeneity (β-diversity) of ectomycorrhizal (EcM) fungal communities. Variation in bacterial and protistan community composition was best predicted by soil properties (pH, inorganic phosphorus and bulk density) and tree traits (hemicellulose, foliar N and P). Tree community characteristics explained additional variation in fungal communities, whilst the basal area of EcM host trees was positively and negatively associated with the relative abundance of EcM and arbuscular mycorrhizal fungi respectively. These findings demonstrate the importance of logging driven changes to forest vegetation as

drivers of soil microbial community structure and highlight the sensitivity of soil fungal communities to logging. Shifts in saprotrophic fungal communities may influence rates of organic matter decomposition whilst declines in EcM abundance could reduce belowground C transport in SL forests decreasing soil C storage. Moreover, reduced EcM abundance in SL forests may control the rate and extent of forest recovery by reducing dipterocarp seedling survival and thus may be important to inform management strategies for tropical forest restoration.

2.2 Introduction

Tropical rainforests hold over 60 % of global plant and animal species (Dirzo and Raven, 2003). However, over recent decades, logging, fire and agricultural expansion have reduced their global extent and ecological intactness, with severe impacts upon biodiversity (Gibson et al., 2011). The situation is particularly acute across tropical forests of South East Asia where high rates of timber extraction and land clearance for oil palm and other plantation cultivation has resulted in greater relative rates of forest degradation and deforestation than in other tropical regions (Achard et al., 2002; Fitzherbert et al., 2008; Sodhi et al., 2004). Whilst the effects of land-use change on aboveground tropical diversity have been studied extensively (Alroy, 2017; Barlow et al., 2007; Barlow et al., 2016; Laurance et al., 2012), the resistance and resilience of soil biotic communities has only recently begun to be investigated (Kerfahi et al., 2014; Lee-Cruz et al., 2013; McGuire et al., 2015; Mueller et al., 2016; Tripathi et al., 2016). This is of central importance given the crucial role that soil microbial communities play in mediating multiple ecosystem functions such as net primary production, litter decomposition, nutrient cycling, biosphere-atmosphere trace gas exchange and carbon sequestration (Van Der Heijden et al., 2008).

Ecosystem disturbance can have persistent impacts on microbial communities, with consequences for the ecosystem processes that they govern (Allison and Martiny, 2008; Griffiths and Philippot, 2013; Shade et al., 2012). In the tropics, conversion from forest to agriculture leads to substantial but inconsistent shifts in bacterial and fungal communities, whilst the effects of selective logging are variable and more subtle (Kerfahi et al., 2014; Lee-Cruz et al., 2013; McGuire et al., 2015; Rodrigues et al., 2013; Tripathi et al., 2016). The greater variability of logging impacts on microbial communities may be due to the complexity of selectively-logged (SL) tropical forests, which comprise a highly heterogeneous mosaic of disturbed and remnant forest patches, and encompass a wide variation in logging management practices, intensities and recovery times (Blonder et al., 2018; Putz et al., 2019).

Logging activities can alter soil properties and nutrient availability through direct mechanical disruption and compaction (DeArmond et al., 2019; Frey et al., 2009; Hartmann et al., 2012) or indirectly by modifying tree communities through the selective removal of economically valuable species. Tree species differ in their effects on the local soil environment, due to variation in the composition and quantity of litter inputs, fine root biomass and root exudates (Russell et al., 2018). As soil properties are strong controls on the distribution of microbial populations, this alone may shift microbial community composition (Bahram et al., 2015; Bates et al., 2012; Fierer and Jackson, 2006; Tedersoo et al., 2014). For example, soil pH has been shown to be important in structuring bacterial and protistan communities in tropical ecosystems (Schulz et al., 2019a; Tripathi et al., 2012). Fungi appear to be more weakly associated with soil pH but have stronger associations with climatic factors (Tedersoo et al., 2014) and altered nutrient availability, which can modify facultative host-microbe interactions such as arbuscular (AM) and ectomycorrhizal (EcM) fungal

symbioses (Albornoz et al., 2016a; Albornoz et al., 2016b), saprotrophic (Kerekes et al., 2013) and pathogenic fungi (Tedersoo et al., 2016).

Microbial communities may also be influenced by selective logging due to a coupling between above and belowground biodiversity (Van Der Heijden et al., 2008; Wardle et al., 2004). Changes to tree species composition and distribution may affect the diversity and abundance of symbiotic rhizobia (Batterman et al., 2018; Wurzburger and Hedin, 2016). However, plant-microbial relationships are most frequently reported in fungal communities, such as mycorrhizal and plant pathogenic fungi due to some level of host specificity or plant-soil feedbacks (Mommer et al., 2018; Peay et al., 2010). Most tropical trees form AM symbioses (Sheldrake et al., 2018). However, a minority form EcM associations and are often associated with local monodominance (Peh et al., 2011). The mycorrhizal ecology of lowland tropical rainforests in SE Asia is unique as, within a hyper-diverse assemblage of AM plants and trees, the canopy is often dominated by a subset of commercially valuable tree species from the Dipterocarpaceae family, all of which form EcM associations (Brearley, 2012). There is limited evidence showing that EcM fungal communities in dipterocarp forests may be sensitive to selective logging (Kerfahi et al., 2014; McGuire et al., 2015). However, it is unknown how AM fungi respond to logging disturbance. Understanding the impact of selective logging on mycorrhizal communities in typically P limited tropical forests is of particular importance as mycorrhizas may enhance plant P uptake, by regulating acquisition of P from inorganic and organic P sources (Condit et al., 2013; Liu et al., 2018), and also influence rates of tree mortality (Bachelot et al., 2017), promoting tree species co-existence and potentially species diversity.

Evidence to support an association between above and belowground biodiversity in forests is limited (Prescott and Grayston, 2013), with some studies showing linkages (Bachelot et al., 2016b; Barberán et al., 2015; Schappe et al., 2017) whilst others show independence (McGuire et al., 2012; Talbot et al., 2014). A number of ecological factors may drive this uncertainty. Local environmental conditions can strongly shape both plant and microbial communities (Bates et al., 2012; Griffiths et al., 2011; Laliberté et al., 2014; Tedersoo et al., 2014). However, if these act independently on above and belowground communities, this would likely confound any association. For example, soil pH is a strong driver of bacterial community composition (Fierer and Jackson, 2006; Griffiths et al., 2011). However, this may or may not drive patterns in plant communities depending on local environmental conditions (Palpurina et al., 2017). Tree functional traits, which may not be strongly phylogenetically conserved, can be important predictors of microbial community composition (de Vries et al., 2012; Sayer et al., 2017). However, few studies have investigated the linkage between plant functional traits and microbial assemblages in tropical forests. In a Panamanian tropical forest, leaf traits were not found to be strong predictors of microbial community composition (Barberán et al., 2015). Resolving the relative importance of interacting above-belowground factors controlling microbial community composition is a central question in community ecology as a greater mechanistic understanding allows for improved model predictions of microbial responses and ecosystem functions to future land-use and climatic change.

To assess whether selective logging of tropical forests altered soil microbial communities we used amplicon sequencing to taxonomically characterize bacteria, protistan and fungal communities and phospholipid fatty acids (PLFA) as a proxy for microbial abundance across old-growth (OG) and SL forest plots in Borneo. To

determine the relative importance of above and belowground drivers of microbial community composition we measured soil exchangeable nutrients and soil physico-chemical properties, censused the taxonomic identity, biomass and productivity of tree communities within plots and measured a comprehensive suite of tree functional traits (Both et al., 2019; Riutta et al., 2018). Using these datasets, we tested the hypotheses that:

1) Soil microbial communities would differ between OG and SL forest but fungal communities would shift more due to stronger purported linkages between fungi and aboveground plant communities relative to bacteria in tropical forests.
2) Community-weighted mean (CWM) plant traits and tree community characteristics would explain additional variation in soil microbial community composition across OG and SL forests, in addition to that explained by soil properties.

2.3 Materials and Methods

2.3.1 Research sites

The study was conducted in Sabah, Malaysian Borneo. The climate is tropical and aseasonal with a mean annual temperature of 26.7 °C and mean annual precipitation of 2600-3000 mm (Walsh and Newbery, 1999). We sampled eight long term 1 ha research plots distributed across two forest types; OG and SL lowland, dipterocarp tropical forests that are part of the pantropical Global Ecosystems Monitoring (GEM) Intensive Carbon Plot network (http://gem.tropicalforests.ox.ac.uk/) (Riutta et al., 2018) (Figure 2.1).

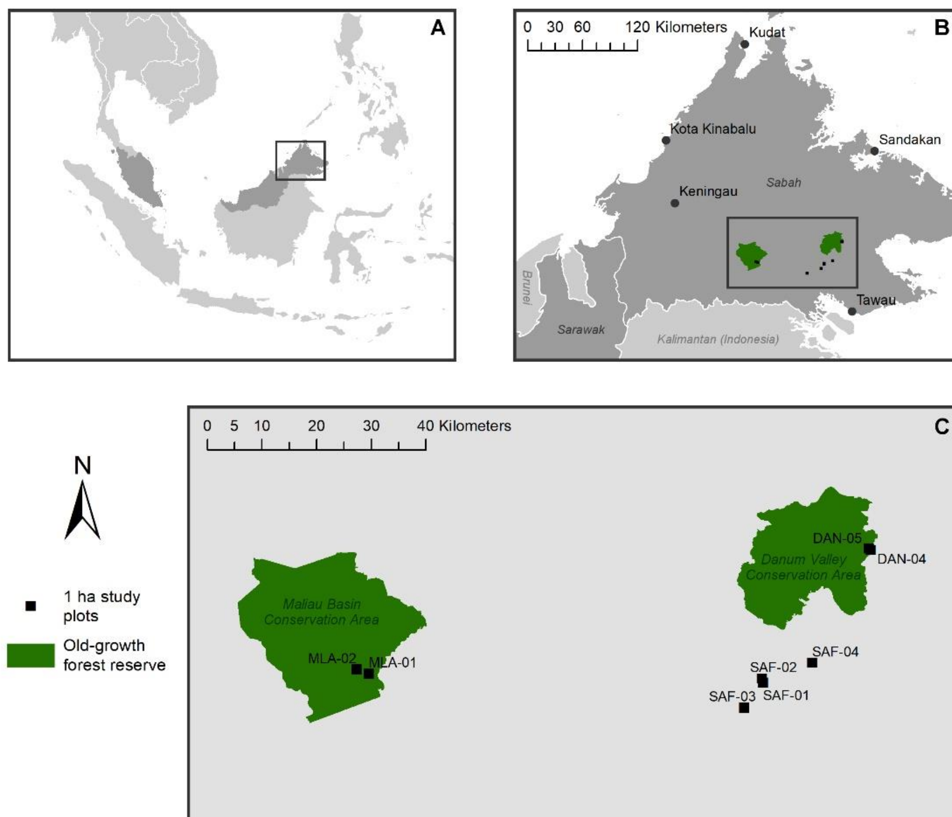

Figure 2.1 *- Map of eight sampling locations A) in northern Malaysian Borneo B) in the state of Sabah, C) with four 1 ha study plots situated within old-growth forest (DAN-04, DAN-05, MLA-01 and MLA-02), four in selectively-logged forest (SAF-01, SAF-02, SAF-03, SAF-04).*

Each 1 ha forest plot was treated as an independent sampling unit. To account for within plot variation, each plot was further subdivided into 25 20 x 20 m subplots with three being randomly selected for soil sampling, CWM trait measurements and identification of tree community composition. These subplots were nested within plots and are treated as pseudo replicates due to geographical proximity to one another. This non-independence is accounted for in all statistics performing comparisons in parameters between OG and SL forest plots (see 2.3.7 for details). Samples representative of OG dipterocarp forest were taken from four plots; two (DAN-04 and DAN-05) are within the 438km^2 Danum Valley Conservation Area (DVCA) (4°6'N, 117°4'E) and two (MLA-01 and MLA-02) are from the 588km^2 Maliau Basin Conservation Area (MBCA) (4°5'N, 116°5'E). DVCA has experienced little disturbance and has been protected since 1976 (Marsh and Greer, 1992). MBCA was protected under law in 1981. Samples from SL forest were taken from four plots covering a range of logging intensities. Two plots were twice-logged (SAF-03, SAF-04) and two four times-logged (SAF-01, SAF-02). All formed part of the Stability of Altered Forest Ecosystems (SAFE) project within the Kalabakan Forest Reserve (Ewers et al., 2011). This area has been logged up to four times with the first round of logging in the mid-1970s and subsequent repeated logging rounds between 1990-2008. Approximately 150-179 m^3 ha^{-1} of timber, predominantly from trees within the Dipterocarpaceae family, were removed over this time period (Struebig et al., 2013), which is higher than the mean extraction volume across other lowland dipterocarp forests of Sabah and South East Asia (100-152 m^3 ha^{-1}) (Curran et al., 2004; Fisher et al., 2011b).

2.3.2 Soil sampling and chemical analysis

Soil sampling was conducted in March 2015. Within each 1 ha plot, three 20×20 m subplots were randomly selected. Five soil samples were collected with a 3 cm diameter gouge auger within each subplot. The organic soil layer depth was measured, separated from the underlying mineral soil, sealed in a plastic bag and transported to a field laboratory. An additional soil sample was taken for bulk density using a volumetric ring (7.5 cm diameter) with bulk density determined using the oven-dried soil weight (dried at 105 °C for 24 hours) after removal of roots and stones (Emmett et al., 2008). Soil samples were homogenised by hand and a subsample taken, frozen at -20 °C on the day of collection and subsequently transported on ice to the UK Centre for Ecology & Hydrology, for microbial analysis. The remaining soils were bulked (n=1 per subplot) and analyzed at the Forest Research Centre, Sepilok, Sabah. pH was measured on fresh soils using a pH meter in a soil water suspension (1: 2.5 ratio of soil to deionised water) after shaking overnight at 100 rpm on an orbital shaker followed by standing for 30 min (Landon, 1984). Soils were air dried at 40 °C, passed through a 2 mm sieve and milled to a fine powder using a mortar and pestle. Subsamples for total C and N analysis were dried at 65 °C for 48 hours and ground as above. Total C and N was determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany). A Bray No. 1 extractant was used to extract inorganic P (Bray and Kurtz, 1945) and Total P was extracted using a mixed acid (sulphuric-nitric-perchloric) (Allen, 1989). The P contents in the extracts and digests were determined using the molybdenum-blue method and read at 880 nm on a spectrophotometer (Hitachi UV-VIS, Japan)

(Anderson and Ingram, 1993). Soil texture (% Sand, Silt & Clay) was determined using the pipette method (Miller and Miller, 1987).

2.3.3 Soil phospholipid fatty acid extraction and analysis

PLFA's were extracted from freeze-dried soils as part of the total lipid extract using a modified Bligh-Dyer extraction (White et al., 1979). Identification of PLFA's was carried out on a GC (Agilent Technologies 6890) fitted with a flame ionization detector (Agilent Technologies 5973). Sample PLFA peaks were identified based on known relative retention times. The terminal and mid-chain branched fatty acids C15:0i, C15:0a, C16:0i C17:0i, and C17:0a were used as indicators of Gram positive bacteria (Whitaker et al., 2014). Cyclopropyl saturated and monounsaturated fatty acids 16:1ω7c, 7,8 cyclic C17:0, C18:1ω7c, and 7,8 cy-C19:0 were used as indicators of Gram negative bacteria (Rinnan and Bååth, 2009). The fatty acids C18:2ω6,9c and C18:1ω9c were taken as indicators of fungi (Willers et al., 2015). Total microbial biomass was calculated as the sum of all identified PLFA's (C13:0, C14:0, C14:1ω5c, C15:0, C15:1ω5c, C16:0, 10Me-C16:0, C16:1ω7t, C16:1ω9c, C16:1ω5c, C17:0, 10Me-C17:0, C18:0i, C17:1ω7c, C18:0a, C18:0, 10Me-C18:0, C18:1ω7t, C18:1ω12c, C18:1ω5c, C18:2ω6t, 9,10-cyC19:0, C19:1ω12c, C20:0, C18:3ω6c, C20:1ω9c, C18:3ω3c, C20:2ω6c, C22:0, C20:3ω6c, C20:4ω6c, C20:5ω3c, C24:0; plus those listed above).

2.3.4 *In situ* measurements of soil exchangeable nutrients

Within each 1 ha plot, ion exchange membranes (PRS^{TM} Probes, Western AG, Saskatoon, Canada) were installed in three 20×20 m subplots (same as described above) to measure the availability of NO_3^-, NH_4^+, P, K, S, Ca, Mg, Fe, Mn, Cu, Zn, B and Al ions (Qian and Schoenau, 2002). These act as dynamic exchangers in soils and

provide a net measure of exchangeable soil nutrient pools. To account for spatial variability we installed four probe pairs (each pair consisting of one cation and one anion probe) vertically in corners of 50x50 cm quadrats to 10 cm depth and replicated these 3 times within each subplot (co-located with 3 of the soil sampling locations). These were collected after 2 weeks, washed thoroughly with distilled water in the field and in the laboratory and then shipped to the manufacturer for analysis. The four probe pairs from each quadrat were pooled prior to elution with 0.5 M HCl for 1 hour. NO_3^- and NH_4^+ were measured colorimetrically using automated flow injection analysis (FIA). All other elements were analyzed using inductively coupled plasma-optical emission spectroscopy (ICP-OES). Results are reported as supply rates per area of membrane available for ion exchange over the burial period (µg/10 cm^2/14 days).

2.3.5 Molecular analyses of soil microbial communities

DNA was extracted from 0.2 g soil using a Powersoil® DNA Isolation Kit according to the manufacturer’s instructions. Amplicon libraries were constructed according to a dual indexing strategy with each primer consisting of the appropriate Illumina adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker and the amplicon specific primer (Kozich et al., 2013). For bacteria, V3-V4 16S rRNA amplicon primers were used (CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC) (Kozich et al., 2013). For eukaryotes, the 18S rRNA gene was targeted using amplicon primers AACCTGGTTGATCCTGCCAGT and GCTATTGGAGCTGGAATTAC (Baldwin et al., 2005) and fungi were targeted by amplifying the ITS2 region using primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). We acknowledge that using ITS2 primers is suboptimal for the identification of Glomeromycota (Hart et al., 2015). However, they can provide good estimates of AM

fungal community structure and relation to environmental variables within sample types (Berruti et al., 2017). Amplicons were generated using a high fidelity DNA polymerase (Q5 Taq, New England Biolabs). After an initial denaturation at 95 °C for 2 minutes, PCR conditions were as follows: denaturation at 95 °C for 15 seconds; annealing at temperatures 55 °C, 57 °C and 52 °C for 16S, 18S and ITS reactions respectively; annealing times were 30 seconds with extension at 72 °C for 30 seconds; cycle numbers were 25 for 16S and ITS, and 30 for 18S; a final extension of 10 minutes at 72 °C was included. Amplicon sizes were determined using an Agilent 2200 TapeStation system and libraries normalized using SequalPrep Normalization Plate Kit (Thermo-Fisher Scientific) and quantified using a Qubit dsDNA HS kit (Thermo-Fisher Scientific). Each amplicon library was sequenced on an Illumina MiSeq using V3 600 cycle reagents at concentrations of 8 pM with a 5 % PhiX Illumina control library. Sequencing runs produced in excess of 21, 18 and 16 million reads passing filter for 16S, ITS and 18S amplicons respectively.

Sequences were processed in R using DADA2 to quality filter, merge (where appropriate), de-noise and assign taxonomies (Callahan et al., 2016). Briefly, 16S and 18S amplicon forward reads were trimmed to 250 and 280 bases respectively, and ITS amplicons reads were trimmed to 225 and 160 bases, forward and reverse respectively. Filtering settings were maximum number of Ns (maxN) = 0, maximum number of expected errors (maxEE) = 1. Sequences were dereplicated and the DADA2 core sequence variant inference algorithm applied. ITS sequences were merged using the *mergePairs* function, whilst forward reads were used for 16S and 18S amplicons. Chimeric sequences were removed using *removeBimeraDenovo* default settings. The actual sequence variants (ASV) were subject to taxonomic assignment using *assignTaxonomy* at default settings; the training databases used were

GreenGenes v13.8, Protist Ribosomal Reference database (PR^2) v4.12.0 and Unite v7.2 for 16S, 18S and ITS respectively. The 18S library was filtered to exclude all non protist sequences by removing unclassified Opistokhonta, Streptophyta, Chlorophyta, Fungi and Metazoa. Prior to analysis, low prevalence taxa were filtered (only taxa detected in at least 3 out of 120 samples were retained) and normalized by rarefying to 5917, 161 and 4698 reads for 16S, 18S and ITS respectively. To assess relationships between microbial community composition and environmental variables measured at the subplot scale, the sample reads from each subplot (n=5) were merged using the *merge_samples* function in the phyloseq R package. Sequences have been deposited at the European Nucleotide Archive (ENA) under project accession number PRJEB36080.

2.3.6 Measurement of plant traits and tree community characteristics

Within each selected subplot (n=24), every individual stem with a diameter at breast height (DBH) of ≥10 cm was identified and measured for a comprehensive set of plant functional traits (Both et al., 2019). A subset of fifteen traits were included here describing branch wood density, leaf morphology and cellular structure (branch wood density, specific leaf area, leaf dry matter content, leaf toughness, leaf thickness, hemicellulose, cellulose, lignin and recalcitrant fibres) and leaf elemental chemistry (foliar C, N, C:N, P, K, Mg, Ca). These traits were selected based on their potential effects on belowground microbial communities: branch wood density, leaf morphology and cellular structure may control resource availability to decomposers whilst the elemental chemistry of leaf litter may determine the extent of soil nutrient heterogeneity. For each selected subplot, stem density, tree species richness, Shannon diversity, total tree basal area and the basal area of putative EcM host trees

(Dipterocarpaceae and Fagaceae families) were calculated. Subplot total litterfall and woody net primary productivity (NPP) (aggregated for all trees ≥10 cm dbh within subplot) was measured during 2011-2016 over a 24 month period as part of the GEM intensive monitoring protocol (Riutta et al., 2018). Aboveground C stocks were estimated using allometric equations for moist tropical forests with diameter, height and wood density as inputs (Chave et al., 2005). Leaf area index (LAI) was calculated from hemispherical photographs at the centre of each subplot (Riutta et al., 2018). The subplot design implemented here allowed for the fine scale taxonomic and trait identification of trees allowing correlative analyses between tree community characteristics, CWM traits and microbial communities.

2.3.7 Data Analyses

Subplot CWM values (i.e. subplot-level trait values weighted by a measure of tree species abundance) for each trait were calculated using tree basal area as a measure of abundance (Etienne Laliberté et al., 2014; Pla et al., 2011). This was done by multiplying trait values for the species that occur within each subplot by their basal area, summing these values and then dividing by the sum of species basal area values. This calculation is a useful way to calculate community trait values weighted by abundance (in this case basal area) of species in a community. To visualize the distribution of soil properties and CWM traits across OG and SL forest plots, principal component analyses were performed after scaling by unit variance and zero centering. Where necessary, variables were log-transformed in order to improve their fit to a normal distribution. Tree community composition was represented by non-metric multidimensional scaling (NMDS). This was performed on Bray-Curtis dissimilarities calculated from a subplot × tree species matrix using basal area as a measure of importance. To aid interpretation, vectors of soil properties, CWM traits and tree

community characteristics with significant ($p < 0.05$) correlation to the first two ordination axes were plotted using the *envfit* function in the *Vegan* R package. Non parametric (permutational) multivariate analysis of variance (PERMANOVA) was performed using the *nested.npmanova* function in the BiodiversityR package (99,999 permutations) to evaluate the effect of forest type on soil properties, CWM traits and tree community composition. This function accounts for the nesting of subplots within plots by estimating the correct F-ratio for the main and nested factors (assuming the nested factor is random) and using the recommended permutation procedures to test the significance. The significance of the F-ratio of the main factor (plot) is tested by permuting entire blocks belonging to levels of the nested factor. The significance of the F-ratio of the nested factor (subplot) is tested by permuting sample units within strata defined by levels of the main factor (Kindt, 2019).

Fungal taxa were assigned to ecological guilds (EcM, AM, saprotrophic and pathogenic) using FunGuild (Nguyen et al., 2016). Only those taxa with non-ambiguous classifications and assignments classified as “probable” or “highly probable” were retained for further analysis (see Appendix 1: Table 8.2, Table 8.3, Table 8.4 and Table 8.5 for a complete list of fungal genera assigned to each ecological guild). To test the similarity of OG and SL microbial community composition (hypothesis 1), Bray-Curtis dissimilarities for bacteria, protists and fungal groups were calculated using square-root transformed actual sequence variant (ASV) counts and visualized using NMDS. We used a nested PERMANOVA as described above to test for differences in microbial community dissimilarity between OG and SL forest whilst accounting for nesting of subplots within plots. Differences in the heterogeneity of microbial communities within OG and SL forest was tested using the PERMDISP2 algorithm (Anderson et al., 2006). Microbial richness and

Shannon diversity was calculated from rarefied ASV counts for each microbial group and the relative abundance of fungal functional groups was calculated as the percentage of sequence reads assigned to functional groups relative to the total sample reads. The differences between forest types were tested using linear mixed effects models. Plot was included as a random term to account for the nested sampling design of subplots within plots and significance was assessed using F-tests implementing the Satterthwaite denominator degrees of freedom approximation. Homogeneity of variances between OG and SL forest was tested using Fligner-Killeen tests.

To examine the relative importance of drivers of microbial community composition (hypothesis 2) we used distance-based redundancy analysis (db-RDA) and performed variation partitioning (Peres-Neto et al., 2006). Tree community characteristics were represented by the two NMDS axes describing variation in tree community composition, subplot tree basal area, aboveground C stocks, woody net primary productivity (NPP), stem density, subplot basal area of EcM host trees, tree species richness, Shannon diversity, LAI and total litterfall. Within groups of measured variables (soil properties, CWM traits and tree community characteristics), those highly correlated ($r \geq \pm 0.7$) were removed a-priori by inspecting correlograms (See Appendix 1: Figure 8.1, Figure 8.2 and Figure 8.3 for correlograms reflecting final variable selection). For each variable group, the best subset of predictors was chosen via forward selection using the ordiR2step function in *vegan* implementing the double stopping criteria proposed by Blanchet et al. (2008). Variation partitioning was then conducted using db-RDA and adjusted R^2 (Peres-Neto et al., 2006). The significance of unique fractions was tested using partial redundancy analysis. All p-values were generated using 9999 permutations. To assess relationships between EcM fungi, AM fungi and host trees, the total basal area of EcM host species was summed within each

subplot (See Table 8.1 for a complete list of genera included). Linear regression was used to determine the relationship between mycorrhizal relative abundance, richness, Shannon diversity and EcM host tree basal area within subplots. Significance was assessed using linear mixed effect models as described above. Model R^2 was calculated following the method of Nakagawa and Schielzeth (2013). All analyses were conducted using R version 3.5.2 and packages Phyloseq, lme4, MuMin, labdsv and vegan.

2.4 Results

2.4.1 Site characteristics, soil properties, CWM traits and tree communities

Study plots varied in altitude with OG forest plots at lower elevation (222–299 m) than SL forest plots (368-576 m) (Table 2.1). Average slope angle differed between individual plots but did not differ systematically between OG and SL forest plots (Table 2.1). Soils in all plots were characterized as orthic acrisols with similar soil texture (sandy loam or sandy clay loam) but varied in soil moisture, temperature and key soil properties (Bulk density, pH and soil carbon (C)). pH and soil C did not differ systematically between plots of OG and SL forest although C was higher in SAF-04 relative to all other plots (Table 4.1). The magnitude of variation in soil moisture (22.1-33.5 %) and temperature (24.2-25.5 °C) between plots was small. The only soil property to vary between OG and SL forest plots was bulk density (Table 2.2).

Multivariate analysis (PCA) of soil properties and CWM traits showed clustering by study plots (PERMANOVA Soil: $F_{7,23} = 4.99$, $p = <0.001$, $R^2 = 0.69$; CWM: $F_{7,23} = 2.55$, $p = <0.001$, $R^2 = 0.53$) but did not differ significantly by forest type (PERMANOVA Soil: $F_{1,6} = 3.42$, $p = 0.18$, $R^2 = 0.13$; CWM: $F_{1,6} = 1.64$, $p = 0.60$, $R^2 = 0.07$) (Figure 2.2). However, heterogeneity in soil properties was higher in SL forest relative to OG (PERMDISP2, $F_{1,23} = 6.15$, $p = 0.04$) (Figure 2.2). Tree community composition was significantly different between OG and SL forest (Figure 2.3) ($F_{1,6} = 2.63$, $p = 0.03$, $R^2 = 0.11$). LAI was higher in OG forest ($F_{1,6} = 25.28$, $p = 0.002$) whilst woody NPP ($F_{1,6} = 6.73$, $p = 0.04$) was higher in SL forest. Subplot basal area and aboveground C stocks were also marginally significantly higher in OG relative to SL subplots (Basal Area: $F_{1,6} = 3.69$, $p = 0.07$, C Stock: $F_{1.6} = 5.11$, $p = 0.06$) (Table 2.4).

Table 2.1 *- Characteristics of the study plots. Mean of individual subplots ±1 SD. Soil textural class was calculated from measured percentage sand, silt and clay. Soil type was taken from descriptions of study areas in Marsh and Greer (1992) and Nainar et al. (2015). In each subplot slope was measured using a handheld clinometer and altitude was determined using a GPS barometric altimeter. Soil moisture and temperature were logged at hourly intervals between September 2015 and May 2016 using DeltaT SM200 probes buried horizontally to 5cm depth. Superscript letters denote whether parameters were significantly different between study plots from Tukey's HSD test. Significant differences (p <0.05) between plots are indicated when letters are different. Non – significant differences (P >0.05 between plots are indicated when letters are shared. MBCA = Maliau Basin Conservation Area; DVCA = Danum Valley Conservation Area, SAFE = SAFE project area within the Kalabakan Forest Reserve.*

Location	Forest Type	Plot Code	Soil type	Soil texture	Soil Bulk Density (g cm^{-3})	Soil pH	SOC (%)	Altitude (m)	Slope (°)	Soil Moisture (%)	Soil Temperature (°C)	Mean Annual Rainfall (mm)
DVCA	OG	DAN-04	Orthic Acrisol	Sandy Clay Loam	^{cd}0.59 (0.14)	^{a}6.83 (0.32)	^{b}5.86 (2.61)	^{e}237 (7)	^{ab}26 (7)	^{a}33.5 (5.7)	^{a}25.5 (0.8)	3052
DVCA	OG	DAN-05	Orthic Acrisol	Sandy Clay Loam	^{cd}0.55 (0.08)	^{ab}6.16 (0.05)	^{b}4.32 (1.05)	^{e}222 (7)	^{c}12 (2)	^{d}28.8 (6.2)	^{b}25.2 (0.4)	3052
MBCA	OG	MLA-01	Orthic Acrisol	Sandy Clay Loam	^{d}0.41 (0.11)	^{bcd}5.37 (0.28)	^{b}4.84 (0.08)	^{d}292 (8)	^{bc}19 (4)	^{c}29.5 (8.6)	^{b}25.2 (0.7)	2838
MBCA	OG	MLA-02	Orthic Acrisol	Sandy Clay Loam	^{d}0.50 (0.06)	^{cde}5.25 (0.61)	^{b}4.47 (0.25)	^{d}299 (12)	^{abc}22 (4)	^{e}27.5 (4.3)	^{e}24.3 (0.5)	2838
SAFE	SL	SAF-01	Orthic Acrisol	Sandy Clay Loam	^{bc}0.71 (0.05)	^{bc}5.91 (0.60)	^{b}6.76 (1.80)	^{c}368 (8)	^{ab}25 (9)	^{f}24.8 (5.7)	^{c}24.8 (0.8)	2717
SAFE	SL	SAF-02	Orthic Acrisol	Sandy Clay Loam	^{bc}0.73 (0.10)	^{bc}5.61 (0.45)	^{b}4.79 (0.33)	^{a}576 (7)	^{ab}26 (4)	^{g}22.1 (6.4)	^{e}24.2 (0.6)	2717
SAFE	SL	SAF-03	Orthic Acrisol	Sandy Loam	^{a}0.94 (0.10)	^{de}4.79 (0.16)	^{b}3.98 (0.21)	^{bc}385 (26)	^{a}30 (1)	^{b}32.4 (2.3)	^{b}25.2 (0.5)	2717
SAFE	SL	SAF-04	Orthic Acrisol	Sandy Loam	^{ab}0.79 (0.08)	^{e}4.47 (0.24)	^{a}13.73 (4.74)	^{b}399 (8)	^{c}11 (6)	^{b}32.6 (4.2)	^{d}24.4 (0.5)	2717

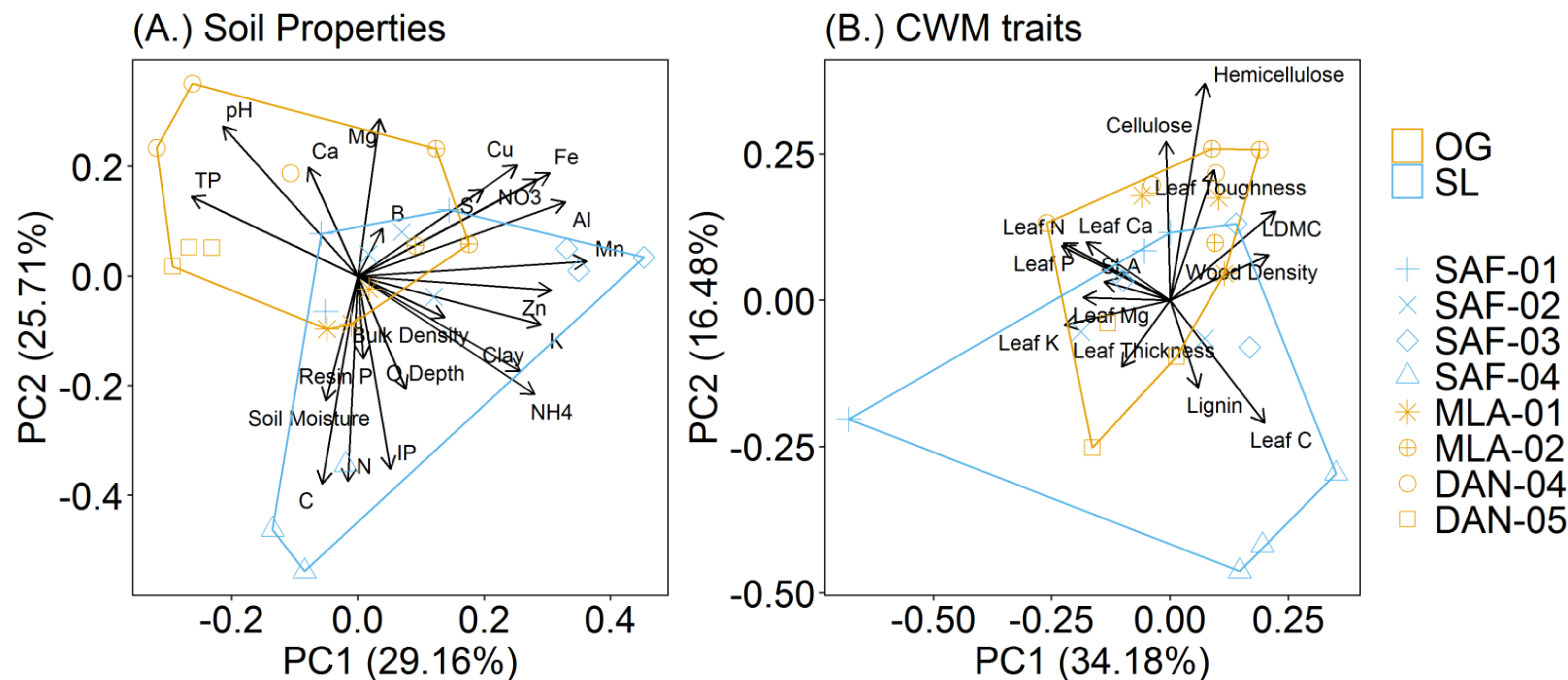

Figure 2.2 *- Principal Component Analysis (PCA) biplots of soil properties (A.) and community-weighted mean (CWM) tree traits (B.) To group points, convex hulls (polygons) were drawn around outermost points of OG and SL plots. Relative differences in the heterogeneity of soil properties and CWM traits between OG and SL forest are indicated by the polygon area. A polygon with a larger area indicates greater heterogeneity. Abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, TP = total soil phosphorus, IP = soil inorganic phosphorus, O depth = organic horizon depth.*

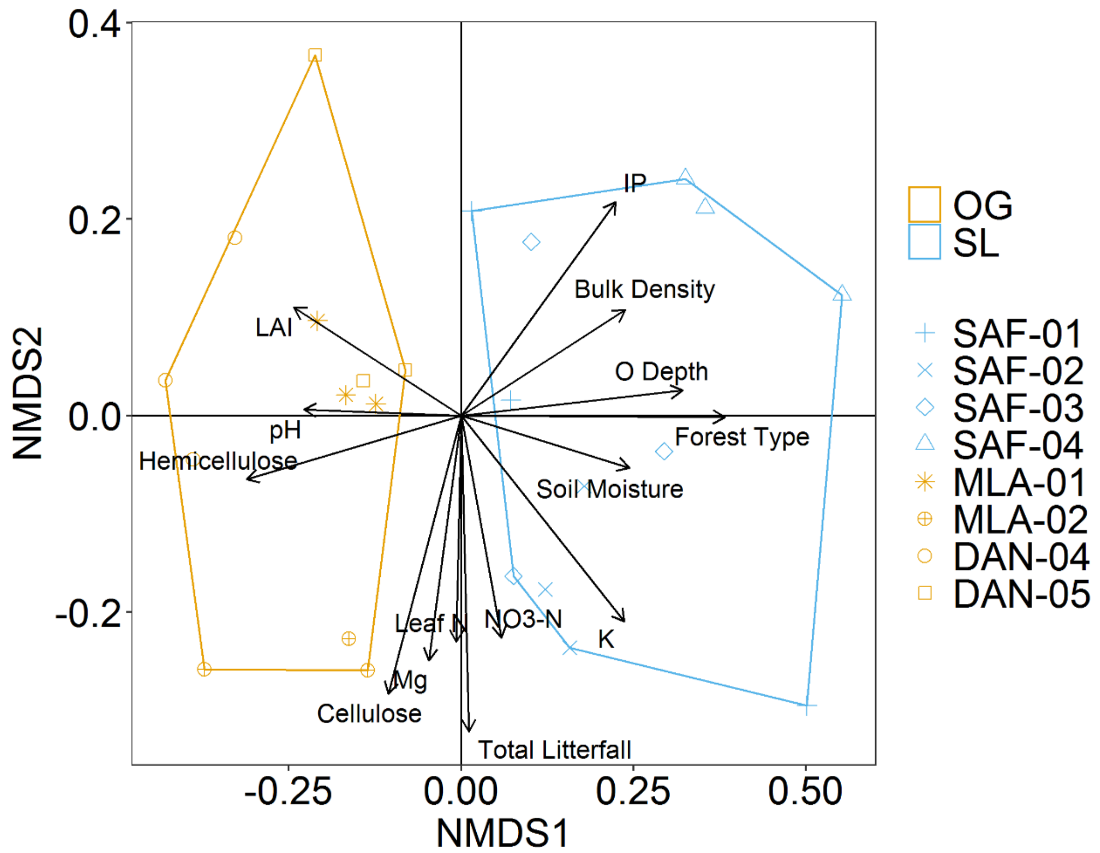

***Figure 2.3**- Non-metric multidimensional scaling (NMDS) plot of tree community composition (C.) (Stress = 0.11). Black arrows represent fitted vectors of soil properties, CWM traits and tree community characteristics with significant correlations ($p < 0.05$) to the 2 unconstrained ordination axes (NMDS1 & NMDS2).*

***Table 2.2** - Summary of measured soil properties in OG and SL forest. Data are means ± 1 standard deviation in brackets.*

Variables	**OG Forest**	**SL Forest**
Organic Horizon Depth (cm)	[a]2.96 (0.56)	[a]4.69 (1.34)
Gravimetric Soil Moisture (%)	[a]25.94 (4.45)	[a]30.42 (8.44)
Bulk Density (g cm^{-3})	[b]0.54 (0.13)	[a]0.81 (0.13)
Soil pH	[a]5.09 (0.89)	[a]4.22 (0.97)
Total C (%)	[a]3.96 (0.85)	[a]5.8 (3.11)
Total N (%)	[a]0.29 (0.07)	[a]0.38 (0.13)
Total P (mg kg^{-1})	[a]308.31 (116.67)	[a]226.01 (64.12)
Inorganic P (mg kg^{-1})	[a]18.35 (6.94)	[a]30.58 (21.05)
C:N	[a]14.14 (2.95)	[a]14.78 (2.45)
Sand (%)	[a]23.48 (3.56)	[a]21.04 (7.18)
Silt (%)	[a]19.74 (3.53)	[a]17.71 (6.49)
Clay (%)	[a]56.78 (5.59)	[a]61.25 (9.23)
NO_3^- (µg 10 cm^{-2} 14 $days^{-1}$)	[a]88.32 (73.09)	[a]147.12 (155.02)
NH_4^+ (µg 10 cm^{-2} 14 $days^{-1}$)	[a]5.25 (4.04)	[a]14.41 (13.35)
Ca (µg 10 cm^{-2} 14 $days^{-1}$)	[a]556.78 (578.17)	[a]402.84 (472.50)
Mg (µg 10 cm^{-2} 14 $days^{-1}$)	[a]224.22 (124.86)	[a]194.09 (139.14)
K (µg 10 cm^{-2} 14 $days^{-1}$)	[a]126.82 (110.24)	[a]304.78 (132.11)
Resin P (µg 10 cm^{-2} 14 $days^{-1}$)	[a]0.51 (0.60)	[a]1.17 (1.36)
Fe (µg 10 cm^{-2} 14 $days^{-1}$)	[a]8.85 (8.25)	[a]12.39 (9.83)
Mn (µg 10 cm^{-2} 14 $days^{-1}$)	8.52 (7.34)	[a]18.81 (21.02)
Cu (µg 10 cm^{-2} 14 $days^{-1}$)	[a]0.17 (0.19)	[a]0.21 (0.18)
Zn (µg 10 cm^{-2} 14 $days^{-1}$)	[a]0.88 (0.76)	[a]1.05 (0.52)
B (µg 10 cm^{-2} 14 $days^{-1}$)	[a]0.11 (0.10)	[a]0.14 (0.13)
S (µg 10 cm^{-2} 14 $days^{-1}$)	[a]13.38 (8.11)	[a]27.29 (20.32)
Al (µg 10 cm^{-2} 14 $days^{-1}$)	[a]16.78 (13.86)	[a]25.59 (18.95)

Table 2.3 *- Summary of measured subplot community-weighted mean (CWM) plant traits in OG and SL forest. Data are means ± 1 standard deviation. The hypothesised effect on microbial communities is the potential mechanism through which CWM traits may influence microbial communities and provides a basis for their selection and measurement in the study.*

Variables	**OG Forest**	**SL Forest**	**Hypothesised Effect on Microbial Communities**
Leaf K (mg g^{-1})	11.25 (3.00)	12.50 (3.98)	
Leaf Ca (mg g^{-1})	10.20 (3.25)	8.67 (7.21)	
Leaf Mg (mg g^{-1})	3.61 (1.31)	2.97 (0.61)	
Leaf P (mg g^{-1})	1.19 (0.20)	1.05 (0.21)	Aboveground nutrient inputs and resource heterogeneity
Leaf N (%)	1.88 (0.10)	1.96 (0.32)	
Leaf C (%)	44.26 (0.95)	44.85 (2.34)	
Leaf C:N	24.40 (1.47)	25.11 (5.42)	
Leaf Thickness (mm)	0.25 (0.02)	0.25 (0.04)	
Specific Leaf Area (mm^2 mg^{-1})	11.28 (1.38)	11.12 (0.88)	
Leaf Dry Matter Content (mg g-1)	411.43 (22.59)	407.66 (34.90)	
Leaf Toughness (N mm^{-1})	0.27 (0.06)	0.22 (0.05)	Modulation of decomposition rates, decomposer substrate specificity and soil C storage
Branch Wood Density (g cm^3)	0.53 (0.05)	0.48 (0.07)	
Hemicellulose (%)	12.58 (1.28)	11.40 (1.51)	
Cellulose (%)	20.80 (2.23)	20.06 (2.28)	
Lignin & Recalcitrants (%)	17.17 (2.03)	17.79 (2.27)	

Table 2.4 *- Summary of measured subplot tree community characteristics in OG and SL forest. EcM host trees were from the Dipterocarpaceae and Fagaceae families. Data are means ± 1 standard deviation. The hypothesised effect on microbial communities is the potential mechanism through which tree community characteristics may influence microbial communities. This provides a rationale for the selection and measurement of these variables.*

Variables	OG Forest	SL Forest	Hypothesised Effect on Microbial Communities
Basal Area (m^2 0.04 ha^{-1})	1.23 (0.49)	0.89 (0.38)	Root biomass and belowground carbon allocation
Aboveground Carbon Stock (Mg C Ha^{-1})	153.79 (76.42)	78.78 (41.92)	
Woody NPP (Mg C Ha^{-1} yr^{-1})	5.03 (2.47)	12.34 (7.47)	
Stem Density (per 0.04 ha)	19 (5)	18 (8)	
EcM host tree basal area (m^2 0.04 ha^{-1})	0.38 (0.37)	0.15 (0.16)	Density dependence, Mycorrhizal host specificity
Tree species richness	11 (3)	12 (6)	Mycorrhizal host specificity, litter diversity
Tree Shannon Diversity	2.18 (0.47)	2.28 (0.41)	
Leaf Area Index	4.27 (0.22)	3.28 (0.59)	Temperature, moisture, plant tissue quality, tree community
Total Litterfall (Mg C ha^{-1} yr^{-1})	4.17 (1.36)	4.81 (1.68)	Aboveground nutrient inputs

2.4.2 Logging effects on soil microbial communities and relationships to soil properties, CWM traits and tree communities

Across all samples and after filtering of rare taxa, 5287 bacterial, 1680 protistan and 4181 fungal ASVs were detected. Species richness of bacteria, protists and fungi did not differ between OG and SL forest plots, however the heterogeneity of bacterial and fungal community richness between samples was higher in SL relative to OG forest (Bacteria: $\chi^2 = 6.82$, $p = 0.009$; Fungi: $\chi^2 = 4.22$, $p = 0.04$) (Table 2.5). EcM richness ($F_{1,6} = 103.05$, $p = <0.001$) and Shannon diversity ($F_{1,6} = 31.49$, $p = 0.001$) was lower in SL relative to OG forests (Table 2.5). Neither total microbial (total PLFA), fungal (Fungal PLFA) or bacterial (bacterial PLFA) biomass varied between OG and SL forest, nor did fungal:bacterial ratios (Table 2.5). However, fungal biomass was more heterogeneous in SL relative to OG forest ($\chi^2 = 4.68$, $p = 0.03$).

Soil bacterial communities in both OG and SL plots predominantly comprised taxa within the phyla Acidobacteria (OG – 17.7±10.2 (±1SD)), SL – 22.8±8.9%), Proteobacteria (OG – 40.8±10.2%, SL – 35.6±11.0%) and Actinobacteria (OG – 10.7±7.6%, SL – 21.9±13.8%) (Figure 2.4). Soil protistan communities were dominated by Alveolata (OG – 47.2±20.9%, SL – 49.0±20.4%) and Rhizaria (OG – 33.5±19.7%, SL – 35.0±18.9%) (Figure 2.4). Fungal communities mainly comprised taxa within the phyla Basidiomycota (OG – 31.7±18.9%, SL – 28.0±19.6%) and Ascomycota (OG – 64.1±19.7%, SL – 68.9±19.6%) (Figure 2.4). Glomeromycota constituted 0.26% and 0.25% of relative abundance in OG and SL respectively.

There was no significant difference in bacterial community composition between forest types (PERMANOVA: $F_{1,23} = 2.70$, $p = 0.24$, $R^2 = 0.11$) **(**Figure 2.5**).** Protistan communities were marginally significantly different ($F_{1,23} = 2.34$, $p = 0.08$, $R^2 = 0.10$) whilst whole fungal communities varied between land uses (Fungi: $F_{1,23} = 2.85$, $p = 0.03$, $R^2 = 0.12$) (Figure 2.5). Variation in bacteria and protistan communities was explained predominantly by a combination of soil properties and leaf CWM traits. However, tree community characteristics explained an additional 3 % variation in protistan communities (Figure 2.5). In contrast, fungal community composition was best explained by a combination of CWM traits (3 %), soil properties (7 %) and tree community composition (5 %) (Figure 2.5)

Table 2.5 *– Summary of measured subplot bacterial, protistan, fungal richness, Shannon diversity and soil PLFA biomarker concentrations measured across 24 subplots in old growth and selectively logged forest plots. Data are means (± 1 SD) with 1 measure per subplot.*

Variables	**OG Forest**	**SL Forest**
Bacterial Richness	1315 (203)	1093 (458)
Bacterial Shannon Diversity	6.05 (0.19)	5.85 (0.59)
Protist Richness	214 (31)	188 (47)
Protist Shannon Diversity	4.54 (0.36)	4.47 (0.42)
Fungal Richness	664 (107)	634 (203)
Fungal Shannon Diversity	4.73 (0.22)	4.58 (0.41)
Ectomycorrhizal Fungal Richness	25 (7)	10 (3)
Ectomycorrhizal Fungal Shannon Diversity	1.91 (0.49)	1.40 (0.42)
Arbuscular Mycorrhizal Fungal Richness	15 (10)	18 (9)
Arbuscular Mycorrhizal Fungal Shannon Diversity	2.26 (0.64)	2.52 (0.47)
Saprotrophic Fungal Richness	143 (24)	126 (36)
Saprotrophic Fungal Shannon Diversity	3.35 (0.50)	2.98 (0.82)
Pathogenic Fungal Richness	44 (12)	44 (17)
Pathogenic Fungal Shannon Diversity	2.51 (0.48)	2.61 (0.56)
Total PLFA (µg g^{-1} dry soil weight)	30.74 (10.49)	35.75 (12.88)
Fungal PLFA (µg g^{-1} dry soil weight)	2.22 (0.81)	2.94 (1.61)
Bacteria PLFA (µg g^{-1} dry soil weight)	17.13 (6.06)	19.67 (7.60)
F:B Ratio	0.13 (0.02)	0.14 (0.04)
G+ PLFA (µg g^{-1} dry soil weight)	8.99 (3.12)	10.82 (4.50)
G- PLFA (µg g^{-1} dry soil weight)	6.68 (2.89)	7.12 (3.92)

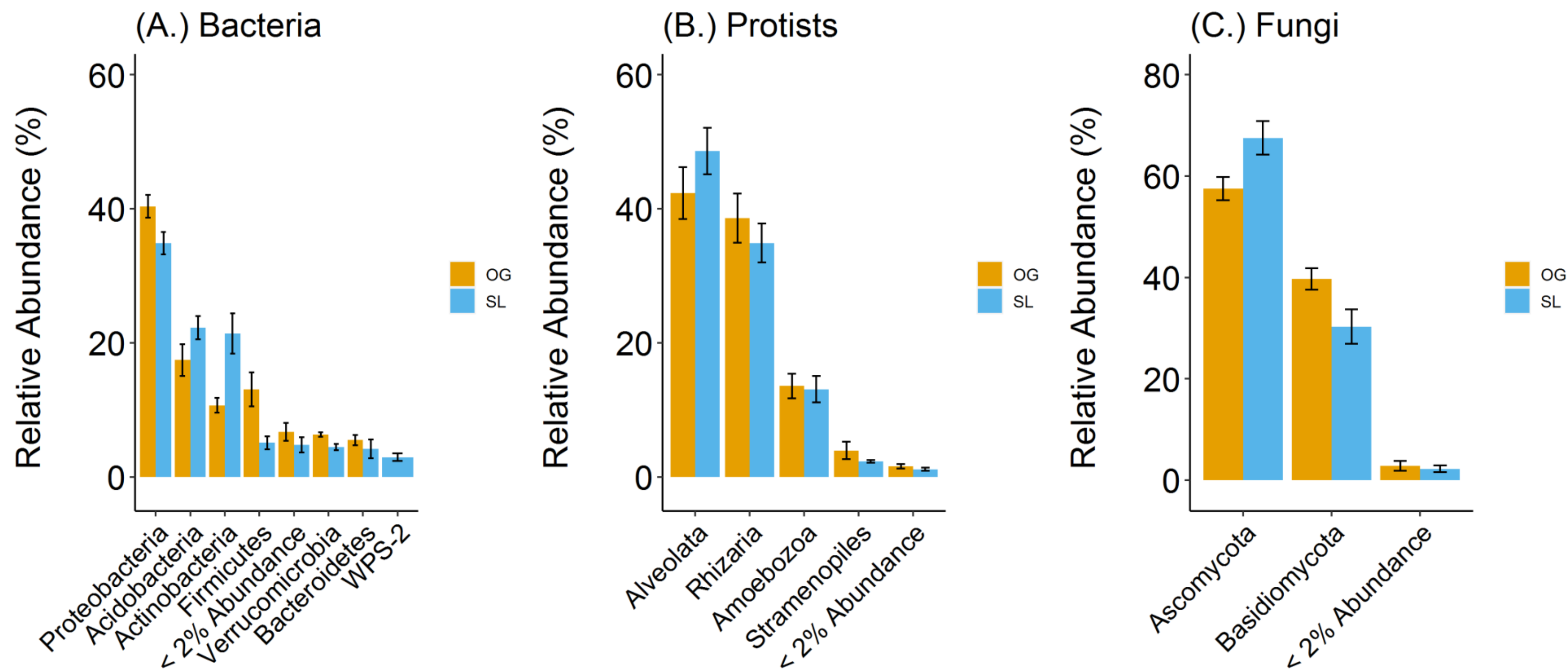

Figure 2.4 *- Relative abundance of phyla belonging to bacteria (A.), protists (B.) and fungi (C.) across old-growth (OG) and selectively logged (SL) forest plots. Relative abundance was calculated as the percent composition of sequence reads assigned to each phyla relative to the total number of sequence reads in each sample. Phyla representing < 2% of relative abundance were grouped into one classification (< 2 % Abundance). Data are means with error bars representing ±1 standard error.*

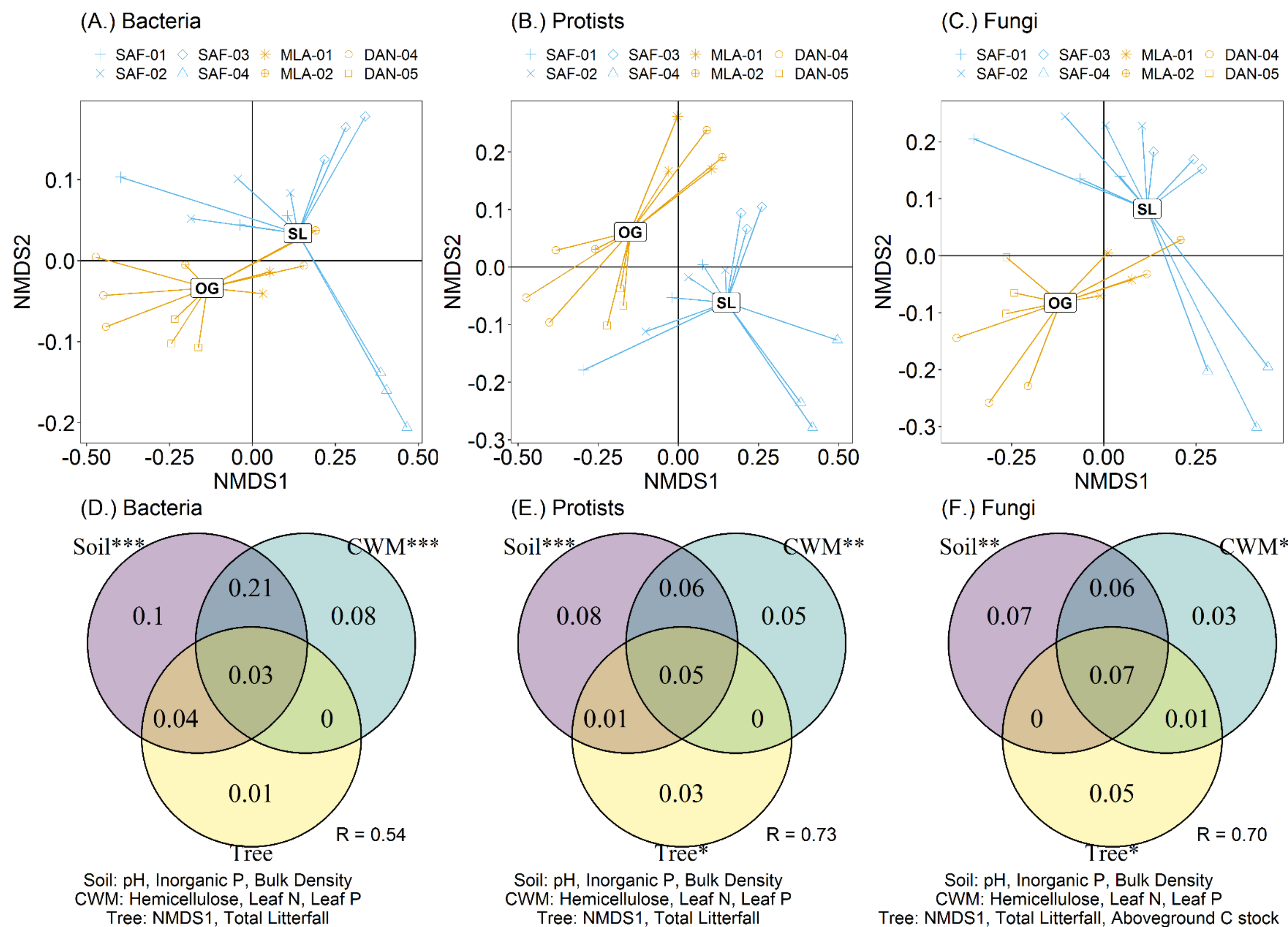

Figure 2.5 *- (A–C): Non-metric multidimensional scaling (NMDS) ordinations of square-root transformed Bray-Curtis dissimilarities of soil bacterial, protistan and fungal community composition across OG and SL forest plots. A: NMDS Stress = 0.05, B: NMDS Stress = 0.09, C: NMDS Stress = 0.12. (D–F): Proportion of variation explained by environmental variables from measured soil properties, CWM traits and tree properties, CWM traits and tree community composition. R = residual unexplained variation. *** = <0.001, ** = <0.01, * = <0.05.*

EcM fungal (PERMANOVA: $F_{1,23} = 3.09$, $p = 0.026$, $R^2 = 0.12$), saprotrophic (PERMANOVA: $F_{1,23} = 2.79$, $p = 0.03$, $R^2 = 0.11$) and pathogenic fungal (PERMANOVA: $F_{1,23} = 3.29$, $p = 0.03$, $R^2 = 0.13$) communities were significantly different between forest types (Figure 2.6, Figure 2.7). EcM fungal community composition was also more homogeneous in SL relative to OG forest (PERMDISP2 – EcM Fungi: $F_{1,22} = 5.11$, $p = 0.03$) (Figure 2.6). AM fungal communities were highly variable and did not cluster between forest types (PERMANOVA: $F_{1,23} = 1.37$, $p = 0.28$, $R^2 = 0.06$) (Figure 2.6).

EcM and AM fungal community composition was best explained by tree community characteristics including tree community composition and EcM host basal area (Figure 2.6). Tree community characteristics explained 7 % and 3 % of variation for EcM and AM fungal communities respectively with soil properties explaining an additional 3 %. However, the total explained variation was very low for AM fungi (8 %) relative to EcM fungi (22 %). Variation in saprotrophic and pathogenic fungal communities was best explained by a combination of soil properties, CWM traits and tree community characteristics although soil properties explained most unique variation (Figure 2.7). Tree community characteristics explained more variation (7 %) than CWM traits (4 %) in pathogenic fungal communities whilst the opposite was true of saprotrophic fungal communities (CWM traits: 6 %, Tree community characteristics: 4 %).

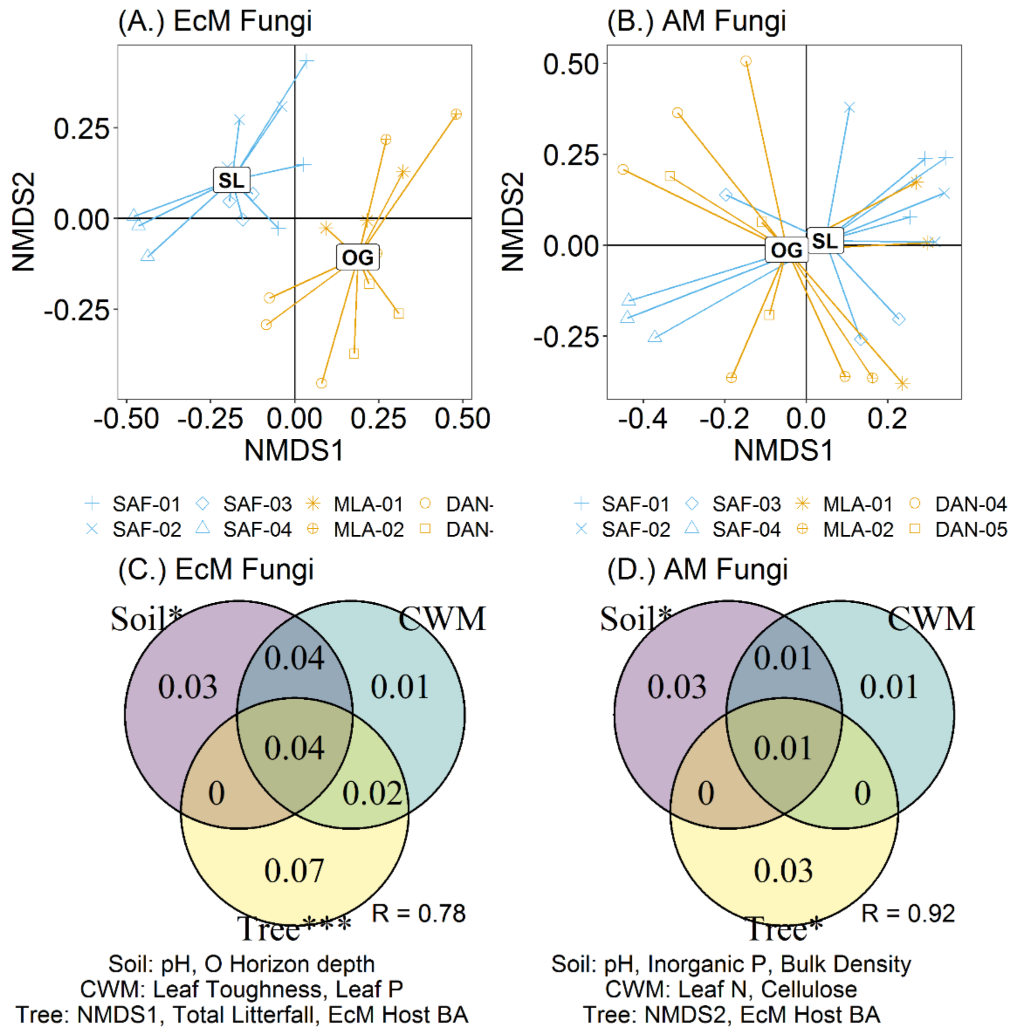

Figure 2.6 *- (A – B): Non-metric multidimensional scaling (NMDS) ordinations of square-root transformed Bray-Curtis dissimilarities of EcM and AM fungal community composition across OG and SL forest plots. A: NMDS Stress = 0.20, B: NMDS Stress = 0.19. (C – D): Proportion of variation explained by environmental variables from measured soil properties, community-weighted mean (CWM) traits and tree community composition. R = residual unexplained variation. *** = <0.001, ** = <0.01, * = <0.05.*

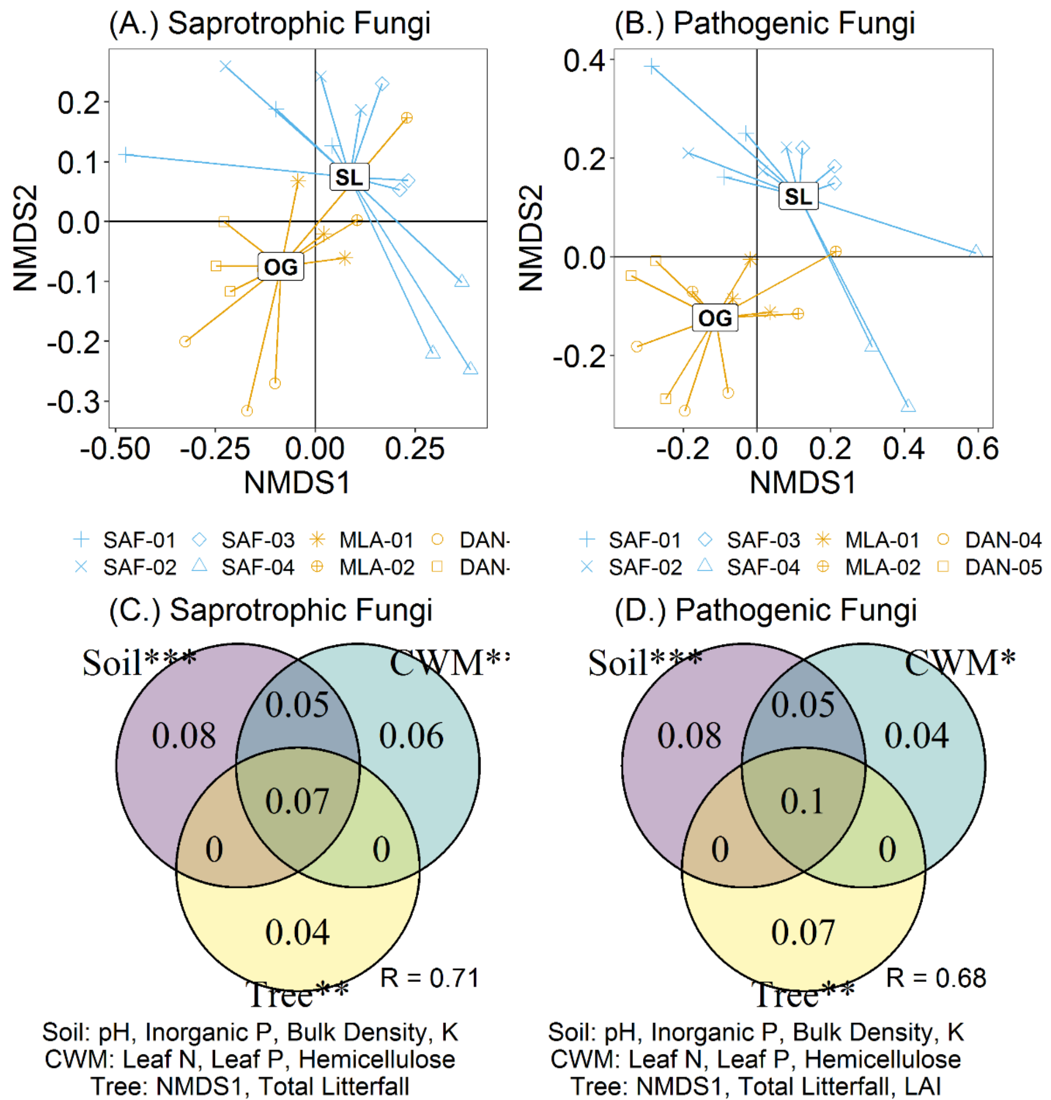

Figure 2.7 *- (A – B): Non-metric multidimensional scaling (NMDS) ordinations of square-root transformed Bray-Curtis dissimilarities of saprotrophic and pathogenic fungal community composition across OG and SL forest plots. A: NMDS Stress = 0.14, B: NMDS Stress = 0.17. (C – D): Proportion of variation explained by environmental variables from measured soil properties, community-weighted mean (CWM) traits and tree community composition. R = residual unexplained variation. *** = <0.001, ** = <0.01, * = <0.05.*

Of those fungal taxa assigned to ecological groups, only the relative abundance of EcM fungi was significantly different between forest types with greater abundance in OG relative to SL forest (OG: 9.76 ± 1.49 %, SL: 2.21 ±0.49 %) ($F_{1,6}$ = 17.48, p = 0.007) (Figure 2.8). Across all forest plots EcM and AM relative abundance were positively and negatively correlated respectively with the basal area of putative EcM host trees within subplots (Figure 2.9). EcM richness and Shannon diversity were also correlated with the basal area of EcM host trees (Appendix 1: Figure 8.4).

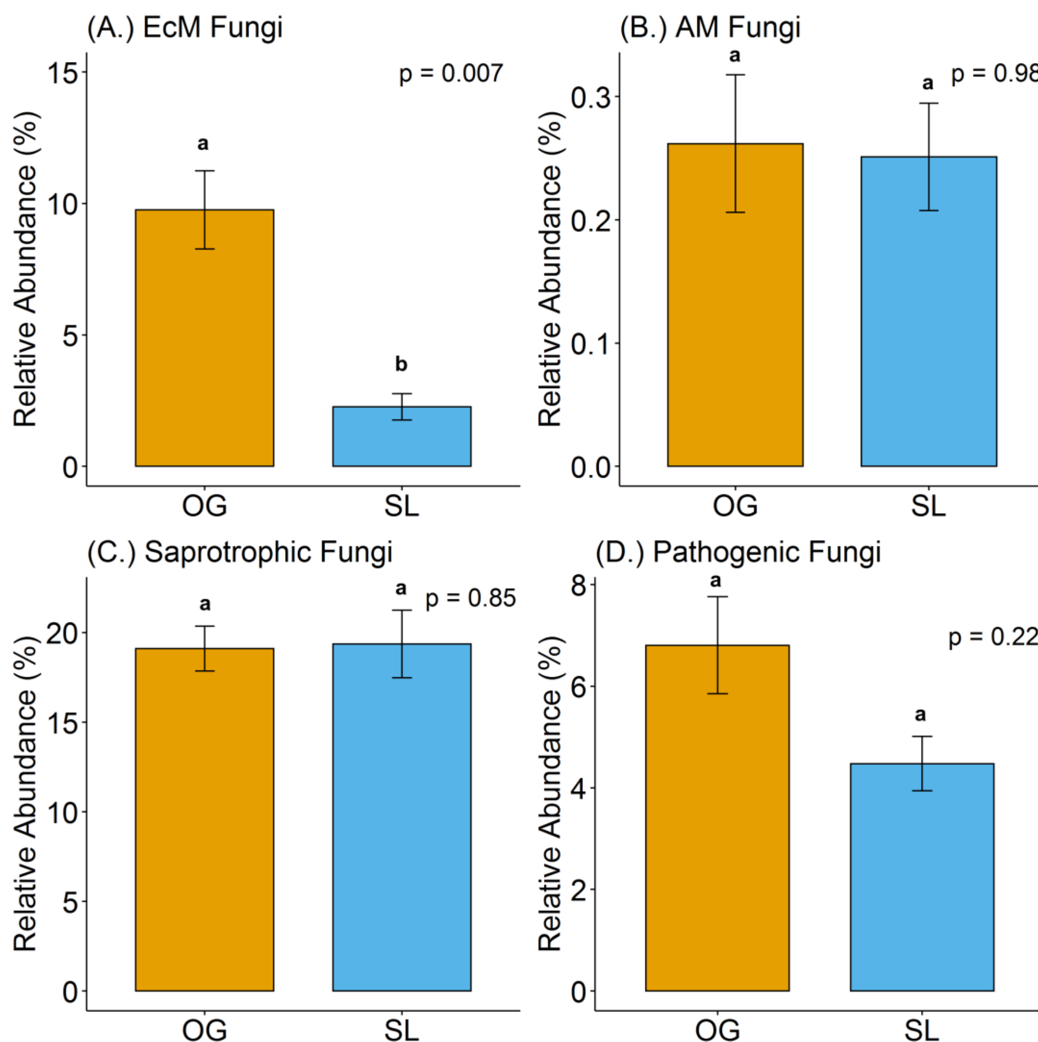

Figure 2.8 *- Relative abundance of soil fungal ecological groups in OG and SL forest plots. Relative abundance was calculated as the percentage of sequence reads assigned to each functional group relative to the total number of fungal sequence reads in each sample. Bars represent data means. Error bars represent ± 1 standard deviation. Letters denote significant differences between OG and SL forest. .*

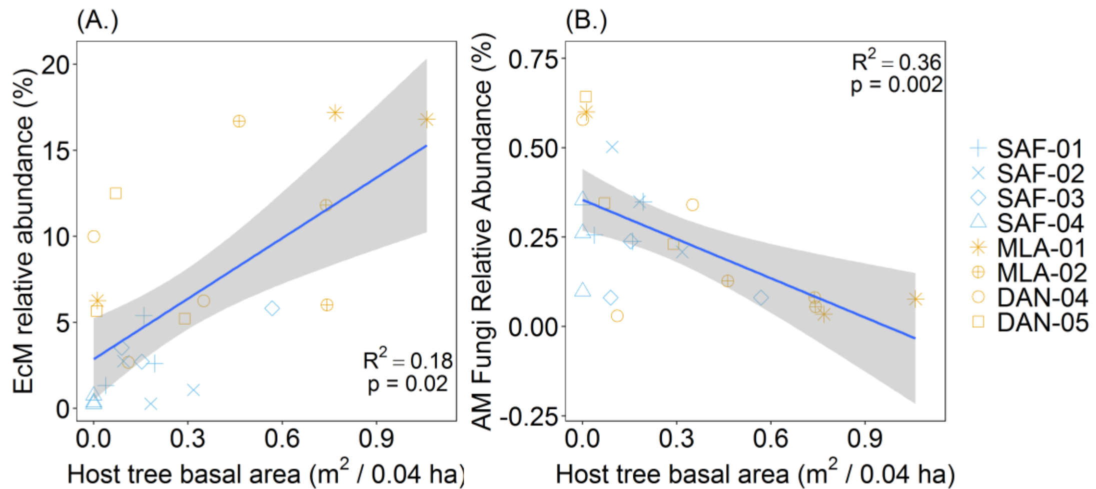

Figure 2.9 *- The relationship between EcM (A.) and AM (B.) fungal relative abundance and the basal area of putative EcM host trees from Dipterocarpaceae and Fagaceae families within subplots (0.04 ha). Statistics represent results from linear mixed effects models with plot as a random term.* R^2 *represents the marginal* R^2 *and p values were calculated using F - tests implementing the Satterthwaite denominator degrees of freedom approximation. Grey shaded envelopes represent the 95% confidence interval.*

2.5 Discussion

Our results show that SL forest had significantly different fungal (whole, EcM, saprotrophic and pathogenic) community composition relative to OG forest (although only EcM relative abundance differed between OG and SL forest) (Figure 2.5, Figure 2.6, Figure 2.7) and marginally significantly different protistan communities, whilst bacterial communities were more resilient to logging disturbance (Figure 2.5). This finding is in partial agreement with hypothesis 1 and other studies conducted in SE Asian tropical forests showing that fungal communities are generally more sensitive to logging disturbance than bacteria (Kerfahi et al., 2014; McGuire et al., 2015). This may be due to higher growth rates of bacteria conferring greater resilience to disturbance relative to fungi, a stronger relative influence of tree communities on soil fungal assemblages (Sun et al., 2017) and greater sensitivity of fungal communities to physical soil disturbance as soil bulk density was higher in SL forest. Higher bulk

density in SL forest might reflect compaction by historical logging activities, which could modifying drainage of soils, decrease soil porosity and microsite variability.

EcM fungal communities were particularly sensitive to selective logging and strongly declined in their relative abundance, richness and diversity, although there was no difference in the relative abundance of AM fungi (Figure 2.8). Although most lowland tropical trees form arbuscular mycorrhizal symbioses (McGuire et al., 2008), the palaeotropical forests of South East Asia are unique, characterised by canopy dominance of a small subset of tree species belonging to the Dipterocarpaceae family, which are obligate EcM symbionts (Taylor and Alexander, 2005). EcM and AM fungal relative abundance was positively and negatively correlated with the basal area of EcM host trees respectively (Figure 2.9). These findings suggest that where EcM hosts and mutualists were most abundant, resource depletion by EcM fungi, or competition between EcM and AM fungi for soil nutrients, may have negatively affected the efficiency of AM fungal associations (Becklin and Galen, 2009). Moreover, it suggests that a reduction in EcM host tree basal area may influence EcM relative abundance across OG and SL forests. Although at the subplot (20×20 m) scale EcM host tree basal area was variable and did not differ significantly between forest types, selective logging did reduce EcM host tree basal area across the 1 ha plots (Both et al., 2019). However, our findings contradict previous work from Malaysia which showed that whilst EcM fungal communities were compositionally distinct between OG and SL forest, their relative abundance was actually higher in SL forest (McGuire et al., 2015). This difference may be linked to the time since logging as the sites surveyed here have been more recently logged (most recently in 2008) in contrast to a 50 year recovery period (McGuire et al., 2015) and highlights the challenge of characterizing heterogeneous, disturbed tropical forests. We also found some evidence

for reductions in the heterogeneity of EcM communities between sampling locations in SL forest, indicative of biotic homogenization, despite greater heterogeneity in soil properties across SL forest (Figure 2.2). Previous work in tropical forests showed more homogeneous fungal communities in cleared forest areas that were linked to a less variable abiotic environment (Bachelot et al., 2016b). We propose that our findings in SL forest may be determined by the removal of large, canopy dominant trees which would ordinarily act as hotspots of mycorrhizal productivity.

Local tree species distributions and their functional trait expression can be influenced by soil properties and nutrient availability, which makes it challenging to disentangle the relative importance of tree community and soil effects on structuring microbial assemblages (Both et al., 2019; John et al., 2007). We used variation partitioning to separate the unique and shared contributions of potential environmental drivers and showed that CWM traits and tree community characteristics both explained additional unique variation in soil microbial communities, thus supporting hypothesis 2. The relative importance of soil properties, CWM traits and tree community characteristics as predictors differed between microbial ecological groups. However, most variance remained unexplained suggesting that either stochastic factors or unmeasured variables (i.e below-ground root traits) are important in structuring microbial communities.

In agreement with previous tropical studies, soil pH was an important predictor for both bacteria and protists (Schulz et al., 2019b; Tripathi et al., 2012). Inorganic P and bulk density also explained variation in bacterial and protistan communities and this subset of soil properties explained 38 % and 20 % of community composition in bacteria and protistan communities respectively (Figure 2.5). However, much of this

variance could equally be explained by foliar nutrient (N and P) concentrations and leaf hemicellulose content (Figure 2.5). This likely reflects the fact that soil properties influence the trait expression of tropical trees via nutrient availability, size of nutrient pools, and pH (Both et al., 2019). Tree community characteristics were not significant predictors of bacterial communities (Figure 2.5). This disagrees with a previous study in a Panamanian tropical forest which found a significant relationship between bacteria and tree community structure but no relationship with plant traits (Barberán et al., 2015). However, Barberán et al. (2015) only surveyed undisturbed forest and the relationships between tree communities and bacteria were weaker than with fungi.

In contrast with bacteria and protists, tree community characteristics explained more unique variation in total fungal communities than CWM traits although soil pH, inorganic P and bulk density were still the most important predictors (Figure 2.5). This agrees with previous studies in tropical forests that found strong associations between fungal and tree communities, but only weak univariate relationships with individual plant traits (Bachelot et al., 2016b; Barberán et al., 2015; Schappe et al., 2017). However, soil properties and CWM traits explained the majority of explained variation in saprotrophic fungal communities (Figure 2.7), likely reflecting the role of aboveground plant traits in controlling aboveground nutrient inputs, resource heterogeneity and modulation of decomposition rates. However, logging also decreases the abundance of key invertebrate decomposers (earthworms and termites) (Ewers et al., 2015). Therefore, fungal saprotrophic community shifts across OG and SL forests may also be as a compensatory response to declines in invertebrate decomposers. Tree community characteristics were important predictors for soil mycorrhizal communities, with the standing basal area of putative EcM host trees and tree community composition influencing EcM and AM fungal community

composition (Figure 2.6, Figure 2.7). This highlights potential linkages between the distribution of tropical tree and mycorrhizal diversity. However, in contrast to our findings, AM fungi in Panamanian tropical forests were not correlated with the structure of tree communities, highlighting that microbial responses to forest disturbance may not be generalizable between palaeo and neotropical forests (Schappe et al., 2017). Pathogenic fungi were also strongly associated with tree community characteristics (Figure 2.7). This suggests that specialized pathogenic fungi may influence patterns of tree mortality in tropical forests and select for specific tree communities, with implications for forest dynamics (Bagchi et al., 2010; Levi et al., 2019). For example, the Janzen-Connell hypothesis suggests that specialized pathogens decrease tree offspring survival at high densities beneath parents, giving locally rarer species an advantage. Such dynamics may prevent dead trees from being replaced by conspecifics, promoting coexistence and maintaining high tree diversity in tropical forests.

2.6 Conclusions

In conclusion we demonstrate that logging disturbance shifts total soil fungal, EcM, saprotrophic and pathogenic fungal communities with a decline in the relative abundance, richness and diversity of EcM fungi. The basal area of EcM host trees, which are targeted during logging, explained variation in mycorrhizal community composition and was positively associated with EcM and negatively to AM fungal relative abundance. This has potential implications for altered biogeochemical cycling and tree species co-existence in disturbed tropical forests (Bagchi et al., 2014; Liang et al., 2015). We also found that CWM traits and tree community characteristics explained additional variation in soil bacterial, protistan and fungal communities above that explained by soil properties. Our findings suggest that disturbance of

tropical forests shifts soil fungal communities, linked to shifts in tree community characteristics and that tree community and CWM traits are useful as general predictors of soil microbial community composition beyond soil properties. However, much of the variation in microbial community composition could still not be explained, highlighting the challenge of predicting patterns and responses of complex soil communities across gradients and to disturbance. Our results also show the need to enhance our mechanistic understanding of the inter-linkages between above-ground plant communities, soil characteristics and complex microbial communities as shifts in soil fungal communities can have wider implications for soil C cycling, storage (Averill et al., 2014) and potential forest recovery.

2.7 Acknowledgments

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3 Ants and termites regulate microbial community structure and function in tropical forest

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3.1 Abstract

Ants and termites are key ecosystem engineers in tropical forests but communities are modified by forest disturbance. Through their activity, invertebrates may influence the composition and activity of soil microbial communities, but how changes to ant and termite abundance might influence soil microbial communities and ecosystem processes is unknown. To address this knowledge gap, ant and termite abundance was experimentally suppressed in an old growth tropical forest in Borneo over three years, using novel, field-scale treatments. The *in situ* response of soil bacterial and fungal communities to ant and termite suppression was then measured after three years. Our findings suggest that ants and termites exert top-down controls on key microbial functional groups as reduced termite activity increased the relative abundance of lignin degrading bacteria and the heterogeneity of lignolytic fungi, whilst ant suppression enhanced rates of fungal foraging by stimulating hyphal production. Despite these observed changes in microbial communities and similar to other perturbation studies, traditional diversity metrics of bacterial and fungal communities were not sensitive to invertebrate suppression. However, microbial interaction patterns inferred from co-occurrence networks revealed reduced modularity and increased

complexity of fungal networks after invertebrate suppression. These network properties have been associated with reduced resilience to climate extremes (e.g. drought). Therefore, changes to ant and termite activity could alter the vulnerability of forest microbial communities to transitions to alternative states (abrupt changes in soil microbial communities) in response to climate extremes, with unknown functional consequences. This is the first indication that interactions between ants, termites and soil microbes in tropical forest may control the response of soil communities to future climate change. Taken together, our results provide new insights into the interactions between ants, termites and microbial communities in tropical forests, with potential implications for forest biogeochemical cycling and hint that the ability of microbial communities to withstand future disturbances might be linked to ant and termite activity.

3.2 Introduction

Tropical forests are globally significant hotspots of biodiversity, have the highest productivity of any terrestrial ecosystem and represent a large store of carbon (C) (Dirzo and Raven, 2003). Within tropical forests, ants (Hymenoptera: Formicidae) and termites (Isoptera) represent key groups of macroinvertebrates. Both are classified as “ecosystem engineers” due to their influence on soil properties, controls on nutrient availability and redistribution of resources for other organisms, including microorganisms and plants (Bignell, 2006; Jouquet et al., 2006). Therefore, the activity, abundance and diversity of ants, termites as well as other macroinvertebrates is important to the maintenance of ecosystem functioning in tropical forests (Ewers et al., 2015; Fayle et al., 2011; Griffiths et al., 2015; Jouquet et al., 2011).

Whilst the direct impacts of invertebrates on soil functions such as C cycling is significant, it is thought that an even greater contribution to soil processes is through complex invertebrate-microbial community interactions (Bray et al., 2019; Grandy et al., 2016). For example, ants are thought to represent ~25 % of all animal biomass in tropical forests (Schultz, 2000) and their activity acts as an important control on nutrient redistribution from organic materials within forest soils (Griffiths et al., 2018). The activity of ants can therefore create both nutrient hotspots around ant nests and areas of resource depletion (Farji-Brener and Werenkraut, 2017; Meyer et al., 2013). This heterogeneity can create localized patches of mycorrhizal enrichment, stimulate the abundance of ammonifying bacteria and increase abundance of mesofauna whilst soil fertility decreases in the surrounding area (Boulton et al., 2003; Dauber et al., 2008; Folgarait, 1998). The activity of ants may thus indirectly influence the composition and distribution of soil microbial decomposers by controlling the availability of organic residues and altering their chemical composition. Whilst ants are generally omnivorous opportunists, many ant species are also generalist or specialist soil invertebrate predators (Luke et al., 2014); preying on oribatid mites (Wilson, 2005) and collembolans (Masuko, 2009), both key fungal grazers (Maraun et al., 2003). This predation pressure may stimulate or suppress the abundance of soil fauna, with cascading impacts on soil microbial communities as it has been shown that fauna can exert top down controls on fungal communities (Crowther et al., 2011a; Crowther and A'Bear, 2012; Crowther et al., 2011b; Crowther et al., 2011c; Crowther et al., 2013). Moreover, two species of specialist ants (*Euprenolepsis procera, Euprenolepsis wittei)* have been found to feed almost exclusively on fungal sporocarps in Malaysian tropical forests, suggesting that this feeding strategy may be more widespread than previously recognized and that ants

could play a direct role in fungal spore dispersal (von Beeren et al., 2014; Witte and Maschwitz, 2008).

Termites are often the dominant macroinvertebrate in tropical ecosystems (Lavelle et al., 1997). They exert strong spatio-temporal controls on soil nutrient availability, as they forage over large spatial scales (metres to tens of metres) and regulate soil moisture (Gautam and Henderson, 2014; Jouquet et al., 2011). They create nest structures which maintain constant temperature and humidity (Jouquet et al., 2011) and create aboveground “sheeting” structures (Jouquet et al., 2015) which confer the ability to maintain high activity, even during drought periods when the activity of other invertebrate detritivores and decomposition rates typically decline (Ashton et al., 2019). Termites consume a diverse range of organic matter (soil organic matter, standing or dead wood, woody litter debris or dead dry standing litter and grasses), modifying its chemical composition and distribution, which can influence soil microbial communities and enhance rates of mineralization (Abe et al., 2000). All termites associate symbiotically with bacteria, archaea and cellulolytic flagellates in their hindgut, which allows for the efficient degradation of cellulose (Bignell and Eggleton, 2000). The Macrotermitinae, a subfamily of Termitidae also maintain a mutualism with *Termitomyces* sp., a genera of white rot fungi, allowing for the complete digestion of woody biomass (cellulose, hemicellulose and lignin) (Rouland-Lefèvre and Bignell, 2002). Only a limited subset of specialist bacteria and fungi possess the ability to produce lignocellulose degrading enzymes such as laccase, lignin peroxidase and manganese peroxidase (Chen et al., 2012). Therefore, termite abundance and diversity are likely key controls on the activity and distribution of lignolytic microorganisms and the mineralization rates of C and nutrients from dead wood in tropical forests (Cheesman et al., 2018). The magnitude of wood

consumption by termites in tropical forests is not well constrained, but estimates suggest that this decomposition pathway is of global significance to the C cycle (Cornwell et al., 2009).

Most studies to date focused on invertebrate-microbial community interactions have been performed in temperate ecosystems and focused on single species of earthworms, isopods and millipedes (Chang et al., 2017; Crowther et al., 2011a; Crowther and A'Bear, 2012; Crowther et al., 2011b; Crowther et al., 2011c; Crowther et al., 2013; Dempsey et al., 2011; McLean et al., 2006). Our understanding is currently limited regarding how ants and termites interact with soil dwelling microbial decomposers in tropical forests and whether these interactions influence the composition, stability and functioning of microbial communities. Whilst traditional microbial diversity metrics have been linked to ecosystem function (Louis et al., 2016; Wagg et al., 2014), they often lack sensitivity to chronic or moderate perturbations (Karimi et al., 2017). Microbial co-occurrence networks offer a unique way to study complex microbial taxa-taxa relationships. They have recently been applied to examine how microbial associations are modified as a result of environmental perturbations (Banerjee et al., 2019; de Vries et al., 2018), to infer and generate hypotheses surrounding community stability to perturbation based upon network topological parameters (Röttjers and Faust, 2018) and have been linked to ecosystem functioning (Wagg et al., 2019). Invertebrates through invertebrate-microbe interactions, may alter the structure of soil microbial networks, which may have implications for the stability of microbial communities and ecosystem functionality. However, this has never been investigated in tropical ecosystems. This represents an important gap in understanding, as both ants and termites are highly responsive to human disturbance, with tropical forest logging

showed to alter species richness, distribution and abundance (Donovan et al., 2007; Folgarait, 1998; Luke et al., 2014).

The aim of this study was to explore the impacts of ants and termites on soil microbial diversity, community structure and function *in situ* within an old growth (OG) tropical forest in Borneo, Malaysia. The abundance of mixed ant and termite communities were experimentally suppressed in the forest for three years. Soil bacterial and fungal community composition was characterized using amplicon sequencing. The putative function of bacterial communities was predicted and hyphal productivity of actively foraging fungi was measured *in situ*. Microbial co-occurrence networks were then used to examine how bacterial and fungal community structure and interactions between taxa were influenced by either ant or termite suppression. We hypothesized that:

[1.] Microbial richness and diversity would decline and community composition would become more homogeneous under invertebrate suppression, due to reductions in soil microhabitat heterogeneity.

[2.] Ant and termite suppression would have contrasting impacts on microbial activity and abundance. Specifically:

[2a] Termite suppression would increase the abundance of microbial lignin degraders due to a compensatory response to reduced wood decomposition rates.

[2b] Ant suppression would stimulate rates of fungal growth due to a reduction in resource redistribution across the forest floor and reduced predatory pressure from ants on fungal grazers.

[3.] Microbial networks would become more complex and less modular under invertebrate suppression due to a more homogeneous soil environment.

3.3 Materials and methods

3.3.1 Field sites and invertebrate suppression

In October 2014, 12 experimental plots were established in a 42 ha area of OG tropical forest, within the Maliau Basin Conservation Area (4°44′35″ to 55″ N and 116°58′10″ to 30″ E; mean annual rainfall 2,838 ± 93 mm) in Sabah, Malaysia. All plots were located on orthic Acrisols. 4 plots were assigned to control treatments, 4 to ant suppression and 4 to termite suppression. Each plot measured 50x50 m and were located at least 100 m apart. Ant and termite suppression was achieved using methods described in detail by Griffiths et al. (2018) and Ashton et al. (2019). Briefly, ants were targeted with two poison baits; Synergy Pro (Active ingredients: hydramethylnon and pyriproxyfen) and a custom bait consisting of Whiskas cat food soaked in a sugar- imidacloprid solution (60 g L^{-1} sugar with imidacloprid at 110 ppm). These were reapplied when ant abundance reached >20 % of that in control plots (measured using bait cards). For the duration of the suppression treatment, ant abundance in leaf litter was reduced by 87 % (assessed by winkler bags) whilst ants measured at bait cards was reduced by 90 % (Griffiths et al., 2018). Initial ant communities in Maliau Basin Conservation Area were comprised primarily of tropical climate specialists (Biogeographically based within the tropics. Few specialised adaptations: *Pseudolasius, Loweriella, Euprenolepis, Proatta, Gnamptogenys, Aenictus, Lordomyrma, Dorylus, Lophomyrmex, Cladomyrma, Tetraponera, Myrmecina, Solenopsis, Dolichoderus, Myrmicaria, Vollenhovia, Epelysidris, Acanthomyrmex, Pristomyrmex, Anoplolepis, Acropyga*), generalized Myrmicinae

(Widespread genera that can dominate resources with chemical defences: *Pheidole, Crematogaster, Monomorium*) and cryptic species (Small species that are either subterranean, or nest in leaf litter or rotting logs. They are abundant and diverse in forests: *Mayriella, Ponera, Carebara, Hypoponera, Pheidologeton, Plagiolepis, Mystrium, Dacetinops, Calyptomyrmex, Amblyopone, Strumigenys, Proceratium, Probolomyrmex, Eurhopalothrix, Centromyrmex, Cryptopone, Discothyrea, Protanilla, Cerapachys*). Ant community composition was not assessed in response to suppression treatment due to the strong reduction in ant activity. However non-ant invertebrate communities shifted as a result of ant suppression with the abundance of flies, crickets, wasps springtails (collembola) and harvestmen recorded in the ant suppression plots 80% higher than observed in the control plots, while the abundance of cockroaches increased by around 50%. Termites were suppressed by initially destructively removing all aboveground termite mounds present and treating the area with a 23 ppm imidacloprid solution. Tea bags (containing *Camellia sinensis*) and standard domestic toilet paper rolls (sawn in half) were soaked in a 5.7 ppm fipronil solution and distributed in a grid across the 4 termite suppression plots. After the initial treatment, toilet roll baits only were reapplied ca. every 6 months. The suppression treatment reduced termite feeding activity (assessed using untreated toilet paper roll) by 45 % (Ashton et al., 2019). 15 m buffer zones were added around each suppression plot so the total area treated with insecticides was 80x80 m. However, sampling occurred only within the central 50x50 m plot areas to avoid any possible edge effects. Initial termite communities were comprised of the following species: *Macrotermes, Bulbitermes, Microcerotermes, Heterotermes, Dicuspiditermes, Globitermes, Malaysiotermes, Pericapritermes, Procapritermes, Schedorhinotermes*. Termite suppression treatment altered termite community composition by primarily

reducing the activity of large bodied, wood feeding termites (*Macrotermes sp., Bulbitermes sp.*) and increasing the activity of small bodied, twig dwelling species (*Microcerotermes sp., Heterotermes sp.).*

3.3.2 Soil sampling and chemical analysis

25 soil samples were collected across each plot (n = 300) during November 2017 using a grid sampling strategy, with each sampling point 5 m apart from the next. Soil samples for microbial sequencing were collected at each sampling point using a 1 cm diameter auger to 10 cm depth (rinsed with 96 % ethanol between samples). For soil chemical characterization a 3 cm window soil corer was used again to 10 cm depth. For both samples, the organic soil horizon was retained for analysis by separating from the underlying mineral soil. Samples for soil characterization were sealed in a Ziploc bag, refrigerated at 4 °C and transported to the Forest Research Centre, Sepilok. Subsamples for microbial sequencing were weighed in the field (0.20 ± 0.02 g) using a calibrated 2 point balance (Kern CM 60-2N, Balingen, Germany) and transferred to 2 ml Zymo Research BashingBead™ tubes prefilled with Xpedition Lysis/Stabilization solution (Edetic Acid, guanidinium thiocyanate, trometamol) (Zymo Research, Irvine, California, USA). These were lysed using a portable bead beater within ~4 hours of collection and transported to the UK for analysis. pH was measured on fresh soils using a pH meter in a soil water suspension (1: 2.5 ratio of soil to deionised water) after shaking overnight at 100 rpm on an orbital shaker followed by standing for 30 min (Landon, 1984). Soils were air dried at 40 °C, passed through a 2 mm sieve and milled to a fine powder using a mortar and pestle. Subsamples for total C and N analysis were dried at 65 °C for 48 hours and ground as above. Total C and N was determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany).

A Bray No. 1 extractant was used to extract inorganic P (Bray and Kurtz, 1945) and total P was extracted using a mixed acid (sulphuric – nitric - perchloric) (Allen, 1989). The P contents in the extracts and digests were determined using the molybdenum blue method and read at 880 nm on a spectrophotometer (Hitachi UV-VIS, Japan) (Anderson and Ingram, 1993).

3.3.3 Molecular analysis of soil microbial communities

DNA was extracted from lysates using a Zymo Research Quick-DNA Fecal/Soil Microbe Miniprep Kit (Zymo Research, California, USA) according to the manufacturer's instructions. Amplicon libraries were constructed according to a dual indexing strategy with each primer consisting of the appropriate Illumina adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker and the amplicon specific primer (Kozich et al., 2013). For bacteria, V3-V4 16S rRNA amplicon primers were used (CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC) (Kozich et al., 2013). For eukaryotes, the 18S rRNA gene was targeted using eukaryotic amplicon primers AACCTGGTTGATCCTGCCAGT and GCTATTGGAGCTGGAATTAC (Baldwin et al., 2005) and fungi were targeted by amplifying the ITS2 region using primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). Amplicons were generated using a high fidelity DNA polymerase (Q5 Taq, New England Biolabs). After an initial denaturation at 95 °C for 2 minutes, PCR conditions were as follows: denaturation at 95 °C for 15 seconds; annealing at temperatures 55 °C, 57 °C and 52 °C for 16S, 18S and ITS reactions respectively; annealing times were 30 seconds with extension at 72 °C for 30 seconds; cycle numbers were 25 for 16S and ITS, and 30 for 18S; a final extension of 10 minutes at 72 °C was included. Amplicon sizes were determined using an Agilent 2200 TapeStation system and libraries normalized using SequalPrep Normalization

Plate Kit (Thermo-Fisher Scientific) and quantified using a Qubit dsDNA HS kit (Thermo-Fisher Scientific). Each amplicon library was sequenced on an Illumina MiSeq using V3 600 cycle reagents at concentrations of 8 pM with a 5 % PhiX Illumina control library.

Sequences were processed in R using the DADA2 pipeline to quality filter, merge (where appropriate), de-noise and assign taxonomies (Callahan et al., 2016). Briefly, 16S and 18S amplicon forward reads were trimmed to 250 and 280 bases respectively, and ITS amplicons reads were trimmed to 225 and 160 bases, forward and reverse respectively. Filtering settings were maximum number of Ns (maxN) = 0, maximum number of expected errors (maxEE) = 1. Sequences were dereplicated and the DADA2 core sequence variant inference algorithm applied. ITS sequences were merged using the *mergePairs* function, whilst forward reads only were used for 16S and 18S amplicons. Chimeric sequences were removed using *removeBimeraDenovo* default settings. The actual sequence variants (ASV) were subject to taxonomic assignment using *assignTaxonomy* at default settings; the training databases used were SILVA v138, Protist Ribosomal Reference database (PR^2) v4.12.0 and Unite v7.2 for 16S, 18S and ITS respectively. The 18S library was pre-filtered to include only metazoan sequences. Prior to estimation of bacterial and fungal alpha diversity, samples were normalized by rarefying to 6969 and 2013 reads for 16S bacterial and ITS fungal amplicons respectively. 6 samples were dropped from bacterial richness estimates and 9 samples were dropped from fungal richness estimates due to a low read count.

3.3.4 Measurements of hyphal productivity

Fungal hyphal productivity was measured *in situ* at 3 randomly selected locations within each experimental plot installed in April 2017 as described in detail by Robinson et al. (2020). At each location, 10 hyphal in-growth bags were buried 50 cm apart along 2 transects (n = 5 per transect), spaced 1 m apart. In-growth bags (5x5 cm) were constructed from 41 µm pore-size nylon mesh (Plastok, UK). This mesh size allows for hyphal in-growth but excludes root access (Langley et al., 2006; Wallander et al., 2013). The bags were each filled with 25 g of sterilized (150 °C for 24 hours) fine quartz sand and sealed using a soldering iron. These were buried vertically between 0-5 cm encompassing the organic layer and the interface between the underlying mineral soil (Lindahl et al., 2007; Wallander et al., 2013). In-growth bags were harvested after ~ 6 months, frozen at -20 °C on the day of collection and subsequently transported on ice to the UK. Hyphae were then extracted from 3 intact bags from each sampling location. Sand from the three bags was bulked, hand mixed and hyphae were extracted from a subsample using an adapted flotation method (Bakker et al., 2015). 5 g of sand was vortexed in 10 ml 4M KCl solution. Hyphae were stained in the tube by adding 20 µl Lactophenol cotton blue and shaking on an orbital shaker at 300 rev min^{-1} for 10 minutes. A further 40 ml 4M KCl was added to sample tubes before vortexing at full speed for 1 minute, leaving to stand for 1 minute to allow hyphal material to reach the surface of the solution, and aspirating the top 15 ml of the extract to a new sample tube in three steps using a 5 ml pipette. Hyphal material was prepared for measurement using the membrane filtration technique (Hanssen et al., 1974). Extracts were transferred to a food processor, diluted with 200 ml of DI water and 20 ml 1M sodium hexametaphosphate solution was added to disperse hyphal fragments and any other remaining colloidal matter (Bardgett, 1991;

Moutoglis et al., 1995). 15ml aliquots were then vacuum filtered onto nitrocellulose filter membranes, air dried and mounted onto microscrope slides.

Hyphae were photographed on filter membranes using a microscope-mounted Canon 400D camera. All coarser hyphae with diameters ≥ 10 µm were identified and photographed in their entirety at ×250 magnification for measurement. Overlapping photographs were taken along hyphal fragments and composite images were created using the Stitching plugin for ImageJ (Preibisch et al., 2009). For finer hyphae with diameters < 10 µm, the filter membrane was divided into six equally-sized segments and one photograph was randomly taken within each segment at ×500 magnification. All visible finer hyphae in these photographs were then identified and measured. Hyphae were measured using the ObjectJ plugin for ImageJ. Length was measured along the centre of each section and widths were measured at five points along section lengths. Widths were averaged for each section and volume was estimated using the formula for cylinder volume. The total hyphal lengths and volumes of hyphae in each subsample was estimated as the sum of: 1) lengths and volumes of all coarse hyphal sections; and 2) total length and volume of fine hyphal sections per area in photographs multiplied by the area of membrane used for filtration. Hyphal length and volume was then calculated in mm g^{-1} and mm^3 g^{-1} dry sand based on sand oven dry weight (105 °C).

3.3.5 Data Analyses

All analyses were performed using R version 3.5.2 or Python 3.7. To visualize the taxonomic composition of bacterial and fungal communities, heat trees of the relative abundance of bacterial and fungal genera were generated using the *metacoder* R package (Foster et al., 2017). All taxa with a relative abundance contribution of less

than 0.005 % for fungi and 0.001 % for bacteria were filtered and taxa were agglomerated at genus level.

To address hypothesis 1, bacterial and fungal richness, Shannon diversity and Pielou evenness were calculated on rarefied 16S and ITS amplicon ASV tables using the *Phyloseq* R package (McMurdie and Holmes, 2013). Differences between treatments were tested using linear mixed effects models implemented in the *lme4* R package. Plot was included as a random term in models to account for the non-independence of multiple measurements made within each plot (n=25 per plot) and specified as follows: *richness ~ treatment + (1|plot), data = data*. Response variables were square root transformed prior to analysis which improved normality (assessed graphically using Q-Q plots and residual vs fitted value plots) and p-values for fixed effects were estimated using the Satterthwaite degrees of freedom approximation. Bray-Curtis dissimilarities were calculated for bacteria and fungal communities using square root transformed and rarefied ASV count data and the effect of ant and termite suppression on microbial community composition was tested using a nested permanova (Accounting for plot as a random factor) as implemented in the *BiodiversityR* package (Anderson, 2001; Kindt, 2019). Multivariate dispersions were used as a measure of community heterogeneity (β diversity) and differences between treatments was tested using the PERMDISP2 algorithm (*betadisper* function in the *vegan* R package) (Anderson, 2006; Anderson et al., 2006). *Post hoc* tests of differences in multivariate dispersions was tested using the *tukeyHSD* function in the *vegan* R package.

To address hypothesis 2a, the FAPROTAX database was used to map bacterial taxa to ecologically relevant functions and convert microbial taxonomic community profiles (ASV table) into putative functional profiles (Louca et al., 2016). These were

calculated on relative abundance normalized ASV data. Fungal ASV tables were normalized to relative abundance and assigned to ecological guilds and traits (e.g. mycorrhizal, saprotrophic and pathogenic) using FunGuild (Nguyen et al., 2016). Only those taxa with non-ambiguous classifications and assignments classified as “probable” or “highly probable” were retained for further analysis. We subset ASVs assigned as wood degrading fungi by filtering those assigned to the wood saprotrophic guild and listed as having wood rot traits (white rot, brown rot and soft rot). Differences in the relative abundance of wood rot fungi, lignolytic and aromatic compound degrading bacteria were tested using mixed effects, beta regression models implemented in the *glmmTMB* R package using the same random structure as described above to account for multiple measurements within each plot. This approach overcomes problems inherent in applying classic statistical approaches to proportional data (Douma and Weedon, 2019). Significance of fixed effects was assessed using likelihood ratio tests (LRT) and *post hoc* comparisons between treatment levels were conducted using the *emmeans* R package (Lenth, 2019). Differences in the variance between treatments was tested using robust Fligner - Killeen tests.

To address hypothesis 2b, differences in fungal hyphal productivity were tested using linear mixed effects models as specified above. To investigate changes in the abundance of soil fauna between control and invertebrate suppression plots, differential abundance analysis was performed on raw ASV count data of metazoa using a zero inflated negative binomial model as implemented in DESeq2 (Love et al., 2014). Low prevalence taxa (that were not present in ≤ 1% of samples) were filtered prior to analysis.

To address hypothesis 3, cross-domain (bacterial and fungal) and fungal only taxon co-occurrence networks were constructed using the *SpiecEasi* R package version 1.0.7 (https://github.com/zdk123/SpiecEasi). This technique uses LASSO regularization and cross validation to detect the most parsimonious network structure in high dimensional microbial data (Kurtz et al., 2015; Tipton et al., 2018). We used the default inverse-covariance selection method (glasso) and selected the optimal sparsity parameter lambda (γ) based on the Stability Approach to Regularization Selection (StARS) (Liu et al., 2010). The lambda ratio was set to 0.01 and the network was assessed over 100 values of γ to detect the least variable network links. The StARS variability threshold was set to 0.05 for all networks. To improve sensitivity of the analysis and reduce spurious links between rare taxa, network analysis was performed on highly prevalence filtered ASVs where only those ASVs with ≥2 reads detected in at least 20 % of samples within each treatment were retained. Network topological parameters were calculated using the *igraph* R package (Csardi and Nepusz, 2005). Nodes represent individual ASVs whilst edges represent relationships between nodes. Degree represents the number of edges connecting to a node whilst the clustering coefficient is a measure of the degree to which nodes in a graph tend to cluster together. Closeness centrality measures the average distance between a node and all other nodes in the network. Betweenness centrality represents the role of nodes as a bridge between different components of the network. As centrality is not well defined for networks with disconnected components, we extracted the largest connected component of each network using the *giant_component_extract* function in the *CINNA* R package and calculated centrality indices (betweenness centrality, closeness centrality) on this component (Ashtiani et al., 2018). We then used bootstrapping followed by two sample Kolmogorov-Smirnov tests to assess the difference in the

node degree distribution between networks and two sample Wilcoxon rank sum tests to identify differences in means of node attributes (node degree, betweenness centrality, closeness centrality, clustering coefficient). Modularity describes the degree to which the network can be split into highly connected “modules” with few connections between modules. This analysis was performed using the cluster fast greedy algorithm (Clauset et al., 2004) A modularity score of > 0.4 suggests that a network has a modular structure. Final networks were visualized using ggnet2 in the *GGally* R package (Schloerke et al., 2011).

3.4 Results

3.4.1 Influence of invertebrate suppression on soil properties and microbial communities

Bulk soil properties (pH, total C, N, inorganic P and total P) did not vary significantly across treatments (

Table **3.1**). Across all samples 54808 bacterial, 2765 metazoan and 37480 fungal ASV's were detected prior to any filtering of rare taxa for analysis**.** Across the 3 treatments, Proteobacteria were the dominant bacterial phylum followed by Acidobacteria and Verrucomicrobia (Figure 3.1). Basidiomycota were the dominant fungal phylum across all treatments with fungi from the class Agaricomycetes accounting for ~50 % of relative abundance (Figure 3.2). Fungi from the ectomycorrhizal genus Russula, were particularly abundant across all treatments (Figure 3.2).

Table 3.1 *- Bulk soil properties measured across control, ant suppression and termite suppression treatment plots. Data are means (n = 100 per treatment) ± 1 standard deviation. Superscript letters denote whether parameters were significantly different between study plots from Tukey's HSD test. Significant differences (p <0.05) between plots are indicated when letters are different. Non – significant differences (P >0.05 between plots are indicated when letters are shared.*

	Control	**-Ant**	**-Termite**
Soil pH	^{a}4.87 (0.77)	^{a}4.45 (0.59)	^{a}4.51 (0.57)
Total N (%)	^{a}0.29 (0.08)	^{a}0.30 (0.10)	^{a}0.28 (0.08)
Total C (%)	^{a}3.62 (1.38)	^{a}3.74 (1.52)	^{a}3.56 (1.79)
Inorganic P (mg kg^{-1})	^{a}17.81 (8.16)	^{a}21.06 (8.53)	^{a}18.49 (6.30)
Total P (mg kg^{-1})	^{a}236.91 (65.97)	^{a}214.21 (42.97)	^{a}235.42 (82.39)

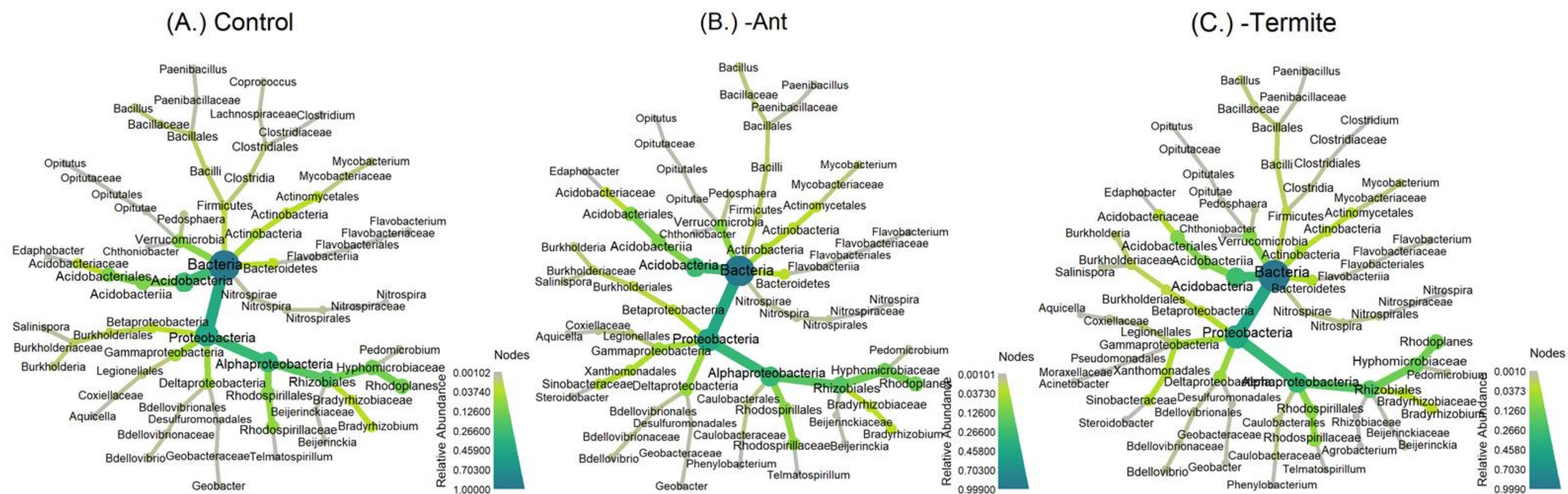

Figure 3.1 *- Heat trees representing the relative abundance of bacterial genera across control, ant suppression and termite suppression treatments. All taxa with a relative abundance contribution of <0.001% were filtered for visualisation. ASV's were agglomerated at the Genus taxonomic rank prior to plotting.*

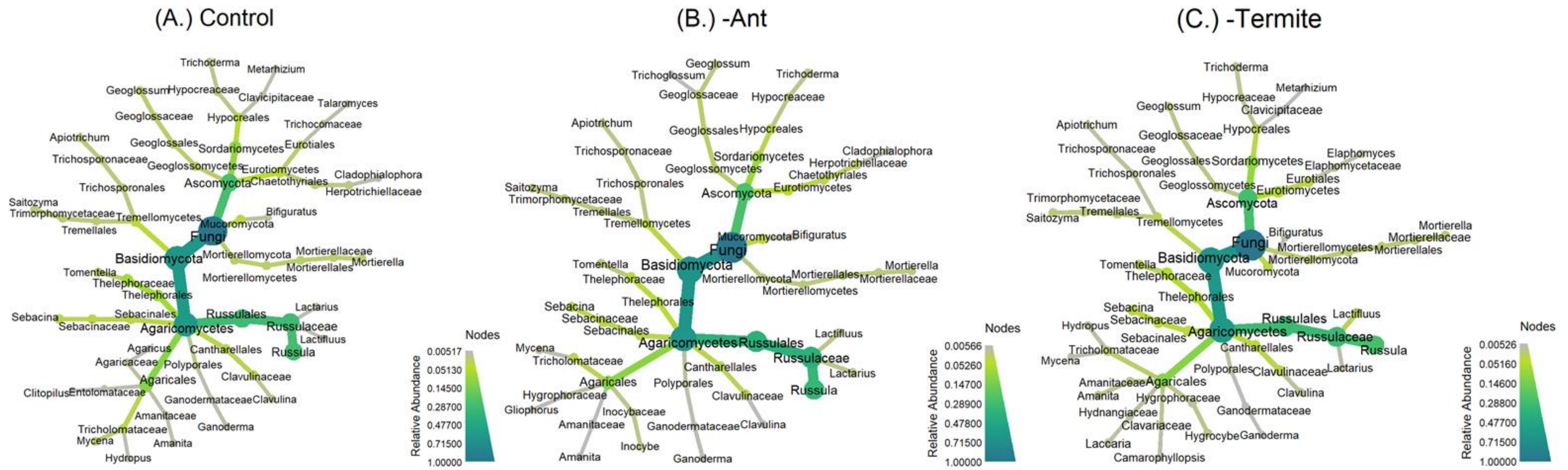

Figure 3.2 *- Heat trees representing the relative abundance of fungal genera across control, ant suppression and termite suppression treatments. All taxa with a relative abundance contribution <0.005% were filtered for visualisation. ASV's were agglomerated at the Genus taxonomic rank prior to plotting.*

Bacterial alpha diversity indices were not significantly different between treatments (richness ($F = 1.36$, $p = 0.26$), Shannon diversity ($F = 1.39$, $p = 0.25$) and evenness ($F = 0.83$, $p = 0.47$) (Figure 3.3). Neither bacterial community composition (Bray-Curtis dissimilarity) ($F_{2,282} = 1.07$, $p = 0.28$) nor multivariate dispersion (β diversity) ($F = 0.90$, $p = 0.41$) differed between treatments (Appendix 2: Figure 8.5). Fungal alpha diversity indices were not significantly different between treatments (Fungal richness ($F = 0.37$, $p = 0.70$), Shannon diversity ($F = 0.52$, $p = 0.61$) and evenness ($F = 0.63$, $p = 0.56$)) (Figure 3.3). Fungal community composition (measured using Bray-Curtis dissimilarities) was significantly different between individual plots ($F = 2.71$, $p = 0.009$) but not between treatments ($F = 0.74$, $p = 0.82$) (Appendix 2: Figure 8.5). However, multivariate dispersion (β diversity) was significantly different between treatments ($F = 6.41$, $p = 0.002$). A Tukey's *post hoc* test showed that the control treatment had lower dispersion than either ant (Tukey: $p = 0.003$) or termite (Tukey: $p = 0.008$) suppression treatments.

The relative abundance of taxa capable of ligninolysis and degradation of aromatic compounds differed between treatments (LRT: $\chi2 = 17.93$, $p = <0.001$) and was higher in termite suppression plots relative to both ant suppression (*emmeans*: $p=<0.001$) and control (*emmeans*: $p=<0.001$) treatments (Figure 3.4). The mean relative abundance of lignolytic fungi did not differ between treatments (LRT: $\chi2 = 0.54$, $p = 0.76$) (Figure 3.5). However, heterogeneity in their relative abundance increased under both ant (Fligner - Killeen: $\chi2 = 6.34$, $p = 0.01$) and termite suppression (Fligner – Killeen: $\chi2 = 14.00$, $p = <0.001$) relative to the control treatment (Figure 3.5). Fungal hyphal productivity also differed between treatments as hyphal length ($F_{2,9} = 5.26$, $p = 0.04$) and volume ($F_{2,9} = 5.47$, $p = 0.03$) was

significantly higher in ant suppression treatments relative to control plots (Figure 3.6). There was no difference between termite suppression and control plots in fungal hyphal productivity (Figure 3.6).

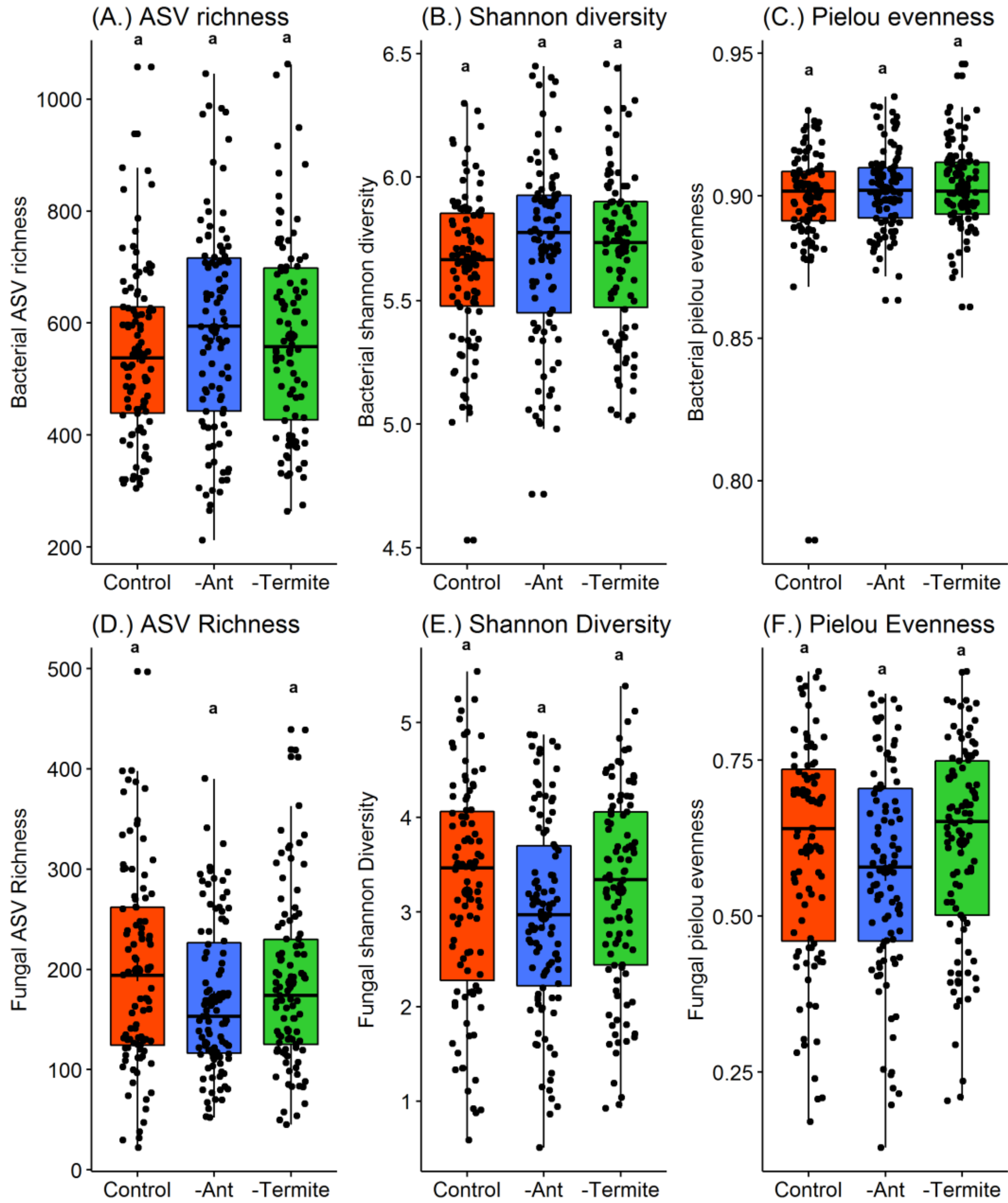

***Figure 3.3** - Bacterial and fungal richness, Shannon diversity and pielou evenness calculated from control, ant suppression and termite suppression treatment plots. Raw data is overlaid as black points for reference. Lowercase letters denote significant differences between treatments.*

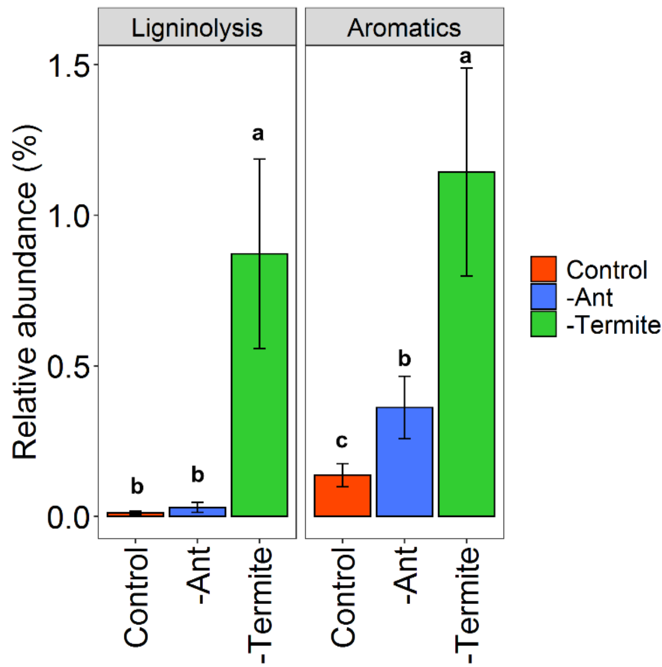

***Figure 3.4** – Relative abundance of Bacterial taxa capable of ligninolysis and aromatic compound degradation. Putative function was assigned to taxonomic data using FAPROTAX. Bars represent means and error bars represent 1 standard error. Lowercase letters denote significant differences between treatments.*

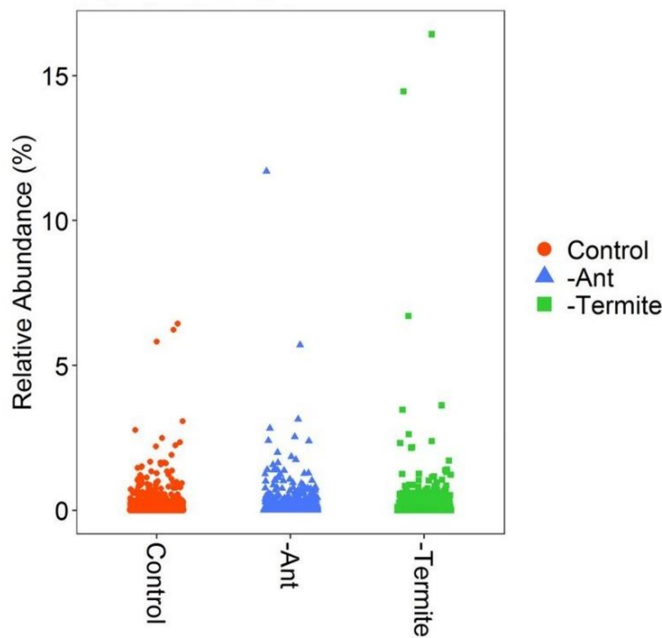

***Figure 3.5** - Relative abundance of lignolytic fungi across control, ant suppression and termite suppression treatments. Differences in variance between Control – ant suppression and Control – termite suppression were tested using Fligner-Killeen tests.*

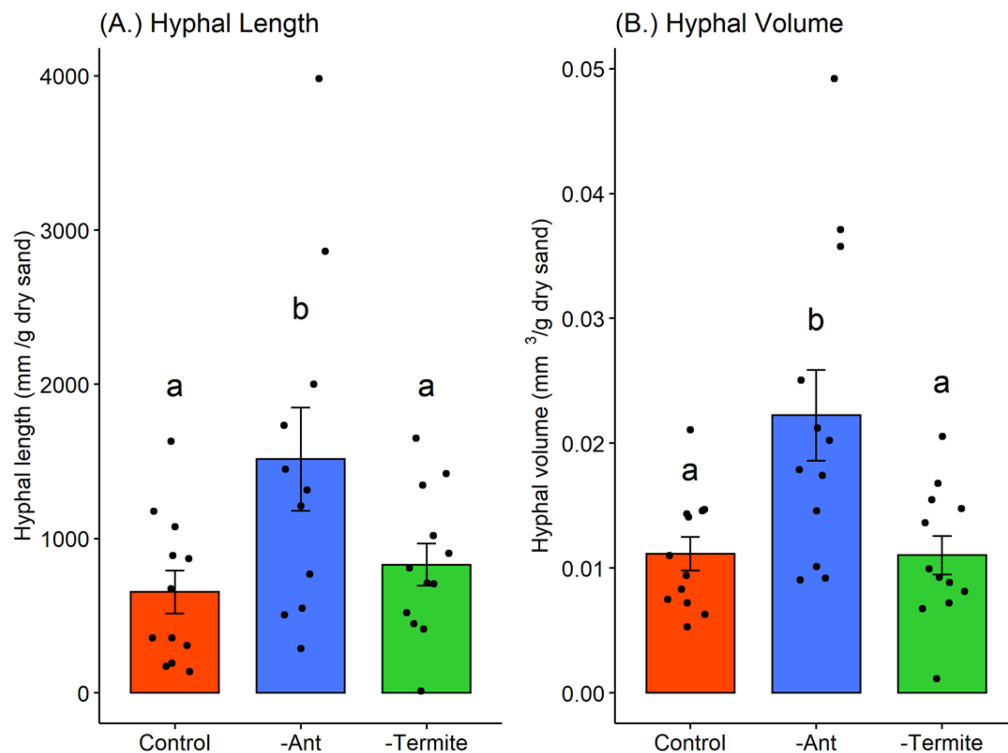

Figure 3.6 *- Fungal hyphal productivity measured using in situ hyphal in-growth bags across control ant and termite suppression treatments. Bars represent means. Error bars represent 1 standard error. Raw data is overlaid for reference. Letters represent whether differences between treatments were significant.*

Differential abundance testing of metazoa showed that read counts representing *Amynthas* (a genus of earthworms) were significantly higher under both ant and termite suppression relative to the control treatment. Collembola were significantly higher under ant suppression relative to control treatment whilst read counts representing *Priopus* (a genus of click beetles) and *Termes* (a genus of higher termites) were lower in both ant and termite suppression treatments relative to the control (Figure 3.7). Parasitic mites (genus: *Polyaspis* and *Varroa*) were also lower under ant and termite suppression (Figure 3.7).

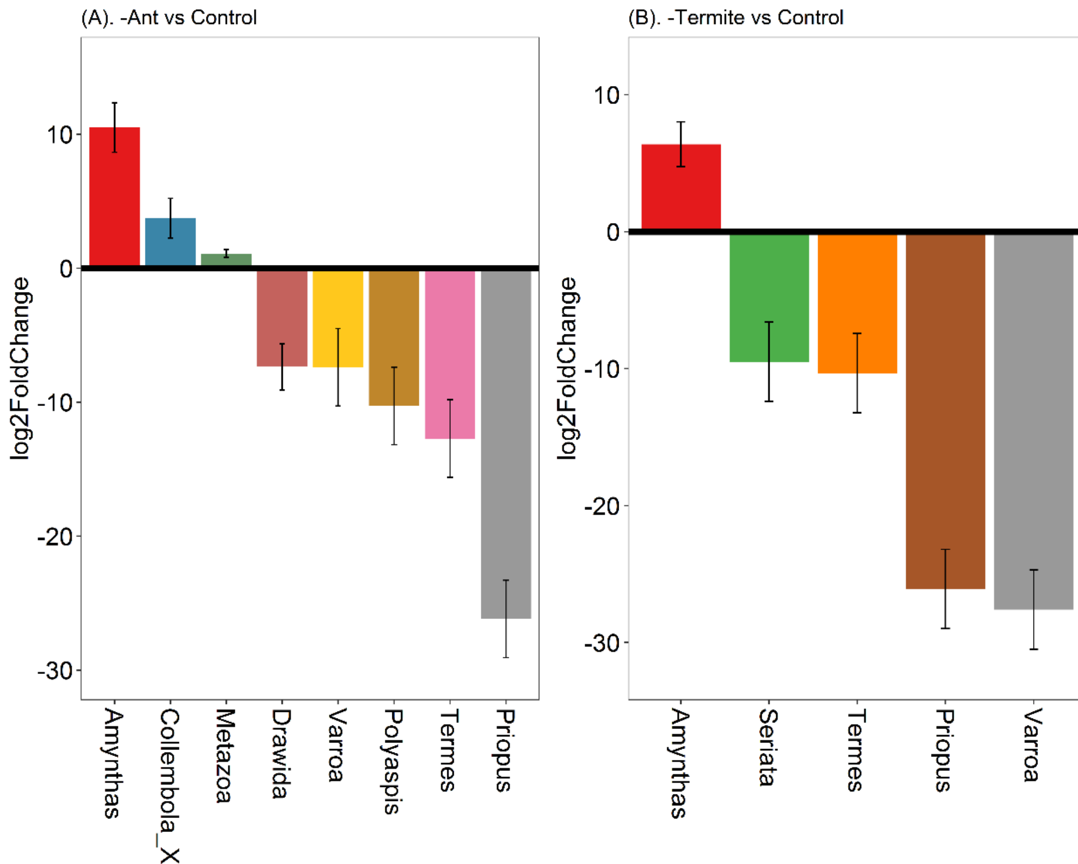

Figure 3.7 *- Differential abundance of soil metazoan genera between control - ant suppression (A.) and control – termite suppression (B.) treatments. Low prevalence taxa (not present in at least 1% of samples) were removed prior to analysis. Only genera that were significantly different between treatments (p-value of <0.05) are presented. A Log2Fold Change (L2FC) can be interpreted as follows: If there is a two-fold increase (fold change= 2, L2FC = 1) between A and B, then A is twice as big as B (or A is 200% of B). If there is a two-fold decrease (fold change = 0.5, L2FC = -1) between A and B, then A is half as big as B (or B is twice as big as A, or A is 50% of B). A positive L2FC represents an increase in the taxon abundance in Ant or Termite suppression treatment plots relative to the Control plots whilst a negative L2FC represents a decrease in the taxon abundance in the in Ant or Termite suppression treatment plots relative to the Control plots.*

3.4.2 Microbial co-occurrence networks

The topology of cross domain soil microbial co-occurrence networks was different between control, ant and termite suppression treatments (Figure 3.8, Table 3.2). The control network consisted of 343 nodes and 2214 edges. The ant suppression network had 341 nodes and 2683 edges whilst the termite suppression network had 309 nodes and 2409 edges (Figure 3.8, Table 3.2). The node degree distribution was different between control – ant suppression (D = 0.15, p = <0.001) and control – termite suppression (D = 0.11, p = <0.001). Mean node degree was significantly different between Control – Ant suppression (p = <0.001), and between Control – Termite suppression (p = 0.005). The global clustering coefficient (measure of the degree to which nodes in a graph tend to cluster together) was higher in ant suppression (p = <0.001) and termite suppression (p = <0.001) relative to control as was closeness centrality (Measure of the average distance between a node and all other nodes in the network) (Control – Ant: p = <0.001, Control – Termite: p = <0.001). Betweenness centrality (Measure of the number of times a node acts as a bridge along shortest paths between other nodes in the network) was not different between control treatment and either ant (p = 0.67) or termite suppression (p = 0.17).

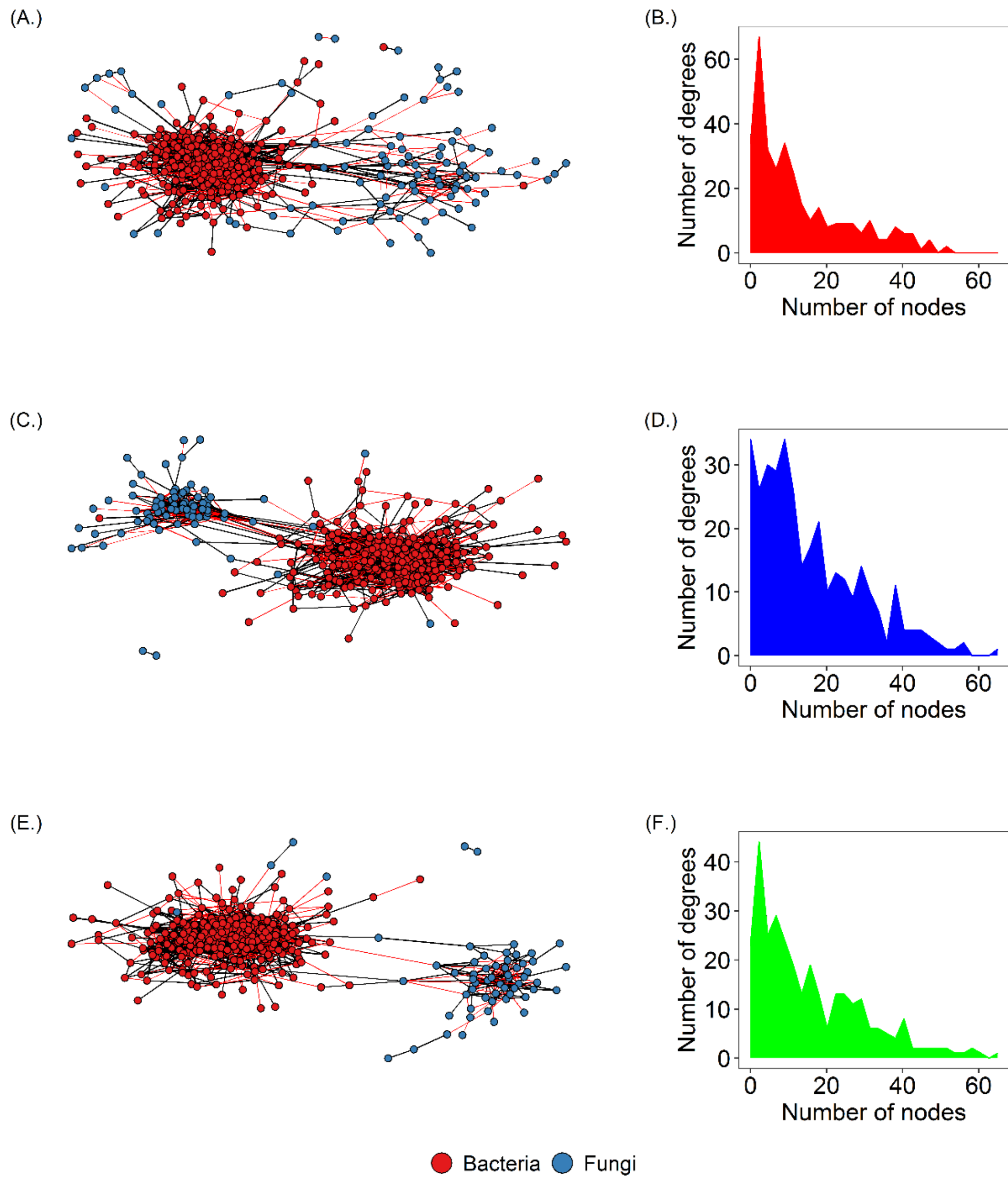

Figure 3.8 *- Soil microbial co-occurrence networks and distribution of node degrees from control (A-B), ant suppression (C-D) and termite suppression (E-F) treatments. Networks were constructed from bacteria and fungal ASV's using cross-domain SPIEC-EASI. In all networks, nodes represent ASV's and are coloured by domain whilst edges represents a predicted interaction, either positive (black) or negative (red). Degree indicates the number of associations shared by each node in a network.*

Soil fungal networks from control, ant and termite suppression treatments displayed marked differences in their structure and topological parameters (Figure 3.9). The control network consisted of 89 nodes and 165 edges. The ant suppression network had 52 nodes and 169 edges whilst the termite suppression network had 52 nodes and 127 edges (Table 3.2). Control networks were more modular (A modularity score > 0.4 suggests that a network has a modular structure) and had lower edge density (ratio of number of edges relative to the number of possible edges) relative to ant and termite suppression (Table 3.2, Figure 3.9). The node degree distribution was different between control – ant suppression ($D = 0.28$, $p = <0.001$) and control – termite suppression ($D = 0.17$, $p = <0.001$). Mean node degree was significantly different between Control – Ant suppression ($p = 0.003$), but not between Control – Termite suppression ($p = 0.23$). The global clustering coefficient was higher in ant suppression ($p = <0.001$) and termite suppression ($p = <0.001$) relative to control as was closeness centrality (Control – Ant: $p = <0.001$, Control – Termite: $p = <0.001$). Betweenness centrality was higher in the control treatment relative to either ant ($p = 0.002$) or termite suppression ($p = 0.004$).

Table 3.2 *- Topological properties describing cross – domain and fungal co-occurence networks. Nodes represent ASV's whilst edges represent positive or negative interactions between nodes. Max degree is the node with most edges linking to other nodes in the network. Mean shortest path length is the average number of steps along the shortest paths for all possible pairs of network nodes. Clustering coefficient is a measure of the degree to which nodes in a graph tend to cluster together. Closeness centrality measures the average distance between a node and all other nodes in the network. Betweenness centrality represents the role of nodes as a bridge between different components of the network. Mean degree is the mean number of edges per node whilst the edge density represents the ratio of the number of edges relative to the maximum number of edges. Modularity describes the presence of distinct sub-communities or "modules" (A modularity score of >0.4 indicates modularity) whilst degree assortativity describes the tendency for nodes with similar degree to connect to each other (positive) or not (negative).*

	Cross Domain networks			**Fungal networks**		
	Control	**-Ant**	**-Termite**	**Control**	**-Ant**	**-Termite**
Nodes	343	341	309	89	52	52
Positive Edges	1226	1551	1426	105	108	76
Negative Edges	988	1132	983	60	61	51
Total number of edges	2214	2683	2409	165	169	127
Max Degree	52	64	65	14	22	21
Mean shortest path length	3.48	3.21	3.42	3.85	2.48	2.62
Mean Clustering Coefficient	0.29	0.331	0.351	0.254	0.559	0.361
Mean Betweenness Centrality	418.55	374.21	369.86	108.62	36.38	38.13
Mean Closeness Centrality	0.0009	0.001	0.001	0.0036	0.0085	0.0084
Mean degree	12.91	15.74	15.59	3.71	6.5	4.88
Edge Density	0.038	0.046	0.051	0.042	0.127	0.096
Modularity	0.3	0.39	0.35	0.56	0.3	0.32
Degree Assortativity	0.32	0.24	0.22	0.34	0.01	0.01

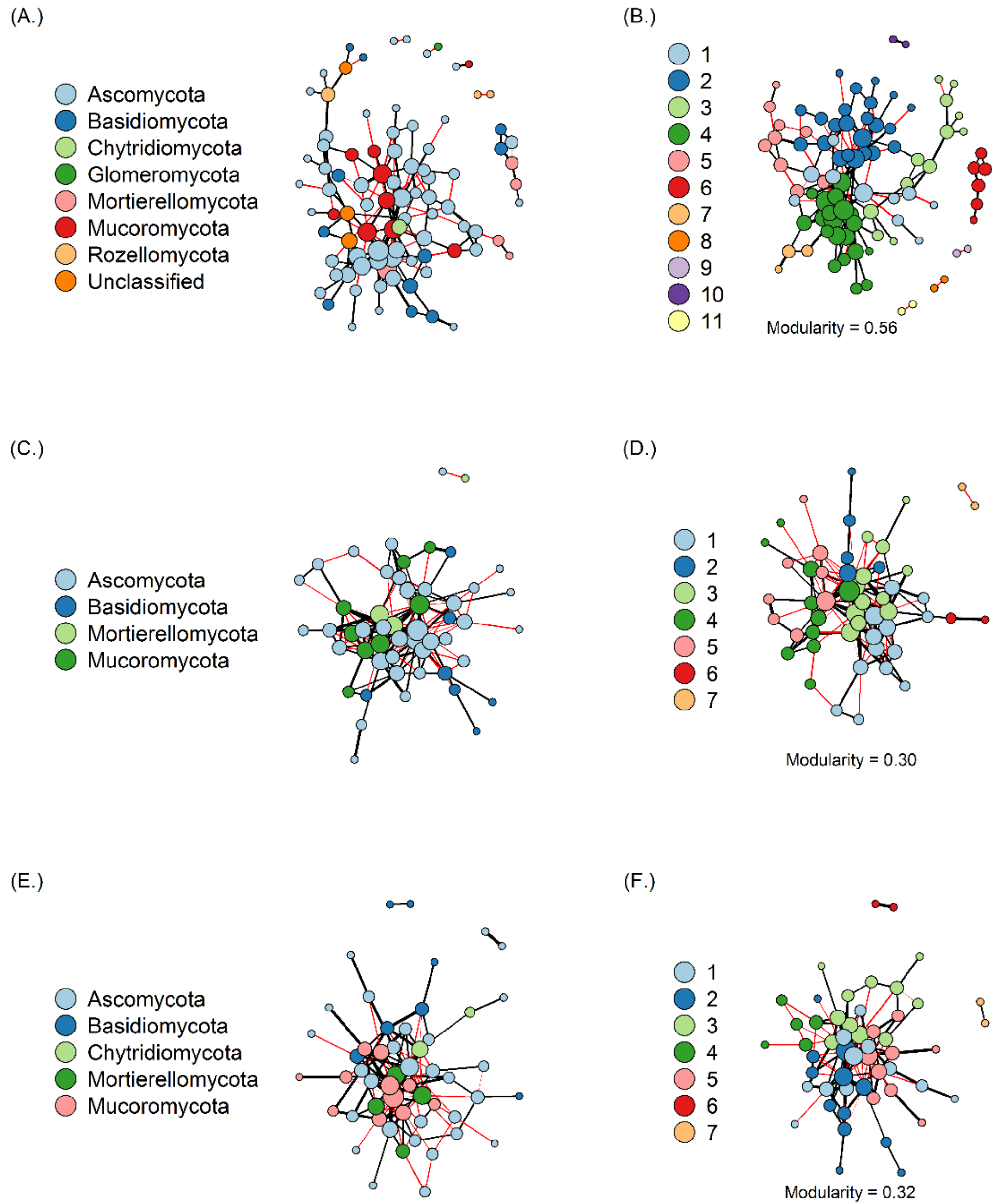

Figure 3.9 *- Soil fungal co-occurrence networks from control (A-B), ant suppression (C-D) and termite suppression (E-F) treatments constructed using SPIEC-EASI. In all networks, nodes represent ASV's whilst edges represents a predicted interaction, either positive (black) or negative (red). Node size is scaled by the node degree and edge width is scaled by the strength of the interaction. Nodes in networks A, C and E are coloured by phyla whilst nodes in networks B, D and F are coloured by module inferred using the fast greedy modularity optimization algorithm for finding community structure in networks.*

3.5 Discussion

Contrary to hypothesis 1, traditional metrics of bacterial and fungal α-diversity were not sensitive to ant or termite suppression and did not differ between treatments (Figure 3.3). Although invertebrate-microbial interactions have not previously been studied at the field scale in tropical forests, α-diversity indices have been shown to lack sensitivity to chronic or low intensity disturbances (Karimi et al., 2017; Wood et al., 2017). We also predicted that microbial communities would become more homogeneous under invertebrate suppression due to reduced soil microhabitat heterogeneity (Donovan et al., 2001; Farji-Brener and Werenkraut, 2017). However, the heterogeneity of fungal communities was actually increased by both ant and termite suppression relative to the control plots (Appendix 2: Figure 8.5). This is surprising as through foraging, nesting and mound building activities, both ants and termites can promote soil heterogeneity by creating nutrient hotspots and areas of relative nutrient depletion (Ashton et al., 2019; Farji-Brener and Werenkraut, 2017; Lu et al., 2019), which are often drivers of fungal community composition (Camenzind et al., 2018; Schappe et al., 2017). It is possible that the sampling scale (regular 5 m spaced grid) used was too coarse to detect finer scale patterns in fungal community composition associated with ant nests, termite mounds and galleries, which could drive fungal community heterogeneity. However, a recent study showed that ants were responsible for greater than 50 % of resource redistribution across the forest floor (Griffiths et al., 2018). Therefore, with a reduction in nutrient transport and soil fertility hotspots under ant suppression, fungi appear to increase spatial coverage to acquire nutrients from more diffuse sources, by investing in increased hyphal networks.

In support of this theory and in agreement with hypothesis 2a, when ant activity was suppressed, fungal hyphal productivity was stimulated (Figure 3.6). This suggests that ant activity may regulate fungal productivity indirectly through modulation of soil nutrient availability and distribution. Increased fungal hyphal productivity under ant suppression may also be linked to interactions with other soil fauna as it has been shown that this can exert top down selective grazing pressure on soil fungi (Crowther and A'Bear, 2012; Crowther et al., 2011b; Crowther et al., 2013). Our findings indicate that the abundance of Collembola sp. (springtails), an important soil mycophage, may have increased under ant suppression (Figure 3.7) in a compensatory response to lower predation pressure. This finding was in agreement with monitoring of non-ant invertebrate abundance at bait cards which also showed an 80 % increase in Collembolan abundance in response to ant suppression (Griffiths et al., 2018). Whilst ants are mainly generalist or opportunistic predators, some genera have specializations to hunt prey such as collembola (e.g. Formicidae: Strumigenys spp) (Ohkawara et al., 2017). Collembolan grazing can suppress fungal hyphal productivity at high population densities, however more often stimulates hyphal growth (Crowther et al., 2011b; Crowther et al., 2011c).

In the tropics, termites play an important role in the mineralization of C and nutrients stored within dead wood on the forest floor (Cornwell et al., 2009; Ulyshen, 2016). In agreement with hypothesis 2b, we found that when termite activity was suppressed, bacteria capable of ligninolysis and aromatic compound degradation was significantly higher relative to both ant suppression and control treatments (Figure 3.4). This suggests an interaction between the activity of large bodied, wood feeding termites, which contribute significantly to deadwood decomposition in tropical forests (and were most affected by the suppression treatments imposed) and the abundance of

bacterial lignin degraders. Although lignin catabolism by wood – feeding termites is somewhat controversial (Geib et al., 2008; Griffiths et al., 2013; Sethi et al., 2013), the Macrotermitinae maintain a mutualism with Termitomyces fungi, which allows for the complete utilization of all constituents of dead wood (cellulose, hemicellulose and lignin) (Aanen et al., 2002). Macrotermes (a genera of Macrotermitinae) abundance was strongly reduced by the suppression treatments imposed here (See supplementary information within Ashton et al. (2019)), which reduced rates of wood decomposition by 58-64 % across these plots over 2 years (Griffiths et al., 2019). This indicates that increased stocks of dead wood and coarse woody debris on the forest floor under termite suppression may have led to increased abundance of bacteria capable of utilizing lignin or lignin depolymerization products as a C source. We did not measure a difference in the mean relative abundance of lignolytic fungi between termite suppression and control treatments although heterogeneity within treatments was significantly higher under termite suppression (Figure 3.5). This also suggests that termites interact indirectly with microbial decomposers by modulating the availability and distribution of dead wood across the forest floor. Although lignin depolymerization results in a wide variety of aromatic compounds (Brink et al., 2019), it must be acknowledged that the insecticides applied to invertebrate suppression treatments may have also influenced the abundance of bacterial aromatic compound degraders. However, the differing abundance of bacterial aromatic degraders between ant and termite suppression treatments, which both received insecticide treatments suggests that reduced termite activity was the strongest driver.

Microbial co-occurrence networks are used to examine the response of soil microbial communities to disturbance and can elucidate community structural changes not observed in standard diversity or relative abundance metrics (Khan et al., 2018;

Lupatini et al., 2014; Wood et al., 2017). In agreement with hypothesis 3, cross-domain and fungal co-occurrence networks were more complex (Higher mean degree, closeness centrality) under ant and termite suppression (Figure 3.8, Figure 3.9, Table 3.2), whilst fungal networks were more modular in the control treatment (Figure 3.9). Network properties such as high degree connectivity and low modularity suggest stronger interactions between species. This may drive instability and low resilience to disturbance (Coyte et al., 2015; de Vries et al., 2018; Peura et al., 2015). This suggests that soil microbial networks may be stabilized by the presence and activity of ants and termites. Network complexity has also recently been associated with increased ecosystem multifunctionality (Wagg et al., 2019), suggesting that ant and termite suppression may have elicited a compensatory functional response in soil microbial communities. Networks are a valuable ecological tool, but the biological implications of network properties are still unclear and therefore solid conclusions should not be drawn solely from the network inferences made (Röttjers and Faust, 2018). However, these findings are useful as a generator of new hypotheses for further experimentation.

3.6 Conclusions

Our findings suggest that ant activity regulates fungal hyphal productivity, likely through controls on nutrient re-distribution and interactions with other soil fauna. Termite activity influenced the distribution of lignolytic fungi and abundance of putative bacterial lignin degraders. Our findings also suggest that both ant and termite activity promotes stabilizing properties of cross-domain and fungal co-occurrence networks in tropical forests. These findings significantly advance our understanding of invertebrate-microbial interactions in tropical forests, which is important as widespread logging has altered the functional diversity of both invertebrates and microbes. Our findings also suggest that the abundance of key invertebrates should be

considered as drivers of microbial composition and stability and change in tropical forests.

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4 Soil microbial community and litter quality controls on decomposition across a tropical forest disturbance gradient

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4.1 Abstract

Industrial logging and agricultural expansion are driving rapid transformations of tropical ecosystems, modifying patterns in above-ground plant and below-ground microbial communities. However, the extent to which these changes in biodiversity drive modifications of ecosystem process rates such as leaf litter decomposition is poorly understood. To determine the relative effects of changes to the chemical quality of litter and shifts in microbial decomposers on leaf litter decomposition rates, we performed a controlled, reciprocal transplant, litter decomposition experiment across a tropical land-use disturbance gradient. Litter mixtures and soils were collected from old growth forest, moderately logged forest, heavily logged forest and oil palm plantation in Sabah, Malaysia, and combined in a fully crossed, factorial microcosm experiment maintained under controlled environmental conditions. We found that whilst litter quality was the most important predictor of litter mass loss, soil origin (land use) was also significant, explaining between 5.17-15.43 % of total variation. Microbial decomposer communities from old growth forest had greater functional breadth relative to those from logged forests and oil palm plantation as all

litter types decomposed faster when combined with old growth soil. The most chemically recalcitrant litter (lowest N, highest lignin, lignin:N and C:N ratio) from moderate logged forest decomposed faster when combine with its “home” soil (Home-Field Advantage) whilst the most labile litter from oil palm decomposed slowest when combined with its “home” soil. This was correlated with lower total soil microbial biomass. Taken together, these findings demonstrate that whilst litter quality regulated rates of litter decomposition across the disturbance gradient, soil microbial decomposer communities were functionally dissimilar between land uses and explained a significant proportion of variation. The impact of disturbance on soil, including microbial community structure, should be considered alongside changes to plant communities when assessing effects on crucial ecosystem processes such as decomposition.

4.2 Introduction

The decomposition of non-living organic matter is a fundamental process in the carbon cycle, releasing CO_2 whilst recycling nutrients to support ecosystem productivity. The chemical quality of organic matter, abiotic environmental conditions and microbial decomposer communities all influence decomposition dynamics (Bradford et al., 2016; Currie et al., 2010; Makkonen et al., 2012). Microclimate and litter traits are widely considered as key constraints regulating rates of litter decomposition (Bradford et al., 2014; Cornwell et al., 2008; Djukic et al., 2018; Gholz et al., 2000; Makkonen et al., 2012; Meentemeyer, 1978; Wall et al., 2008; Zhang et al., 2008). However, litter decomposition is ultimately a microbially mediated process. Therefore, the abundance and structure of soil decomposer communities may also drive local variation in rates of decomposition, but the role of microbial community composition is currently not well understood (Bradford et al., 2017). Identification of the factors regulating litter decomposition rates is necessary to inform biogeochemical models on how ecosystem organic matter stocks and thus the magnitude of biosphere-atmosphere feedbacks will respond to anthropogenic disturbance and future environmental change (Bonan et al., 2013).

Globally, tropical forests are threatened by industrial logging, fire and deforestation for agricultural expansion with degraded and secondary forest now comprising over half of all remaining tropical forests (Laurance et al., 2014; Potapov et al., 2017). Southeast Asia is a deforestation hotspot, driven primarily by agricultural expansion of oil palm and commercial timber plantations (Estoque et al., 2019; Gibbs et al., 2010). Remaining lowland tropical forests in the region are heavily degraded, due in part to the high density of commercially valuable, dipterocarp timber species (Achard et al., 2002; Sodhi et al., 2004). Degradation of tropical forests modifies regional

above - ground species distributions and community composition across the tropics, driving changes to functional diversity and leaf litter traits (Bakker et al., 2011; Baraloto et al., 2012; Both et al., 2019; Carreño-Rocabado et al., 2012; Ding et al., 2019). In South East Asian dipterocarp forests, logging disturbance appears to shift tree communities from those with resource conservative traits, prioritising structural and defence tissues to those with more resource acquisitive traits promoting carbon capture and growth (Both et al., 2019). Given the important role of leaf traits in determining litter quality, this shift may drive changes to rates of litter decomposition within tropical forests (Cornwell et al., 2008). However, evidence from a field experiment showed that subtle differences in microclimate rather than litter quality explained most variation in litter decomposition rates in tropical forest (Both et al., 2017). In contrast to tropical forests where litter inputs are continuous and distributed across the forest floor, oil palm plantation litter is comprised primarily of senesced fronds. These are typically pruned manually twice a year and green fronds may also be pruned during harvesting to access fruit bunches (Corley and Tinker, 2015). These are stacked in piles or rows, therefore significant aboveground C inputs occur only within the vicinity of these frond piles in mature plantations (Ruegg et al., 2019). Leguminous cover crops may also be planted in in young plantations to stabilise soils and improve fertility (Luke et al., 2019).

Tropical land use change can also drive parallel shifts in soil microbial decomposer communities (Kerfahi et al., 2014; McGuire et al., 2015; Mueller et al., 2016; Rodrigues et al., 2013; Shi et al., 2019b; Tripathi et al., 2016; Tripathi et al., 2012). Theory proposes that the immense diversity of microbial communities should confer a high level of functional redundancy, particularly with regard to bulk processes such as litter decomposition (Allison and Martiny, 2008; Nannipieri et al., 2003). However,

experimental work suggests that changes to bacterial and fungal community composition can alter rates of litter decomposition (Allison et al., 2013; Cleveland et al., 2014; Martiny et al., 2017; Strickland et al., 2009b). The specific mechanisms underpinning functional dissimilarity are not well understood, but two hypotheses have been proposed. The functional breadth hypothesis (FBH) states that decomposer communities from recalcitrant litter environments have wider functional abilities. This confers the capability to degrade a wide range of substrates efficiently, at similar rates with low enzyme activities and microbial biomass per unit of decomposition (Keiser et al., 2011; Van Der Heijden et al., 2008). FBH has been demonstrated with decomposer communities from forest habitats decomposing low quality litter (e.g. low N, high lignin content, lignin:N and C:N ratios) faster than communities from other ecosystems whilst high quality litter was decomposed equivalently across ecosystems (Fanin et al., 2016; Strickland et al., 2009a; Strickland et al., 2009b). Alternatively, the home-field advantage hypothesis (HFA) states that litter decomposes more rapidly in an environment dominated by, or in the vicinity of the species it is derived from (Home) rather than in a foreign environment (Away) due to functional specialisation of decomposer communities (Gholz et al., 2000). HFA has been demonstrated in numerous ecosystems but is not universal and appears to be highly context dependent (Ayres et al., 2009b; Lin et al., 2019; Veen et al., 2018; Wang et al., 2013). It has also been shown that the HFA effect becomes more pronounced as home and away litters become more dissimilar (Veen et al., 2015).

In South East Asian dipterocarp forests, most trees and plants form arbuscular mycorrhizal associations but the canopy is often dominated by a subset of commercially valuable tree species from the Dipterocarpaceae family, all of which form ectomycorrhizal (EcM) associations (Brearley, 2012). Selective removal of these

tree species can lead to a reduction in abundance and shifts in community composition of EcM fungi (Kerfahi et al., 2014; McGuire et al., 2015), which may influence decomposition processes through changes to competitive dynamics with saprotrophic fungi (Corrales et al., 2018; Fernandez and Kennedy, 2016). In oil palm plantations, roots are heavily colonized by arbuscular mycorrhizal fungi (AMF) (Phosri et al., 2010), whilst EcM fungi are almost absent (McGuire et al., 2015). Although AMF are not thought to have saprotrophic capabilities, they can enhance rates of litter decomposition (Gui et al., 2017).

To test whether human modification of tropical ecosystems altered the functional capabilities of microbial decomposer communities, and to quantify the relative effects of litter quality and microbial decomposers on litter decomposition rates, we conducted a controlled decomposition experiment with reciprocal litter transplants in microcosms under controlled environmental conditions. Using soil and litter mixtures from a tropical land-use disturbance gradient spanning old growth (OG) forest, moderately logged (ML) forest, heavily logged (HL) forest and oil palm plantation, we tested three non-exclusive hypotheses that: (1) Litter quality would explain the majority of variation in litter decomposition rates and thus be largely independent of the decomposer community; (2) Soil microbial decomposer communities from forests would have greater functional breadth relative to oil palm plantations (i.e. microbial decomposers from forests would decompose all litters faster than those from oil palm) but be functionally equivalent between OG and logged forests; (3) Higher rates of litter decomposition would be observed where litter and soil shared a common origin (HFA).

4.3 Materials and methods

4.3.1 Research sites

The study sites were located on orthic Acrisols in the Malaysian state of Sabah on the island of Borneo. The regional climate is moist tropical with annual daily mean temperature of 26.7 °C and annual precipitation totals of approximately 2,600 – 2,700 mm (Kumagai and Porporato, 2012; Walsh and Newbery, 1999). Four 1 ha research plots comprised of 25 20x20 m subplots were selected that form part of the Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/). These were chosen to represent a tropical land - use disturbance gradient including OG tropical forest, ML tropical forest, HL tropical forest and monoculture oil palm plantation. The OG forest plot was located within Danum Valley Conservation Area (DVCA). This forest has experienced little modern disturbance and has been protected since 1976 (Marsh and Greer, 1992). The most common tree genera within the plot were *Shorea* (Dipterocarpaceae) and *Diospyros* (Ebenaceae) with a low abundance of pioneer trees (0.1 ± 0.0 % of basal area) and high basal area of standing trees (30.6 ± 3.37 m^2 ha^{-1}) (Riutta et al., 2018). Plots representing ML forest, HL forest and oil palm were within research sites located in the Kalabakan Forest Reserve and neighbouring Benta Wawasan oil palm estate. These were established as part of the Stability of Altered Forest Ecosystems (SAFE) project and within the Yayasan Sabah Forest Management Area (Ewers et al., 2011) (www.safeproject.net). In the logged forest sites, the most common tree genera were *Macaranga* (Euphorbiaceae), *Shorea* (Dipterocarpaceae), and *Syzygium* (Myrtaceae). The ML forest plot had medium abundance of pioneer trees (6.9 ± 2.2 % of basal area) and medium basal area of standing trees (19.3 ± 1.7 m^2 ha^{-1}) whilst the HL forest plot had the highest abundance of pioneer trees (28.1 ± 4.3 % of basal area) and lowest standing tree basal area (6.81

± 1.0 m^2 ha^{-1}) of the 3 forest plots (Riutta et al., 2018). Both logged forest plots (ML, HL) were subjected to one round of logging during the 1970's. The ML forest plot was subsequently logged once whilst the HL forest plot was logged three times between 1990-2008. Logging operations targeted primarily hardwoods from the genera *Dryobalanops* sp., *Dipterocarpus* sp., *Shorea* sp. *and Parashorea* sp. Study plot characteristics are summarized in Table 4.1. For more detailed site characteristics and logging history of forest plots refer to Riutta et al. (2018). For further information on tree communities and functional traits, refer to Both et al. (2019) with reference to the following plots: OG Forest = DAN-05, ML Forest = SAF-04, HL Forest = SAF-01. The oil palm plot was on its first rotation with standing palms ~7 years old at the time of sampling. Fertilizer (compound mixture comprised of diammonium phosphate, potassium chloride, ammonium sulphate, magnesium sulphate and borax) was applied twice a year at a rate of 3-4 kg per palm (Julia Drewer, UKCEH - personal communication). Senesced fronds were stacked in rows between palms whilst inter-row and palm circle soils were kept weed free. No cover crops were present.

4.3.2 Sample collection and preparation

Each 1 ha plot was subdivided into twenty-five 20×20 m subplots with five randomly selected for sampling. Samples taken from these 5 subplots were subsequently treated as individual replicates for each land use type in the incubation. In forest plots, freshly senesced mixed litter was first collected from a 40×40 cm sampling area on the soil surface followed by removal of the organic soil to the horizon with underlying mineral soil. Strongly humified litter was considered as part of the organic soil layer. In the oil palm plantation, surface soils were collected at the edge of the frond stacks. Fresh litter was taken from senesced fronds within the adjacent frond stacks. To account for fronds of different ages we randomly selected 5 fronds for sampling and collected all leaflets from each frond. Leaf litter samples were carefully sorted by hand to remove woody debris, partially humified leaves and reproductive material. Only intact leaves were retained, which were air dried until constant weight. Fresh soils were homogenized by passing through a 4 mm sieve to remove stones, coarse woody and litter debris and a subsample frozen for phospholipid fatty acid (PLFA) extraction and microbial sequencing. Soil and dried litter samples were sealed in plastic bags and transported on ice in a cool box to the UK. Fresh soil was stored at 4 °C prior to establishment of the experiment. Soil subsamples for PLFA analysis were freeze – dried, passed through a 2 mm sieve and ground to a fine powder using a pestle and mortar. Subsamples for total C, N and inorganic P analysis were dried at 65 °C for 48 hours and ground as described above. Air dried litter was further hand sorted to remove any remaining coarse woody debris and partially decomposed leaves and then chopped into small (< 5 mm) pieces to create a homogenous litter mixture capturing the high species diversity of these tropical forests. Litter was then sterilised by autoclaving twice at 121 °C and then dried at 65 °C to constant weight. We

acknowledge that autoclaving would likely change the initial chemical composition of litter. To quantify this, a subsample of each initial litter mixture (autoclaved and non-autoclaved) was ground to a fine powder using a pestle and mortar for chemical analysis (See Appendix 3: Table 8.6 for non-autoclaved litter chemistry results).

4.3.3 Microcosm Design

Microcosms were constructed in 9 cm diameter plastic petri dishes (Wardle et al., 1998). Fresh soils were adjusted to 70 % of maximum water holding capacity and 10 g dry weight equivalent soil was added to each microcosm. A fine mesh (1 mm) disk was laid on top of the soil and 1 g of the autoclaved, sterilised litter mixture was then added. Microcosms were then partially sealed by taping the lid around the edge to minimize moisture loss. A small section was left open to allow for gas exchange. Our experimental design was 4×4 fully factorial with all litters being crossed with all soils. This reciprocal transplant design was used in order to separate the relative effects of soil microbial decomposer community and litter quality as well as interactive effects (Reed and Martiny, 2007). Each soil and litter had five true field replicates (n = 80 microcosms). This was replicated three times to allow destructive harvesting at three time intervals to capture progressive stages of litter decomposition. Microcosms were maintained in a controlled temperature incubator at 25 °C and weighed weekly to adjust back to 70 % water holding capacity (WHC) by the addition of de-ionised water. Microcosms were destructively harvested after 31, 105 and 398 days. Remaining litter was removed from the mesh disk with tweezers, dried at 65 °C for 24 hours and weighed. The percentage mass loss was used as a proxy for litter decomposition and calculated as the remaining dry litter weight divided by the initial dry litter weight.

4.3.4 Litter and soil analysis

The chemical composition of initial leaf litter (autoclaved and non-autoclaved) was measured as follows: Total C and N were quantified on an elemental analyser (NCS 2500, CE Instruments, UK). Total P was extracted using a sulfuric acid/hydrogen peroxide digest and analysed on a flow injection auto analyzer (FIAStar 5000, Foss Tecator, Denmark). Ca, K, Mg and Al were extracted by sulfuric acid digestion and measured using atomic absorption spectroscopy (AAS, Perkin Elmer AAnalyst 100, MA, USA). Fibre analysis (soluble cell content, hemicellulose + proteins, cellulose, lignin + recalcitrants) was performed using automated sequential digestion (ANKOM Technology, Macedon, NY, USA).

Soil pH was measured on fresh subsamples in a 2.5:1 water: soil slurry suspension, allowed to rest for 30 minutes and measured using a pH meter calibrated between pH 4 - 7 (pH210 Meter, Hanna Instruments, UK). Total soil C and N was measured using a LECO Truspec Micro elemental analyser (LECO Corporation, USA). Inorganic P was extracted from soils using a Bray No 1 extractant and analysed using colorimetry on a SEAL AutoAnalyzer 3 (Seal Analytical, UK).

PLFAs were extracted from freeze-dried soils as part of the total lipid extract using a modified Bligh-Dyer extraction (White et al., 1979). Identification of PLFA's was carried out on a GC (Agilent Technologies 6890) fitted with a flame ionization detector (Agilent Technologies 5973). Sample PLFA peaks were identified based on known relative retention times. The terminal and mid - chain branched fatty acids C15:0i, C15:0a, C16:0i C17:0i and C17:0a were used as indicators of Gram positive bacteria (Whitaker et al., 2014). Cyclopropyl saturated and monounsaturated fatty acids 16:1ω7c, 7,8 cyclic C17:0, C18:1ω7c & 7,8 cy-C19:0 were used as indicators of

Gram negative bacteria (Rinnan and Bååth, 2009). The fatty acids C18:2ω6,9c and C18:1ω9c were taken as indicators of fungi (Willers et al., 2015). Total microbial biomass was calculated as the sum of all identified PLFA's (C13:0, C14:0, C14:1ω5c, C15:0, C15:1ω5c, C16:0, 10Me-C16:0, C16:1ω7t, C16:1ω9c, C16:1ω5c, C17:0, 10Me-C17:0, C18:0i, C17:1ω7c, C18:0a, C18:0, 10Me-C18:0, C18:1ω7t, C18:1ω12c, C18:1ω5c, C18:2ω6t, 9,10-cyC19:0, C19:1ω12c, C20:0, C18:3ω6c, C20:1ω9c, C18:3ω3c, C20:2ω6c, C22:0, C20:3ω6c, C20:4ω6c, C20:5ω3c, C24:0; plus those listed above).

4.3.5 Molecular analyses of soil microbial communities

DNA was extracted from 0.2 g frozen soil using a Powersoil® DNA Isolation Kit according to the manufacturer's instructions. Amplicon libraries were constructed according to a dual indexing strategy with each primer consisting of the appropriate Illumina adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker and the amplicon specific primer (Kozich et al., 2013). For bacteria, V3-V4 16S rRNA amplicon primers were used (CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC) (Kozich et al., 2013). Fungi were targeted by amplifying the ITS2 region using amplicon primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). Amplicons were generated using PCR and a high fidelity DNA polymerase (Q5 Taq, New England Biolabs). Amplicon sizes were determined using an Agilent 2200 TapeStation system and libraries normalized using SequalPrep Normalization Plate Kit (Thermo Fisher Scientific) and quantified using a Qubit dsDNA HS kit (Thermo Fisher Scientific).

Each amplicon library was sequenced separately on Illumina MiSeq using V3 600 cycle reagents at concentrations of 8 pM with a 5% PhiX Illumina control library.

Sequences were processed in R using DADA2 to quality filter, merge (where appropriate), de-noise and assign taxonomies (Callahan et al., 2016). Briefly, 16S forward reads were trimmed to 250 bases. ITS amplicons reads were trimmed to 225 and 160 bases, forward and reverse respectively. Filtering settings were maximum number of Ns (maxN) = 0, maximum number of expected errors (maxEE) = 1. Sequences were dereplicated and the DADA2 core sequence variant inference algorithm applied. ITS sequences were merged using *mergePairs* function, whilst forward reads were used for 16S amplicons. Chimeric sequences were removed using *removeBimeraDenovo* default settings. The actual sequence variants (ASV) were subject to taxonomic assignment using *assignTaxonomy* at default settings; the training databases used were GreenGenes v13.8 and Unite v7.2 for 16S and ITS respectively. Prior to analysis, samples were normalized by rarefying to 28859 reads for 16S and 4349 reads for ITS. Fungal taxa were classified as saprotrophic using FunGuild (Nguyen et al., 2016). Only those taxa with non-ambiguous classifications and assignments classified as “probable” or “highly probable” were retained.

4.3.6 Data analyses

All analyses were performed using R statistical software (version 3.5.2) or SAS version 8.0 (SAS Institute 2008). Differences in initial leaf litter chemistry, soil properties and PLFA concentrations were tested using ANOVA with land use as the independent variable (5 replicates taken from subplots within each land use). Tukey’s honestly significant difference *post hoc* test was used to report pairwise differences between land uses. Initial PLFA profiles were represented in two dimensions using

principal components analysis (PCA). Bacterial, fungal and saprotrophic fungal community composition was represented in two dimensions by principal co-ordinates analysis (PCoA) ordination of Bray- Curtis dissimilarities. Differences in initial microbial community composition were tested using PERMANOVA. ANOVA was used to test the significance of litter and soil origin as predictors of litter mass loss at each time point. Litter mass loss was the dependent variable whilst litter type and soil origin were included as independent variables with an interaction term. To determine which measured soil covariates were the best predictors of litter mass loss we replaced the factor “soil origin” with measured soil variables (soil chemical properties, PLFA concentrations, bacterial, fungal and saprotrophic fungal richness) and performed multiple linear regression. Highly correlated variables were removed a priori and by inspecting variance inflation factors. The best model was selected by forward and backward stepwise model selection using AIC as a criterion. To determine whether initial microbial community composition was predictive of litter mass loss at the final time point (398 d) we used the two axis scores from PCoA on bacteria, fungal and saprotrophic fungal community composition alongside litter type as independent variables in multiple linear regression, with litter mass loss as the dependent variable. For all regression models, the effect size (relative importance) of each independent variable was estimated by averaging over orderings of regressors using the *relaimpo* package and is presented as a percentage of total variance (Groemping, 2006). The Decomposer Ability Regression Test (DART) was used to determine the relative contribution of litter quality, functional breadth of microbial decomposers and home – field advantage in explaining rates of litter mass loss (Keiser et al., 2014).

$$Y_i = \alpha + \sum_{l=1}^{N} \beta_l \, Litter_{l_i} + \sum_{s=1}^{M} \gamma_s \, Soil_{s_i} + \sum_{h=1}^{k} \eta_h \, Home_{h_i} + \epsilon_i$$

Y_i is the litter mass loss (%) for observation i, β_l is the ability of litter mixture *l* (from species 1 to N), γ_s is the ability of the soil decomposer community *s* (From community 1 to M), η_h is the HFA of *h* (from home combinations 1 to K) where Home = $Litter_l$ x $Soil_s$ when l and s are home field pairings. $Litter_l$, $Soils_s$ and $Home_h$ are dummy variables that equal 1 or 0 depending on the presence or absence of the litter species, soil community or home combination, respectively. The intercept α represents the average mass loss for all observations in the dataset after controlling for litter, soil and home – field pairings and ε represents the error term. The parameters to be estimated are β_l (Litter Quality), γ_s (Decomposer Ability) and η_h (Home – Field Advantage).

4.4 Results

4.4.1 Study plot description

All study plots were located on orthic acrisols with similar soil texture (Table 4.1). Plots did vary in terms of altitude, average slope, soil moisture and temperature (Table 4.1). OG forest was at the lowest altitude followed by oil palm, ML forest and HL forest although the range in plot elevation was small (<200 m). OG and HL forest plots were flatter than ML forest and oil palm plots whilst soil moisture was highest in ML forest and lowest in ML forest and oil palm. Soil temperature was highest in oil palm and lowest in ML forest although the range in temperature was small across all plots (1.1 °C) (Table 4.1).

Table 4.1 *- Characteristics of the study plots. Mean of individual subplots ±1 SD (n=5). Soil textural class was calculated from measured percentage sand, silt and clay. Soil type was taken from descriptions of study areas in Marsh and Greer (1992) and Nainar et al. (2015). Soil bulk density was estimated using a volumetric ring (5cm diameter). In each subplot slope was measured using a handheld clinometer and altitude was determined using a GPS barometric altimeter. Soil moisture and temperature were logged at hourly intervals between September 2015 and May 2016 using DeltaT SM150 probes buried horizontally to 5cm depth. Superscript letters denote whether parameters were significantly different between study plots from Tukey's HSD test. Significant differences (p <0.05) between plots are indicated when letters are different. Non – significant differences (P >0.05 between plots are indicated when letters are shared. DVCA = Danum Valley Conservation Area, SAFE = SAFE project area within the Kalabakan Forest Reserve.*

Location	Land Use	Plot Code	Soil type	Soil texture	Soil bulk density (g cm^{-3})	Altitude (m)	Slope (°)	Soil Moisture (%)	Soil Temperature (°C)	Mean Annual Rainfall (mm)
DVCA	OG Forest	DAN-05	Orthic Acrisol	Sandy Clay Loam	0.55 (0.08)	^{d}222 (7)	^{b}12 (2)	^{b}28.8 (6.2)	^{b}25.2 (0.4)	3052
SAFE	ML Forest	SAF-01	Orthic Acrisol	Sandy Clay Loam	0.71 (0.05)	^{b}368 (8)	^{a}25 (9)	^{c}24.8 (5.7)	^{c}24.8 (0.8)	2717
SAFE	HL Forest	SAF-04	Orthic Acrisol	Sandy Loam	0.79 (0.08)	^{a}399 (8)	^{b}11 (6)	^{a}32.6 (4.2)	^{d}24.4 (0.5)	2717
SAFE	Oil Palm	-	Orthic Acrisol	Clay Loam	1.10 (0.29)	^{c}327 (3)	^{ab}18 (2)	^{c}24.1 (0.8)	^{a}25.5 (0.2)	2717

4.4.2 Litter quality and soil microbial communities

Multiple litter chemistry parameters were different between land uses (Table 4.2). Foliar P ($F_{3,16}$ = 296.55, p = <0.001), hemicellulose + proteins ($F_{3,16}$ = 140.72, p = <0.001) and cellulose ($F_{3,16}$ = 30.07, p = <0.001) were higher in oil palm litter relative to all forest sites, whilst soluble cell content ($F_{3,16}$ = 21.85, p = <0.001) and lignin + recalcitrant ($F_{3,16}$ = 54.09, p = <0.001) were lower. Lignin:N ($F_{3,16}$ = 8.51, p = <0.001) and C:N ($F_{3,16}$ = 22.41, p = <0.001) ratios were highest in ML forest litter relative to OG forest, HL forest and oil palm (Table 4.2). Base cations varied between land uses (K: $F_{3,16}$ = 9.48, p = <0.001), Mg: $F_{3,16}$ = 32.83, p = <0.001, Ca: $F_{3,16}$ = 49.23, p = <0.001). K, and Mg were lowest in ML forest whilst Ca was highest in HL forest (Table 4.2). Foliar C, N and Al were not different between land uses (Table 4.2).

Table 4.2 *- Chemical properties of autoclaved litter mixtures taken from old growth (OG) forest, moderate logged (ML) forest, heavily logged (HL) forest and oil palm plantation. Data are means (n = 5) ± 1 SE. Superscript letters denote whether parameters were significantly different between land uses from pairwise Tukey's HSD test. Significant differences (p <0.05) between land uses are indicated when letters are different. Non – significant differences (P >0.05 between land-uses are indicated when letters are shared.*

	OG Forest	**ML Forest**	**HL Forest**	**Oil Palm**
C (%)	^{a}43.38 (0.91)	^{a}47.95 (7.45)	^{a}39.02 (0.58)	^{a}41.12 (0.77)
N (%)	^{a}1.65 (0.08)	^{a}1.44 (0.35)	^{a}1.78 (0.05)	^{a}1.91 (0.08)
P (µg/g)	^{b}0.64 (0.02)	^{c}0.37 (0.01)	^{b}0.70 (0.02)	^{a}1.21 (0.03)
K (µg/g)	^{a}4.34 (0.22)	^{b}2.18 (0.69)	^{a}4.51 (0.21)	^{a}5.09 (0.35)
Ca (µg/g)	^{b}12.76 (0.44)	^{c}9.06 (0.41)	^{a}14.96 (0.66)	^{c}7.70 (0.32)
Mg (µg/g)	^{a}3.39 (0.06)	^{c}2.06 (0.08)	^{b}2.82 (0.07)	^{b}2.70 (0.15)
Al (µg/g)	^{a}2587.75 (879.88)	^{a}3882.64 (1042.63)	^{a}4392.22 (1530.61)	^{a}4064.65 (825.35)
Soluble Cell Content (%)	^{a}32.26 (0.77)	^{a}31.06 (0.62)	^{a}33.13 (0.67)	^{b}25.24 (0.95)
Hemicellulose + Proteins (%)	^{b}7.41 (0.42)	^{b}9.87 (0.21)	^{c}6.98 (0.24)	^{a}16.25 (0.50)
Cellulose (%)	^{b}22.02 (0.32)	^{b}21.76 (0.27)	^{b}22.56 (0.61)	^{a}29.46 (1.11)
Lignin + Recalcitrants (%)	^{a}38.25 (0.42)	^{a}40.14 (0.62)	^{b}34.39 (1.03)	^{c}29.00 (0.39)
C:N Ratio	^{b}26.57 (1.57)	^{a}35.33 (2.05)	^{b}21.98 (0.46)	^{b}21.66 (0.59)
Lignin:N Ratio	^{ab}23.43 (1.31)	^{a}32.58 (4.77)	^{b}19.40 (0.84)	^{b}15.31 (0.67)

Soil properties also differed between land uses (

Table **4.3**). Soil moisture ($F_{3,16}$ = 39.32, p = <0.001), total C ($F_{3,16}$ = 3.64, p = 0.04) and C:N ratio ($F_{3,16}$ = 27.76, p = <0.001) were lowest in oil palm and highest in ML forest whilst soil pH ($F_{3,16}$ = 20.73, p = <0.001) was lowest in ML forest and highest in OG forest (

Table **4.3**). Total PLFA ($F_{3,16}$ = 4.38, p = 0.02), bacterial PLFA ($F_{3,16}$ = 4.25, p = 0.02) and G- PLFA ($F_{3,16}$ = 7.66, p = 0.002) concentrations were all highest in ML forest and lowest in oil palm (

Table **4.3**). Bacterial, fungal and saprotrophic fungal richness varied according to land use (Bacteria: $F_{3,16}$ = 7.48, p = 0.002, Fungi:, $F_{3,16}$ = 3.59, p = 0.04, Saprotrophic Fungi:, $F_{3,16}$ = 5.21, p = 0.01) with lower richness in ML forest relative to OG forest, HL forest and oil palm (

Table **4.3**). Initial bacterial (16S) and fungal (ITS) community composition also differed between land uses (Figure 4.1) (PERMANOVA: Bacteria: $F_{3,19}$ = 1.87, p = <0.001, R^2 = 0.26, Fungi:, $F_{3,19}$ = 2.47, p = <0.001, R^2 = 0.32, Saprotrophic Fungi:, $F_{3,19}$ = 1.58, p = <0.001, R^2 = 0.23). PLFA profiles were also significantly different between land uses (Figure 4.1) (PERMANOVA: PLFA: $F_{3,19}$ = 5.16, p = <0.001, R^2 = 0.49). Initial bacterial communities across all land uses were comprised primarily of Acidobacteria, Actinobacteria and Proteobacteria whilst fungal communities were dominated by taxa from the phyla Ascomycota, Basidiomycota and Mortierellomycota (Figure 4.2).

Table 4.3 *- Soil properties, PLFA concentrations and microbial richness (number of observed ASV's) measured across old growth (OG) forest, moderate logged (ML) forest, heavily logged (HL) forest and oil palm plantation. Data are means (n = 5) ± 1 SE. Superscript letters denote whether parameters were significantly different between land uses from Tukey's HSD test. Significant differences (p <0.05) between land uses are indicated when letters are different. Non – significant differences (P >0.05 between land-uses are indicated when letters are shared.*

Parameter	OG Forest	ML Forest	HL Forest	Oil Palm
Gravimetric Moisture Content (%)	^{a}28.14 (1.66)	^{b}52.20 (7.35)	^{ab}41.80 (2.40)	^{c}11.42 (0.57)
pH	^{a}6.32 (0.08)	^{b}4.12 (0.26)	^{ac}6.06 (0.31)	^{c}5.34 (0.14)
Total C (%)	^{ab}10.25 (1.32)	^{a}26.11 (7.33)	^{ab}11.75 (1.23)	^{b}6.41 (1.40)
Total N (%)	^{a}0.58 (0.06)	^{a}1.07 (0.27)	^{a}0.72 (0.06)	^{a}0.46 (0.10)
Inorganic P (µg/g)	^{a}24.02 (2.64)	^{a}57.69 (16.56)	^{a}47.67 (9.80)	^{a}246.16 (165.04)
C:N Ratio	^{a}17.65 (0.67)	^{b}23.51 (1.03)	^{a}16.32 (0.84)	^{c}14.06 (0.38)
Total PLFA (µg/g soil dry weight)	^{ab}72.42 (7.44)	^{a}93.51 (20.41)	^{ab}77.03 (6.40)	^{b}36.72 (3.05)
Fungal PLFA (µg/g soil dry weight)	^{a}6.27 (0.78)	^{a}14.17 (4.62)	^{a}6.25 (0.65)	^{a}4.20 (0.58)
Bacteria PLFA (µg/g soil dry weight)	^{a}35.10 (2.52)	^{a}44.82 (9.80)	^{a}39.90 (3.20)	^{b}16.83 (1.47)
F:B Ratio	^{ab}0.18 (0.01)	^{a}0.30 (0.06)	^{b}0.16 (0.01)	^{ab}0.25 (0.03
G+ PLFA (µg/g soil dry weight)	^{a}15.86 (1.48)	^{a}21.31 (4.74)	^{a}17.24 (1.17)	^{a}9.64 (0.83)
G- PLFA (µg/g soil dry weight)	^{a}18.07 (1.00)	^{a}22.64 (4.93)	^{a}22.06 (2.13	^{b}6.83 (0.74)
Bacterial Richness	^{a}2247 (56)	^{b}1352 (199)	^{a}2032 (135)	^{a}2340 (213)
Fungal Richness	^{a}394 (13)	^{b}260 (30)	^{a}364 (49)	^{a}285 (31)
Saprotrophic Fungal Richness	^{a}93 (5)	^{b}56 (9)	^{ab}76 (10)	^{b}55 (8)

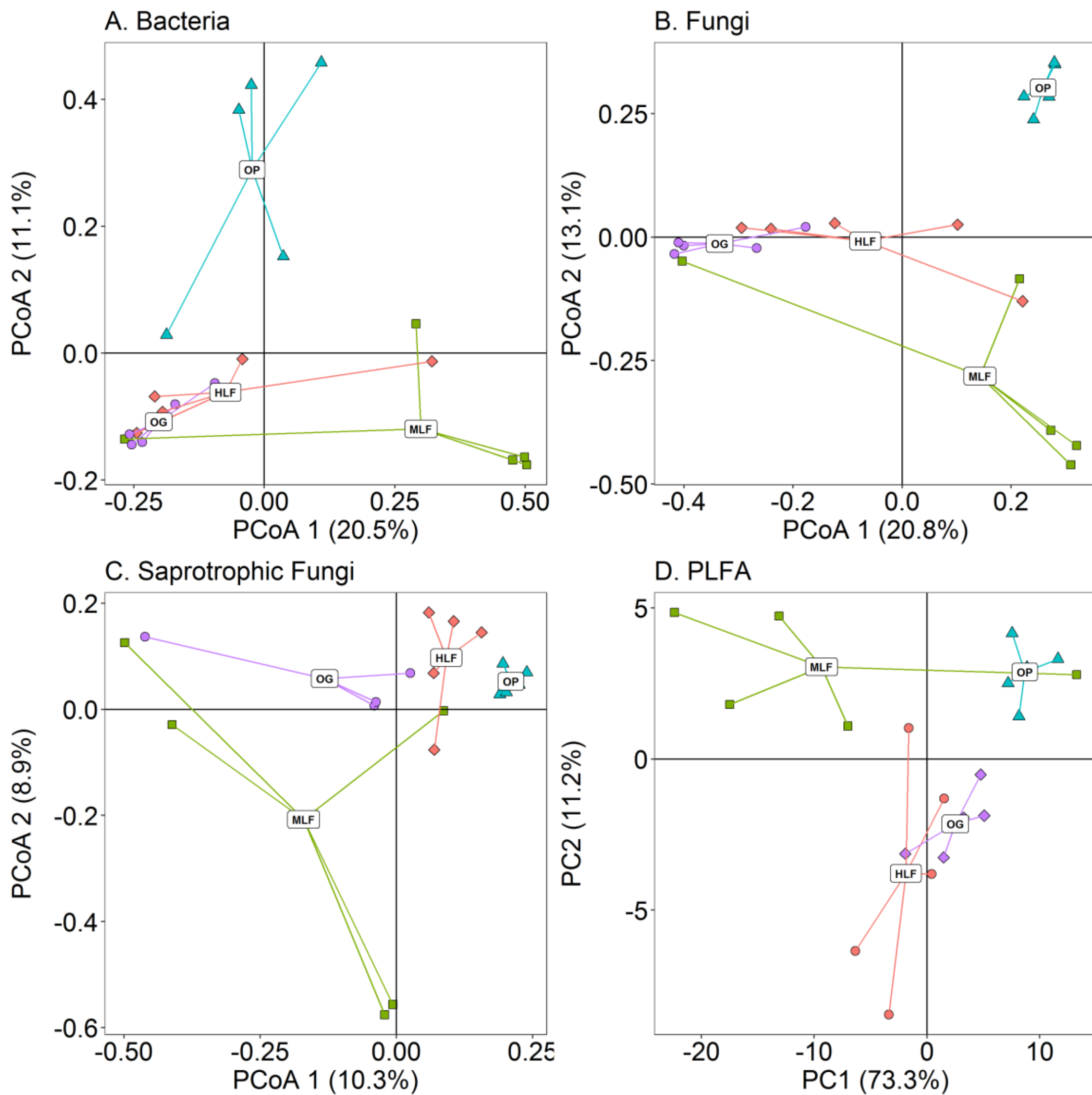

Figure 4.1 *- A – C: Principal coordinates analysis (PCoA) ordinations of Bray – Curtis dissimilarities of bacteria, fungal and saprotrophic fungal microbial community composition. D: Principal components analysis of PLFA concentrations across old – growth forest (OG), moderate logged forest (MLF), heavily logged forest (HLF) and oil palm plantation (OP).*

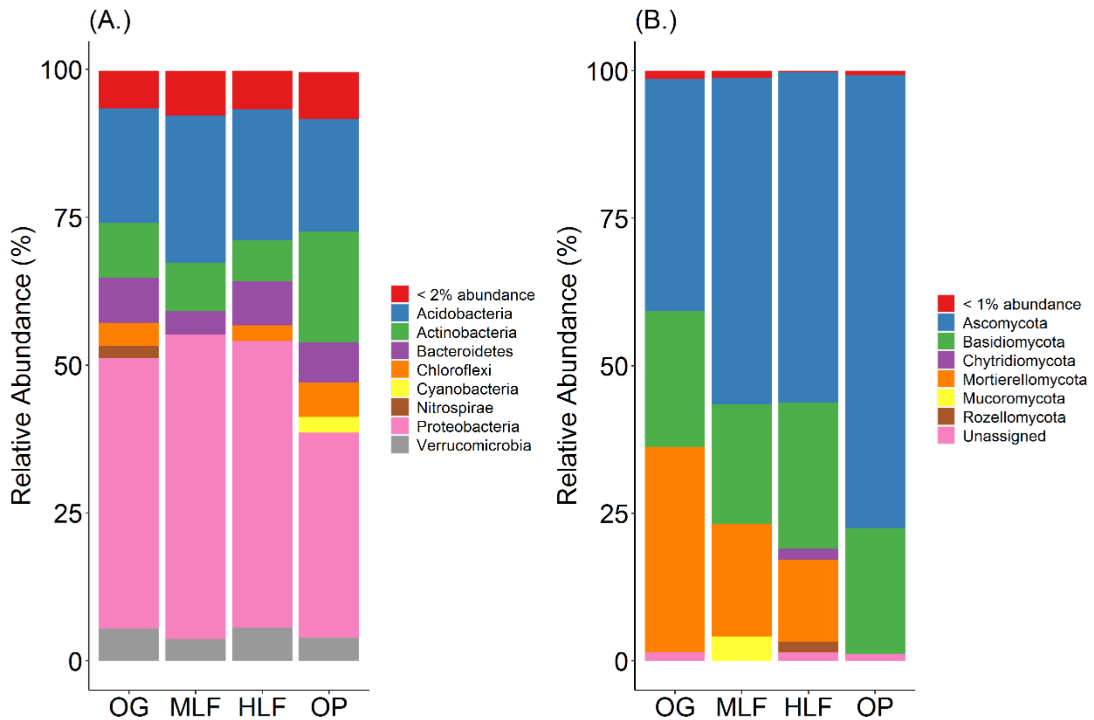

***Figure 4.2** - Relative abundance of phyla belonging to kingdoms Bacteria (A.) and Fungi (B.) across old-growth (OG), moderately logged forest (MLF), heavily logged forest (HLF) and oil palm (OP). Bacterial phyla representing < 2% abundance were grouped into one category (< 2% Abundance) whilst fungal phyla representing < 1% abundance were also grouped into one category (< 1% Abundance).*

4.4.3 Controls on rates of litter decomposition

Over the course of the 398 day experiment, significant differences in the rates of mass loss were observed between litter mixtures although there was no difference in rates of litter decomposing at "home" between the four sites. Overall, oil palm litter decomposed faster than all forest litters losing 12.48 ± 0.59 % 1SE after 31 days, 34.97 ± 1.49 % 1SE after 105 days and 42.51 ± 1.48 % 1SE after 398 days (Figure 4.3) in line with its higher chemical quality (low lignin: N ratio). ML forest litter decomposed slowest losing 8.31 ± 0.54 % 1SE after 31 days, 19.05 ± 0.54 % 1SE after 105 days and 23.85 ± 1.82 % 1SE after 398 days. Both litter and soil origin were

significant predictors of litter mass loss across all three time points (Table 4.4). Litter type accounted for between 34.51-66.28 % of total variance whilst soil origin accounted for between 5.17-15.43 % (Table 4.4). To explore whether soil properties, microbial abundance or richness may be driving the effect of soil origin, we “decomposed” the factor soil origin into measured soil properties (soil chemical properties, PLFA concentrations, bacterial, fungal and saprotrophic fungal richness) using multiple regression. This showed that at the 398 d time point, soil inorganic P, total PLFA concentrations and bacterial richness best explained variation in litter mass loss rates (Table 4.5). Initial bacterial, fungal and saprotrophic fungal community composition was also predictive of litter mass loss at 398 d. However, these models explained less variation than the previous model (Table 4.6)

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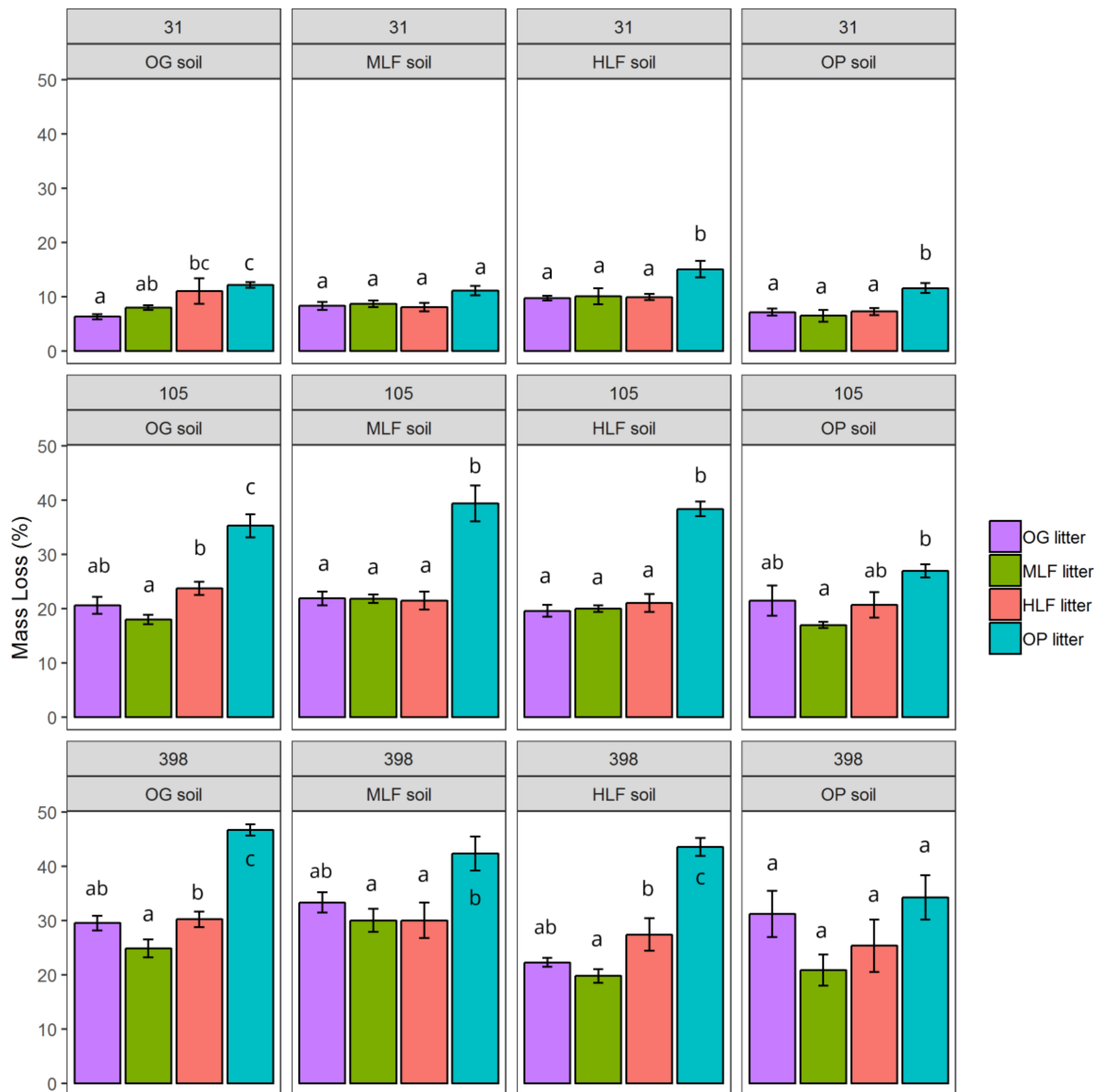

Figure 4.3 *- Mean litter mass loss from microcosms consisting of soils and mixed litter collected from old growth (OG) forest, moderate logged forest (MLF), heavily logged forest (HLF) and oil pam (OP). The four litter mixtures and soils were combined in a fully – factorial design (16 unique combinations) and destructively harvested after 31, 105 and 398 days. Values are mean percentage mass loss ± 1 SE of OG, MLF, HLF and OP litter after 31, 105 and 398 days of decomposition. Superscript letters denote pairwise significant differences at P <0.05 within each panel from ANOVA and Tukey's honestly significant difference post hoc tests.*

Table 4.4 *- Two way ANOVA results for the effects of soil origin, litter type and an interaction term on litter mass loss (log – transformed) after 31, 105 and 398 days. Relative importance was calculated using the method of Lindeman, Merenda and Gold, (1980) (lmg), by partitioning R^2 and averaging over orders of regressors and is presented as percentages which sum to the overall model R^2.*

Source of variation	**df**	**Relative Importance (%)**	**F**	**P - value**	R^2
31 d					
Litter type	3	34.51	17.81	<0.001	0.59
Soil origin	3	15.43	7.96	<0.001	
Litter type x Soil origin	9	8.73	1.5	0.17	
Error	64				
105 d					
Litter type	3	66.28	61.76	<0.001	0.78
Soil origin	3	5.17	4.61	0.006	
Litter type x Soil origin	9	6.1	1.9	0.07	
Error	63				
398 d					
Litter type	3	45.98	26.74	<0.001	0.65
Soil origin	3	11.17	6.02	0.001	
Litter type x Soil origin	9	8.14	1.62	0.21	
Error	62				

Table 4.5 *- Multiple linear regression results from a model with litter mass loss (log - transformed) at 398 d as the dependent variable and litter type, soil inorganic P, total PLFA concentrations and bacterial richness as independent variables. Relative importance was calculated using the method of Lindeman, Merenda and Gold, (1980) (lmg), by averaging over orders of regressors and is presented as percentages which sum to the overall model R^2.*

Source of variation	**Sum of Squares**	**df**	**Relative Importance (%)**	**F**	**P - value**	R^2
Litter Type	3.67	3	47.66	33.67	<0.001	0.66
Soil Inorganic P	0.36	1	3.41	10.03	0.002	
Total PLFA	0.36	1	7.1	9.96	0.002	
Bacterial Richness	0.33	1	7.8	9.08	0.003	
Error	2.58	71				

***Table 4.6** - Multiple linear regression results from a model with litter mass loss (log - transformed) at 398 d as the dependent variable, litter type and axis scores 1 and 2 from principal co-ordinates analysis (PCoA) of initial bacteria, fungal and saprotrophic fungal community composition as independent variables. Relative importance was calculated using the method of Lindeman, Merenda and Gold, (1980) (lmg), by averaging over orders of regressors and is presented as percentages which sum to the overall model R^2.*

Source of variation	Sum of Squares	df	Relative Importance %	F	P - value	R^2
Litter Type	3.33	3	45.52	22.69	<0.001	0.53
Bacteria PCoA1	0.21	1	2.69	4.24	0.04	
Bacteria PCoA2	0.27	1	5.24	5.58	0.02	
error	3.52	72				
Litter Type	3.32	3	45.43	23.49	<0.001	0.55
Fungi PCoA1	0.02	1	0.41	0.46	0.5	
Fungi PCoA2	0.61	1	9.4	12.92	<0.001	
error		72				
Litter Type	3.42	3	46.1	24.99	<0.001	0.57
Saprotrophic Fungi PCoA1	0.31	1	4.82	6.76	0.01	
Saprotrophic Fungi PCoA2	0.42	1	5.7	9.26	0.003	
error	3.28	72				

Final litter mass loss (after 398 d) of the lowest and highest chemical quality litters from ML forest and oil palm respectively, was significantly correlated with initial bacterial and fungal community composition whilst PLFA profiles were significantly correlated with mass loss of all litters (Appendix 3: Table 8.7). To assign a quality index to each litter and determine whether microbial decomposer communities were different in terms of their functional breadth and whether they perceived their "home" litter differently (HFA), we applied the DART regression framework. This showed that oil palm litter was of the highest quality whilst ML forest litter was the lowest (Table 4.7, Figure 4.4). OG and HL forest litter mixtures had intermediate qualities. After 398 d, the functional breadth of decomposer communities was significantly higher in OG forest and lower in HL forest relative to the average across all sites (Table 4.7, Figure 4.4). A positive HFA was detected for ML forest litter as it

decomposed significantly faster when combined with its “home” soil whilst a negative HFA was observed for oil palm litter which decomposed slower in combination with its “home” soil (Table 4.7, Figure 4.4).

Table 4.7 *- Output from the decomposer ability regression test (DART) using mass loss of litter mixtures from old growth (OG) forest, moderate logged (ML) forest, heavily logged (HL) forest and oil palm after 31, 105 and 398 days as a proxy for decomposition. Quality Index (QI) relates both the physical/chemical quality of the litter and how all decomposer communities perceive the relative litter quality. Ability quantifies the overall functional capacity of decomposer communities relative to each other across land uses (functional breadth). Home – Field Advantage (HFA) represents whether litter combined with its home soil decomposes faster than when combined with other soils and is given for the four home litter x soil combinations designated by soil community origin.*

Timepoint	Variable	Parameter Estimate	SE	P-value
31 d				
	Intercept	9.54	0.3	<.0001
	QI: OG	-0.96	0.42	0.0249
	QI: MLF	-1.67	0.55	0.0036
	QI: HLF	-0.05	0.63	0.9352
	QI: OP	2.67	0.55	<.0001
	Ability: OG	0.55	0.64	0.3913
	Ability: MLF	-0.93	0.48	0.0578
	Ability: HLF	2.06	0.54	0.0003
	Ability: OP	-1.69	0.49	0.0009
	HFA: OG	-2.83	1.03	0.0074
	HFA: MLF	1.74	1.03	0.0952
	HFA: HLF	-1.61	1.18	0.176
	HFA: OP	1.04	1.18	0.3793
105 d				
	Intercept	24.72	0.49	<.0001
	QI: OG	-3.87	0.94	<.0001
	QI: MLF	-6.16	0.64	<.0001
	QI: HLF	-2.66	0.95	0.0068
	QI: OP	12.68	1.02	<.0001
	Ability: OG	-0.37	0.84	0.6663
	Ability: MLF	0.78	1.05	0.4644
	Ability: HLF	0.37	0.75	0.6276
	Ability: OP	-0.78	0.92	0.4026
	HFA: OG	0.08	2.07	0.9704
	HFA: MLF	2.49	1.61	0.1264
	HFA: HLF	-1.38	2.04	0.5021
	HFA: OP	-9.7	2.07	<.0001

Table 4.7 - Continued

Timepoint	Variable	Parameter Estimate	SE	P-value
398 d				
	Intercept	30.85	0.73	<.0001
	QI: OG	-1.03	1.48	0.4912
	QI: MLF	-8.54	1.16	<.0001
	QI: HLF	-3.52	1.57	0.028
	QI: OP	13.09	1.12	<.0001
	Ability: OG	2.71	1.04	0.0112
	Ability: MLF	1.5	1.45	0.3026
	Ability: HLF	-3.51	1.09	0.0019
	Ability: OP	-0.7	1.71	0.6829
	HFA: OG	-3.03	2.44	0.2189
	HFA: MLF	6.19	2.9	0.0362
	HFA: HLF	3.58	3.54	0.316
	HFA: OP	-9.04	4.24	0.0365

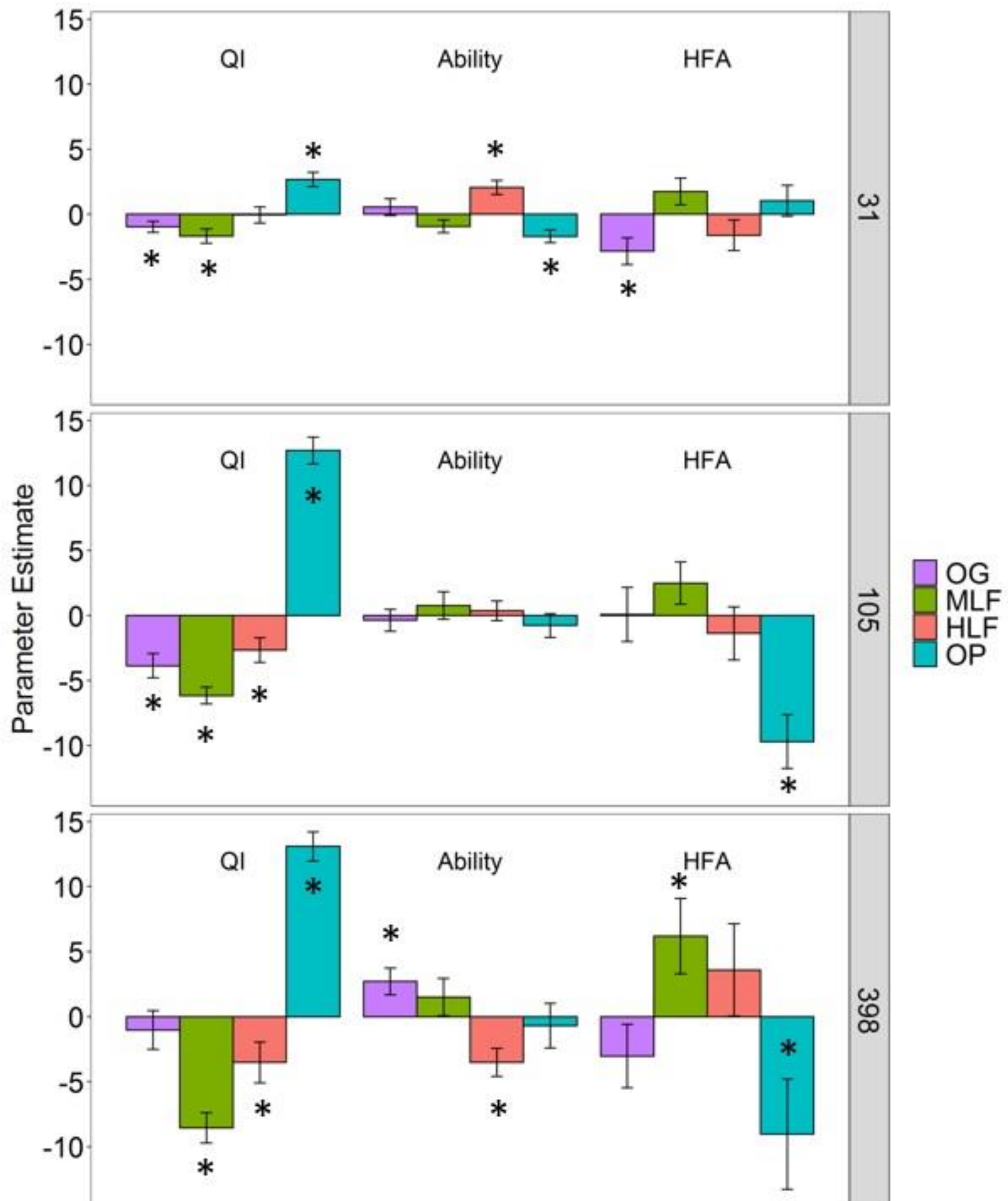

Figure 4.4 *- DART output calculated from % litter mass loss from litter decomposition microcosms after 31, 105 and 398 days: QI (litter quality index ranking the chemical quality of litters within the study), Ability (the functional capabilities of the microbial decomposer community to decompose all litters) and HFA (home – field advantage or the relative advantage of a decomposer community decomposing its "home" litter type). The bars are parameter estimate means ± 1 SE. "*" above or within bars represent a statistically significant difference from the intercept (y = 0) at $p < 0.05$. The intercept represents the average litter mass loss for all observations in the dataset after controlling for litter, soil and home – field pairings. A positive and negative estimate indicates faster or slower decomposition than the intercept (average litter mass loss) respectively.*

4.5 Discussion

Alongside climate, litter quality has been shown to be a dominant control on rates of litter decomposition (Cleveland et al., 2014; Cornwell et al., 2008; Fanin et al., 2016; Makkonen et al., 2012). Our results broadly agree with these studies and lend support to Hypothesis 1 as we found that litter type explained the most variation in litter mass loss at all stages of decomposition across OG, ML, HL forest and oil palm plantation (34.5-66.3 %) (Table 4.4). Variation in forest chemical litter quality was not aligned with logging history as ML forest litter had lower quality litter than HL and OG forest, which had similar litter qualities (Table 4.2, Appendix 3: Table 8.6). This probably reflects the higher heterogeneity in functional diversity of logged tropical forests as it does not agree with a recent study of tree community-weighted mean traits across this gradient (Both et al., 2019). This showed that whilst leaf tissue nutrient concentrations were primarily controlled by soil nutrient availability, logging did drive shifts from resource conservative to acquisitive traits (Both et al., 2019). Oil palm litter had the highest foliar P concentrations and lowest lignin: N ratios (Table 4.2) and decomposed ~40 % faster than all forest litters (Figure 4.3). This is comparable to another study comparing forest to oil palm litters in mesocosms under field conditions in Borneo (Kerdraon et al., 2020). The mean mass loss of forest litters after 105 days in microcosms was 20.9 ± 1.6 % (1SD). This was lower than those in a field decomposition experiment in Bornean tropical forest (30.3 %) over a similar time period (24 weeks) (Both et al., 2017). Moreover, exclusion of fauna reduced decomposition rates by 24 % highlighting that ex-situ decomposition excludes an important component of litter decomposition.

We found that, in addition to litter quality, soil origin was also a significant predictor of litter mass loss at all time points and across all land uses explaining 5.2-15.4 % of

total variation (Figure 4.3). This finding is in agreement with similar studies in temperate ecosystems and indicates that litter decomposition rates, whilst largely regulated by litter quality, are not decoupled from microbial decomposer community composition under controlled, microclimatic conditions (Ayres et al., 2009b; Cleveland et al., 2014; Fanin et al., 2016; Strickland et al., 2009b).

Hypothesis 2 (Functional Breadth Hypothesis) was not supported as microbial decomposer communities from OG forest had significantly higher functional breadth (i.e. they decomposed all 4 litter types faster than the average of decomposer communities from other land uses) whilst decomposer communities from HL forest had the lowest functional breadth (i.e. they decomposed all 4 litter types slower than the average of decomposer communities from other land uses) (Figure 4.4). OG and HL forest were the most similar in terms of both microbial decomposer community composition (Figure 4.1), microbial biomass and soil abiotic properties (

Table **4.3**) suggesting that even subtle shifts to the compositional make-up of microbial communities can lead to significant functional dissimilarity. Microbial decomposer communities from the oil palm plantation had a functional ability that was not significantly different from the average across all plots (Figure 4.4). This was surprising as total microbial biomass (Total PLFA), which has been positively associated with rates of litter decomposition and is represented in most decomposition models (Bradford et al., 2017; McGuire and Treseder, 2010), was much lower in oil palm (Table 4.2) relative to all forest plots. This could be explained by the loss of soil structure in microcosms. Soils in oil palm lacked the distinct horizon structure of forest soils and were more compacted and clay rich than forest soils. Compacted soils can reduce microbial activity and rates of decomposition (Carlesso et al., 2019).

Therefore, loosening of the soil structure may have enhanced litter decomposition rates relative to forest soils. High decomposition rates in oil palm may also have been due to past fertilisation with inorganic nutrients as fertilization with N, P, K and micronutrients has been shown to increase both cellulose and leaf litter decomposition rates in tropical forest (Hobbie and Vitousek, 2000; Kaspari et al., 2008). Soil inorganic P concentrations were higher in oil palm than forests (

Table **4.3**). When soil origin was replaced with soil properties, inorganic P concentrations as well as total PLFA and bacterial richness were positively associated with litter mass loss after 398 d. As P is thought to be a key limiting nutrient in lowland tropical forest ecosystems, alleviation of this limitation by fertilization may have increased rates of forest litter decomposition in oil palm, despite a lower abundance of microbial decomposers (Camenzind et al., 2018).

Numerous previous studies have shown that microbial communities decompose litter from their “home” site more quickly than exogenous litter (The Home-Field Advantage Hypothesis) (Austin et al., 2014; Ayres et al., 2009b; Gholz et al., 2000; Lin et al., 2019; Veen et al., 2015). However, evidence for this appears variable and context dependent with other studies showing no or even negative HFA (Gießelmann et al., 2011; McGuire et al., 2010; St. John et al., 2011). In partial support of Hypothesis 3, we found that after 398 d, the lowest quality litter mixture from ML forest decomposed significantly faster than all other litters when combined with its home soil (Figure 4.4). This is consistent with findings suggesting that HFA effects are stronger for recalcitrant litter and become more pronounced as litter types become more dissimilar (Veen et al., 2015). This may be explained by the higher concentrations of complex compounds in low quality litter, which require specialist

decomposers (i.e. lignocellulolytic fungi) that can secrete specific enzymes to break them down (Ayres et al., 2009b; Lin et al., 2019; Milcu and Manning, 2011; Veen et al., 2015). We found evidence for this specialisation as initial soil bacterial, fungal, saprotrophic fungal community composition and PLFA profiles were correlated to rates of ML forest litter mass loss after 398 d (Appendix 3: Table 8.7). A HFA effect can also be present for labile litter decomposition, explained by stimulation of competition for resources amongst copiotrophic microbial decomposers (Lin et al., 2019; Wang et al., 2013). Between 31-105 d and 105-398 d, labile oil palm litter decomposed slower in its "home" soil environment relative to all forest soils indicating a negative HFA effect at this stage of decomposition (Figure 4.4). The decay of labile compounds is thought to be primarily mediated by generalist microbial decomposers, which may be abundant in soil microbial biomass (Ayres et al., 2009a; Lin et al., 2019; López-Mondéjar et al., 2018; Milcu and Manning, 2011). Therefore, this negative HFA may be explained by lower microbial biomass (total PLFA) and thus abundance of generalist decomposers in oil palm relative to all forest sites (

Table **4.3**). In support of this, initial total PLFA (Table 4.5) and PLFA profiles (First two principal components from PCA analysis) (Appendix 3: Table 8.7) were positively correlated with final mass loss of all litter mixtures. This suggests that generalist species found across land uses, rather than specialist decomposers regulated the decomposition of oil palm litter.

4.6 Conclusions

These data provide evidence that under controlled climatic conditions, litter quality regulates rates of litter decomposition across tropical OG forest, logged forests and oil palm plantations. However, differences in soil microbial decomposer community

explained a smaller but significant portion of variation in litter mass loss with OG forest decomposer communities retaining greater functional breadth, decomposing all litter mixtures faster relative to communities under logged forest and oil palm. We found evidence for a HFA in the most recalcitrant litter mixture from ML forest and significant correlations between initial decomposer community composition, microbial abundance, richness and litter mass loss after 398 d. These findings suggest that shifts in soil microbial decomposer community structure should be considered when assessing the impacts of disturbance on crucial process rates, such as decomposition, in tropical forest ecosystems.

4.7 Acknowledgments

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5 Drought intensity and land use regulates the resistance and resilience of tropical soil microbial communities to drought

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5.1 Abstract

Climate change and deforestation are modifying precipitation patterns across the tropics, resulting in longer droughts and more intense rainfall events. Such events alter soil drying-rewetting (D-RW) dynamics, shifting microbially mediated biogeochemical processes. An understanding of how soil moisture fluctuations influence microbial processes is therefore crucial to better predict future responses to global change. Using microcosms, we determined how land use and the intensity of drought interacted to influence soil microbial production of greenhouse gases (GHG) upon rewetting of 3 soils taken from old growth (OG) tropical forest, selectively logged (SL) tropical forest and oil palm (OP) plantation in Sabah, Malaysia. We also investigated microbial tolerance (“resistance”) to soil drying and the ability to recover following rewetting (“resilience”), measured in terms of soil respiration and microbial community composition. We found that the effect of drought intensity on soil GHG emissions was land use specific, as more intense drought increased CO_2 emissions in OG forest and OP but reduced CO_2 emissions in SL forest. However, the size of the CO_2 flush across land uses was strongly related to soil C:N ratio, suggesting that soil

properties may be a simple measure to generalize microbial responses across tropical landscapes to future hydrological changes. Intense drought also reduced CH_4 uptake from forest soils and drove short term “hot moments” in N_2O emissions from OP soils. OG forest microbial communities had greater functional resilience. However, bacterial community composition was strongly modified by D-RW in OG and SL forest relative to OP soils with drought tolerant genera becoming dominant members of disturbed communities. Taken together these findings suggest that interactions between drought intensity and land use could drive divergent trajectories for the GHG balance of tropical landscapes but that soil properties may be useful as predictors of microbial responses to climate change.

5.2 Introduction

Climate change is predicted to drive alterations to the global water cycle resulting in greater spatio-temporal variability in precipitation patterns (Cai et al., 2014; Dai, 2013; Stocker et al., 2013). Consequently, drought periods are likely to increase in duration interspersed with intense precipitation events (Dai, 2013; Fischer and Knutti, 2016). In tropical regions, many of which have experienced high rates of deforestation (Hansen et al., 2013), drought periods may be further amplified as tropical forest cover loss has been related to increased air temperature and reduced daily precipitation totals (Alkama and Cescatti, 2016; Kumagai et al., 2013; McAlpine et al., 2018). The resultant changes to soil biophysical conditions and moisture regimes have important implications for biogeochemical cycling as soil moisture and temperature are the primary controls on soil microbial activity, which regulates greenhouse gas (GHG) exchange between soils and the atmosphere (Le Quéré et al., 2009; Oertel et al., 2016). An improved understanding of how drought-rewetting (D-RW) events influence the magnitude and dynamics of soil heterotrophic respiration and trace gas production is therefore crucial to inform predictions of how future changes to drought periods may influence the terrestrial carbon (C) cycle (Reichstein et al., 2013).

Soil microbes are the dominant contributors to soil heterotrophic respiration and require soil pore water to access nutrients, sustain growth, disperse and maintain metabolic function (Tecon and Or, 2017; Vos et al., 2013). Soil drying reduces microbial metabolic activity, typically resulting in reduced soil respiration and nutrient mineralization (Manzoni et al., 2012). When soils are rewetted after a period of drought, a transient pulse of CO_2 known as the "Birch" effect after Birch (1958) is released, which may be many times higher than basal respiration and nutrient

mineralization rates may also increase (Borken and Matzner, 2009; Kim et al., 2012). The source of this respired C is debated but likely originates from bioavailable C pools and mobilised C from soil aggregates by rewetting, after incorporation into microbial biomass (Schimel, 2018).

Soil CH_4 is produced by the anaerobic decomposition of organic matter by methanogens and mineralized under aerobic conditions by methanotrophic bacteria (Topp and Pattey, 1997). Well aerated soils typically act as a net sink for atmospheric CH_4 as biological consumption processes dominate over production processes in aerobic soils (Topp and Pattey, 1997). Over prolonged drought periods soil CH_4 consumption rates typically increase (Liu et al., 2019; Oertel et al., 2016) but the effect of rewetting aerated soils on the CH_4 flux is not well constrained. Rewetting appears to reduce CH_4 uptake in tropical forest soils but may also activate anaerobic CH_4 production processes (Matson et al., 2017; Welch et al., 2019). Soil nitrogen (N) availability has also been associated with reduced CH_4 uptake and increased emissions (Liu and Greaver, 2009).

Soil N_2O is produced by microbial nitrification (oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) or nitrate (NO_3^-) and denitrification (the anaerobic reduction of NO_2^- or NO_3^- to nitric oxide, N_2O or N_2) (Butterbach-Bahl et al., 2013). Thus soil moisture is a major driver of N_2O emissions as it regulates oxygen availability to soil microbes (Butterbach-Bahl et al., 2013). Thus rapid changes from drought to rewetting can result in significant N_2O emission, with larger differences between soil dry and wet states, resulting in greater hotspots in N_2O emissions (Barrat et al., 2020). This may be due to increased metabolism of microbial denitrifying taxa and enhanced substrate

supply to support both nitrification (N substrates) and denitrification (C & N substrates) (Barrat et al., 2020).

Although the effects of D-RW cycles on soil GHG emission and nutrient mineralization have been studied extensively, the impact of the intensity (level of drying or drought duration) of the preceding drought on the magnitude of the rewetting GHG pulse has received less attention (Barrat et al., 2020; Borken and Matzner, 2009; Lu et al., 2020; Navarro-García et al., 2012; Sun et al., 2018). The few studies that have studied different drying duration or intensities suggest that the magnitude of the rewetting GHG pulse may increase with longer drought duration (Navarro-García et al., 2012), as may rates of N mineralization (Lu et al., 2020; Sun et al., 2018) and P leaching (Khan et al., 2019). However, studies to date have only been performed in temperate agricultural and grassland ecosystems and it is unclear as to whether these findings apply to tropical ecosystems.

Changes to soil C and N cycling driven by altered D-RW dynamics may also be governed by the inherent resistance (the ability to maintain structure and function during drought) and resilience (ability to return to a pre drought state and maintain structure and function) of soil microbial communities (Griffiths and Philippot, 2013; Shade et al., 2012). However, our understanding of the mechanisms that control the resistance and resilience of microbial communities is currently limited (Bardgett and Caruso, 2020). Numerous biotic and abiotic factors have been suggested as determinants of microbial resistance and resilience. For example species richness or diversity has been proposed as an important intrinsic measure of resilience as this may confer functional redundancy due to the “insurance” hypothesis, whereby the loss of a particular species is less likely to reduce ecosystem function if there is a high diversity

of other species to perform compensatory functions (Yachi and Loreau, 1999). Functional diversity may also determine microbial resistance and resilience as traits such as physiological plasticity and the capacity to enter dormancy may increase resistance, whilst sporulation and rapid growth may result in low resistance but increased resilience (Griffiths and Philippot, 2013; Lennon and Jones, 2011; Shade et al., 2012). These traits may drive divergent species responses to D-RW, which have recently been used to identify broad life history strategies associated with microbial resistance and resilience (Evans and Wallenstein, 2014; Meisner et al., 2018).

Demand for timber products and land for monoculture oil palm plantations are driving rapid land use change across the tropics of SE Asia (Reynolds et al., 2011; Wilcove and Koh, 2010). Most remaining lowland tropical forests in the region are heavily degraded with old growth forest restricted to isolated protected areas and oil palm plantations expanding rapidly over the last three decades (Gaveau et al., 2019; Gaveau et al., 2014). Previous studies of microbial responses to drought across land uses have been restricted to temperate arable and grasslands (Ingrisch et al., 2020; Kaisermann et al., 2013; Karlowsky et al., 2018). However, it is unknown how microbial resistance and resilience to drought varies across tropical land uses. Evidence suggests that environmental characteristics such as the historical climate and soil physico-chemical conditions may influence microbial resistance and resilience, by modifying intrinsic community attributes and selecting for certain taxa with environmental preferences and life histories (Bardgett and Caruso, 2020). For example, soil microbial activity appears to be more sensitive to changes in soil moisture when microbial assemblages have experienced drier or more constant historical moisture regimes (Averill et al., 2016; Hawkes and Keitt, 2015; Ochoa-Hueso et al., 2018). Therefore, land use change from humid tropical forest to oil palm plantation could influence the

drought sensitivity of soil microbial communities due solely to changes in soil microclimate. Soil properties can also vary widely across tropical land uses. Few studies have examined the interaction between soil microbial community resistance and resilience to climatic perturbations and soil abiotic properties (although see de Vries and Shade (2013); Orwin et al. (2006)). However soil resource availability may play an important role, as high availability selects for copiotrophic microbial taxa with rapid growth rates, which could confer increased resilience (Wallenstein and Hall, 2012).

Here we tested whether the intensity of drought prior to rewetting influenced microbial GHG emissions across old growth (OG) tropical forest, selectively logged (SL) tropical forest and oil palm (OP) plantation and whether any effect of land use was explained by contrasting soil properties or microbial community composition. We also investigated whether the resistance and resilience of soil microbial communities to drought differed across land uses. We hypothesised that:

[1]. Rewetting peak and cumulative microbial GHG (CO_2, CH_4 and N_2O) emissions would be positively related to drought intensity with no interaction of land use. However, the magnitude of trace gas emissions (CH_4 and N_2O) upon rewetting would vary between land uses as hypothesised below:

[1a] Net CH_4 sink would be weaker upon rewetting in OP relative to OG and SL forest soils as CH_4 uptake is common in forests and soil N availability may be higher in OP plantations (due to fertilization), which can inhibit methanotrophy.

[1b] N_2O emissions would be higher upon rewetting in OP relative to OG or SL forest soils, driven by higher soil N availability in oil palm plantations.

[2]. The resistance and resilience of soil microbial activity (CO_2 respiration) and microbial community composition to D-RW across land uses would be higher in OP relative to OG and SL forests due to a less buffered field soil moisture regime.

5.3 Materials and methods

5.3.1 Site description and plot selection

The study sites were in the Malaysian state of Sabah on the island of Borneo. The regional climate is moist tropical with annual daily mean temperature of 26.7 °C and annual precipitation of approximately 2600-2700 mm (Kumagai and Porporato, 2012; Walsh and Newbery, 1999). We sampled from three long-term, 1 Ha research plots that form part of the pantropical Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/). Two plots were representative of lowland dipterocarp tropical forest and one of mature oil palm plantation. These represent the current dominant land uses across the island of Borneo (Gaveau et al., 2019; Gaveau et al., 2014). One “old growth” forest plot (OG) was located within the Danum Valley Conservation Area (DVCA). This forest has experienced little modern disturbance and has been protected since 1976 (Marsh and Greer, 1992). The most common tree genera within the OG forest plot were Shorea (Dipterocarpaceae) and Diospyros (Ebenaceae) with a low abundance of pioneer trees (0.1 ± 0.0 % of basal area) and high basal area of standing trees (30.6 ± 3.37 m^2 ha^{-1}) (Riutta et al., 2018). The second “selectively logged” forest (SL) and oil palm (OP) plot were located within the Kalabakan Forest Reserve and neighbouring Benta Wawasan oil palm estate. These were established as part of the Stability of Altered Forest Ecosystems (SAFE) project

(www.safeproject.net) and are situated within the wider Yayasan Sabah Forest Management Area (Ewers et al., 2011). The SL forest plot is part of a forest contiguous with the Danum Valley Conservation Area but has been lightly logged once during the 1970's and once during the period 1990-2008. Logging operations targeted primarily hardwoods from the genera *Dryobalanops* sp., *Dipterocarpus* sp., *Shorea* sp. and *Parashorea* sp. The most common tree genera within SL forest were *Macaranga* sp. (Euphorbiaceae), *Shorea* sp. (Dipterocarpaceae), and *Syzygium* sp. (Myrtaceae) with higher abundance of pioneer trees (6.9 ± 2.2 % of basal area) and lower basal area of standing trees (19.3 ± 1.7 m2/ha) relative to OG forest (Riutta et al., 2018). The OP plot was established in 2000 but standing palms were ~7 years old. Fertilizer (compound mixture comprised of diammonium phosphate, potassium chloride, ammonium sulphate, magnesium sulphate and borax) was applied twice a year at a rate of 3-4 kg per palm (Julia Drewer, UKCEH: personal communication). Site characteristics are summarized in

Table **5.1.** For further forest site characteristics, refer to Riutta et al. (2018) for the following plots: OG Forest: DAN-05, SL Forest: SAF-04.

5.3.2 Field microclimate measurements

To characterize field microclimates across land uses, soil moisture, soil temperature and air temperature were measured *in situ* for a period of ~6 months between November 2016 and April 2017. Soil temperature and moisture were measured hourly using an SM150T moisture/temperature probe buried horizontally at a depth of 5 cm and logged with a GP1 Datalogger (Delta T Devices, Cambridge, UK). Sub-canopy air temperature was measured with a shielded Hobo Pendant UA-002-64 Temperature data logger (Onset, Massachusetts, USA). Due to logger failure in the OP plot,

monthly manual measurements of soil moisture and soil temperature data were used. These were measured using a hand-held moisture probe (ML3 Thetaprobe, Delta T Devices, Cambridge, UK) and a soil temperature stab probe to 5 cm depth.

5.3.3 Soil collection, processing and chemical analysis

Soil sampling was conducted in March-April 2017. Each 1 Ha plot was subdivided into twenty five 20x20 m subplots and five subplots were randomly selected for soil sampling. Samples taken from these 5 subplots were subsequently treated as individual replicates for each land use type in the incubation. The fresh litter layer was removed and five co-located individual plastic cores (8 cm depth, 4 cm diameter) were hammered into the soil within each subplot. These were dug out of the ground with a trowel, sealed at the top and bottom with rubber caps and transported to a field lab where they were stored at 4 °C. Cores were then transported to the UK in an icebox and stored at 4 °C for ~2 weeks prior to the establishment of the D-RW experiment. One intact core per subplot was used to determine the maximum water holding capacity using the method of Öhlinger and Kandeler (1996). An additional core per subplot was used for initial soil characterisation. This was removed from the plastic tube and homogenised by passing the fresh soil through a 4 mm aperture sieve. Any stones and coarse roots retained on the sieve were air-dried at 25 °C and weighed for correction of bulk density estimates. A 10 g fresh soil subsample was taken for determination of pH. The remaining soil was left to air dry for ~1 week at 25 °C in a drying room. This was then homogenised by passing through a 2 mm sieve (stones and coarse roots retained on sieve were weighed) and ground to a fine powder using a pestle and mortar. Bulk density was determined using the oven-dried soil weight (dried at 105 °C for 24 hours) and corrected for the volume of roots and stones

(Emmett, 2008). Soil pH was measured using fresh soil in a 2.5:1 water: soil slurry suspension, allowed to rest for 30 minutes and measured using a calibrated pH meter (pH210 Meter, Hanna instruments, UK). Total soil C and N was determined using oven-dried (65 °C), 100 mg powdered subsamples and analysed using a LECO Truspec Micro elemental analyser (LECO Corporation, USA). Inorganic P was extracted from 0.2 g air dried soil using a Bray No. 1 extractant and analysed using colorimetry on a SEAL AutoAnalyzer 3 (Seal Analytical, UK).

5.3.4 Microcosm design and set up

The remaining 3 cores per subplot were set up intact as soil microcosms in 45 1L glass kilner jars. We did not remove roots and repack cores as forest soils had a distinct horizon structure. We acknowledge that fine root decomposition is likely to influence CO_2 efflux during the experimental period. However, soil structure and porosity are also major drivers of GHG fluxes from soils and therefore cores were incubated intact to preserve field differences between sites. 15 intact cores from each land use were sealed at the bottom and placed on end within the glass jars. The water holding capacity (WHC) of each core was adjusted to 70 % of maximum water holding capacity by the addition of an artificial rainwater solution based on precipitation chemistry for Danum Valley taken from the World Data Centre for Precipitation Chemistry (http://wdcpc.org/) (Vet et al., 2014). Jars were then placed in a temperature controlled walk-in incubator at 25 °C and sealed with perforated parafilm to minimise evaporation but prevent anaerobicity. Microcosms were left for 3 weeks to equilibrate during which moisture was adjusted daily to maintain 70 % WHC. Cores were then assigned to one of 3 treatments: Low intensity drought (LID) (dry down period of 4 days), high intensity drought (HID) (dry down period of 14 days)

and a control treatment which was maintained throughout at 70 % WHC. Each land use had 5 field replicates (representing the five discrete subplots sampled within each 1 Ha) per treatment (n = 45). Upon rewetting, artificial rainwater was added to each core to achieve 70 % WHC. Cores were maintained at 70 % WHC for a further 30 days after rewetting.

5.3.5 *In situ* inorganic nitrogen determination

NH_4^+ and NO_3^- availability was measured *in situ* prior to and immediately after re-wetting. Commercial anion (Part No: 551642S) and cation (part No: 551652U) exchange membranes (VWR International, Pennsylvania, USA) were cut into 4x1 cm rectangles and buried vertically in pairs (one cation exchange, one anion exchange) in two slits within the top of each core. Anion exchange membranes sorbed nitrate (NO_3^-) ions and cation exchange membranes sorbed ammonium ions (NH_4^+). These were removed after 24 hours during the pre-drought burial and 14 days during the post re-wetting period, washed thoroughly with deionised water and extracted by shaking in 25 ml of 1M KCl for 1 hour. Extracts were measured using colorimetry on a Seal AutoAnalyzer 3 (Seal, UK). As N supply rates to membranes are not linear with burial time, all data are shown as available NH_4^+ or NO_3^- in µg per membrane area available for ion exchange over the burial period. Ion exchange membranes have been shown to be well correlated with traditional measure of N availability and production in soil and provide an integrated measure of mineral N availability, with minimal soil disruption (Durán et al., 2013).

5.3.6 Greenhouse gas measurements and flux calculations

To validate that intact cores in microcosms reflected microbial activity *in situ*, field soil CO_2 respiration measurements were made prior to core collection using an EGM-

4 infrared gas analyser and SRC-2 soil respiration chamber (PP Systems, Amesbury, MA, USA) using a two minute enclosure period. In the laboratory GHG measurements in microcosms were made using a Picarro G2508 cavity ring down (CRDS) analyser (Picarro Inc. Santa Clara, USA) prior to drying (70 % WHC), immediately prior to rewetting (after 4 or 14 days) and at 1, 3, 5, 7 hours, 1, 2, 3, 7, 14, 22 and 30 days following rewetting. We used a closed loop gas recirculation system by using a custom kilner jar lid fitted with two leak tight compression fittings (Swagelok, Manchester, UK). These fittings were connected via stainless steel tubing to the inlet and outlet of the analyser and vacuum pump respectively. Prior to measurements being made, the analyser was calibrated using gas standards (508, 1063, 4211 ppm CO_2, 0.99, 3.03, 10.5 ppm CH_4, 0.45, 1.01, 2.04 ppm N_2O) (Air Products, Walton on Thames, UK) in flow through mode. At each sampling we first removed the parafilm, allowed jars to vent for 15 minutes and then connected each jar in turn to the sampling loop (using the custom lid). These were left to equilibrate for 60 seconds and then measurements of CO_2, CH_4 and N_2O were made for 5 minutes. Each measurement yielded a time series of approximately 300 data points of trace gas concentrations. A custom R script was used to convert gas concentrations to mass units and corrected to incubation conditions through application of the ideal gas law. Fluxes were then calculated using linear regression as enclosure times were short and there was no indication of non-linearity following visual inspection (Holland et al., 1999). The minimum detectable flux (MDF_{SE}) for CO_2, CH_4 and N_2O ($\mu mol/m^2/h$) was calculated for the system described using the approach first proposed by Christiansen et al. (2015) and extended to high frequency measurements by Nickerson (2016) (Equation 1):

Equation 1 – Minimum detectable flux for high frequency measurements

$$MDF_{SE} = \left(\frac{A_A}{\sqrt{\frac{1}{t_C P_S}}}\right)\left(\frac{VP}{SRT}\right)$$

where A_A is the analytical accuracy of the instrument (ppm), t_C is the enclosure time of the chamber in hours, P_S is the sampling periodicity in hours, V is the chamber volume (m^3), P is the atmospheric pressure (Pa), S is the chamber surface area (m^2), R is the ideal gas constant (m^3 Pa K^{-1} mol^{-1}) and T is the ambient temperature (K). This was then converted to mg CO_2-C m^{-2} hr^{-1}, µg CH_4-C m^{-2} hr^{-1} or µg N_2O-N m^{-2} hr^{-1} by multiplying by the molar mass of CO_2, CH_4 or N_2O divided by molar mass of C or N_2. MDF_{SE} was 0.23 mg CO_2-C m^{-2} hr^{-1}, 1.41 µg CH_4-C m^{-2} hr^{-1} and 4.14 µg N_2O-N m^{-2} hr^{-1}. Any flux values < MDF_{SE} were replaced with zero flux following guidelines in Venterea et al. (2020). 480 flux measurements were made for each GHG. 72 CH_4 and 32 N_2O fluxes fell below the MDF_{SE} and were replaced with zero flux.

5.3.7 Molecular analysis of soil microbial communities

After the final gas sampling at 30 days post rewetting, soil cores from LID, HID and control treatments were destructively harvested. Soil was homogenised by passing through a 4 mm sieve and frozen at -80 °C. DNA was subsequently extracted from 0.2 g frozen soil using a Powersoil® DNA Isolation Kit according to the manufacturer's instructions. Amplicon libraries were constructed according to a dual indexing strategy with each primer consisting of the appropriate Illumina adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker and the amplicon specific primer (Kozich, Westcott et al. 2013). For bacteria, V3-V4 16S rRNA amplicon primers were used (CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC) (Kozich,

Westcott et al. 2013). Fungi were targeted by amplifying the ITS2 region using amplicon primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark, Bodeker et al. 2012). Amplicons were generated using PCR and a high fidelity DNA polymerase (Q5 Taq, New England Biolabs). Amplicon sizes were determined using an Agilent 2200 TapeStation system and libraries normalized using SequalPrep Normalization Plate Kit (Thermo Fisher Scientific) and quantified using a Qubit dsDNA HS kit (Thermo Fisher Scientific). Each amplicon library was sequenced separately on Illumina MiSeq using V3 600 cycle reagents at concentrations of 8 pM with a 5 % PhiX Illumina control library.

Sequences were processed in R using DADA2 to quality filter, merge (where appropriate), de-noise and assign taxonomies (Callahan, McMurdie et al. 2016). Briefly, 16S forward reads were trimmed to 250 bases. ITS amplicons reads were trimmed to 225 and 160 bases, forward and reverse respectively. Filtering settings were maximum number of Ns (maxN) = 0, maximum number of expected errors (maxEE) = 1. Sequences were dereplicated and the DADA2 core sequence variant inference algorithm applied. ITS sequences were merged using mergePairs function, whilst forward reads were used for 16S amplicons. Chimeric sequences were removed using removeBimeraDenovo default settings. The actual sequence variants (ASV) were subject to taxonomic assignment using assignTaxonomy at default settings; the training databases used were GreenGenes v13.8 and Unite v7.2 for 16S and ITS respectively. Diversity metrics were calculated on rarefied data (Bacteria: 2082 reads, Fungi: 5247 reads). All other analyses were performed using normalized relative abundance data.

5.3.8 Calculation of microbial resistance and resilience

To compare the resistance (the amount of change caused by the disturbance) and resilience (the rate of recovery from a disturbance) of soil microbial activity to different intensities of D-RW disturbance we calculated indices of resistance and resilience as described by Nimmo et al. (2015) using soil CO_2 respiration as a response function. Resistance was calculated as the percent change in soil CO_2 respiration (S) from before (T1) to the end (T2, 4 or 14 days) of the drying period = S_{T2}/S_{T1} Resilience was calculated as $(S_{T3}/S_{T1}) - (S_{T2}/S_{T1})$ where S_{T3} = CO_2 respiration 30 days after rewetting. This is a measure of relative resilience as it is weighted by the resistance (percent change in CO_2 respiration as a result of drying). The rationale here is that the ability of microbial activity to return to pre-disturbance levels is dependent upon the impact (reduction in CO_2 respiration) during drying. High resistance reduces the relative resilience, while low resistance increases relative resilience. Values lower than 1 indicate that CO_2 respiration was lower after the D-RW event relative to pre disturbance with lower values indicating decreasing resilience. Values > 1 indicate that CO_2 respiration was higher after the D-RW event relative to pre-disturbance. This resilience index may have negative values if CO_2 respiration following rewetting was lower than performance during drying. Resilience of microbial community composition was assessed by comparison of Bray-Curtis dissimilarities of microbial community structure between cores subjected to D-RW and Control treatments.

5.3.9 Data Analyses

All analyses were performed using R statistical software (version 3.6.1). Differences in soil properties, field microclimates and microbial metrics between land uses were tested using ANOVA. To test hypothesis 1, we calculated the maximum % flux

change in CO_2 relative to the pre-drought baseline following Kim et al. (2012) (*Equation 2*).

Equation 2 *–Maximum percentage flux change relative to pre-drought baseline*

$$\%\ peak\ flux\ change = (peak\ flux_{post-rewet}) - (Flux_{pre-drought}) \div (Flux_{pre-drought}) \times 100$$

The cumulative flux of CO_2, CH_4 and N_2O produced during 30 days after rewetting from LID, HID and Control treatments was estimated between timepoints by linear interpolation using the *agg.fluxes* function in the *gasfluxes* R package. We then tested whether the % peak flux change of CO_2 or total cumulative flux of CO_2, CH_4 or N_2O following rewetting was associated with preceding drought intensity or land use using ANOVA and included an interaction term to determine whether the effect of drought intensity on GHG emission was dependent on land use. *Post hoc* pairwise comparisons between levels of treatment and land use were performed using estimated marginal means (*emmeans* R package) (Lenth, 2019).

To test hypothesis 2 we performed ANOVA's using resistance and resilience indices as response variables with drought intensity and land use as explanatory factors with an interaction term. To detect which abiotic and biotic covariates might be driving variation in microbial GHG emissions, resistance and resilience across land uses, we replaced the land use term with measured soil properties, inorganic N availability following rewetting and metrics of microbial richness, diversity and community composition (NMDS axes scores) and performed multiple linear regression. In order to reflect the experimental design we forced the selection of the fixed factor treatment (drought intensity). Highly correlated variables were removed a priori and by inspecting variance inflation factors. The best model was selected by forward and

backward stepwise model selection using Akaike's information criterion (AIC) as an index of the goodness of model fit. For all models, the effect size (relative importance) of each independent variable was estimated by partitioning R^2 using averaging over the order of regressors using the *relaimpo* R package and is presented as a percentage of total explained variance (Groemping, 2006). The resilience of microbial community composition was assessed by performing ANOVA’s on bacterial and fungal richness and Shannon diversity with drought intensity and land use as explanatory factors with an interaction term. We also calculated Bray-Curtis dissimilarities on square root transformed bacterial and fungal ASV abundance data and performed PERMANOVA as implemented in the *adonis2* function in the *vegan* R package (Jari Oksanen et al., 2019) with drought intensity and land use as explanatory variables and an interaction term. Significance was assessed using 9999 permutations. Pairwise comparisons were performed using the *pairwiseAdonis* R package. Lastly, to identify drought tolerant bacterial taxa within each land use we used Random Forest classification (*randomForest* R package). Genera which were more abundant in D-RW samples and were ranked within the top 15 most important variables for classification accuracy (MeanDecreaseAccuracy) were considered drought tolerant (See Appendix 4: Figure 8.8, Figure 8.9 and Figure 8.10 for variable importance).

5.4 Results

5.4.1 Site characteristics, soil properties and microbial respiration

The three sites varied significantly in terms of field soil moisture ($F_{2,12701} = 4592.6$, $p = <0.001$), soil temperature ($F_{2,12701} = 2952.7$, $p = <0.001$), and air temperature

($F_{2,24996}$ = 549.7, p = <0.001). Soil moisture was lowest in OP and highest in SL forest (

Table **5.1**, Appendix 4: Figure 8.6) whilst soil and air temperature were lowest in SL forest and highest in OP (

Table **5.1**, Appendix 4: Figure 8.6). Field soil respiration was significantly higher in SL forest relative to both OG forest and OP whilst OG forest had higher respiration than OP ($F_{2,12}$ = 16.90, p = <0.001) (

Table **5.1**, Appendix 4: Figure 8.7). Incubated cores also had higher respiration rates in SL forest relative to both OG forest and OP ($F_{2,12}$ = 11.36, p = 0.002) and there was a significant correlation between field and laboratory incubated core respiration (Appendix 4: Figure 8.7). Lab core CO_2 fluxes were lower than field CO_2 respiration measurements although the magnitude of difference varied between land uses (lab core CO_2 fluxes were 12.9 ± 2.0 %, 11.3 ± 1.5 % and 32.5 ± 10.6 1SD % of field CO_2 fluxes for OG forest, SL forest and oil palm respectively) (Appendix 4: Figure 8.7).

Initial soil properties differed between land uses (

Table **5.1**). Soil pH was higher in OG relative to SL forest and OP ($F_{2,12}$ = 40.91, p = <0.001) but not different between SL forest and OP. Soil C was higher in SL and OG forest relative to OP ($F_{2,12}$ = 4.99, p = 0.03) whilst C:N ratio was highest in SL forest followed by OG forest and lowest in OP ($F_{2,12}$ = 25.70, p = <0.001). Inorganic P was higher in SL forest and OP relative to OG forest ($F_{2,12}$ = 8.83, p = 0.004). Soil NH_4 was higher in SL forest than in OG forest or OP ($F_{2,12}$ = 29.30, p = <0.001) whilst soil

NO_3 was lower in SL forest than in either OG forest or OP ($F_{2,12}$ = 29.30, p = <0.001) (

Table **5.1**). Soil bulk density and total soil N were not different between land uses. Upon rewetting of SL forest soils, $NH_{4\text{-rewet}}$ was strongly reduced in LID (p = <0.001) and HID (p = <-0.001) treatments relative to the control. NO_{3}-$_{\text{rewet}}$ increased across all land uses in HID treatment relative to control soils (Table 5.2).

Table 5.1 *- Site characteristics, field microclimate and soil properties. Data represent means ± 1 standard error in brackets.*

	OG Forest	**SL Forest**	**Oil Palm**
Plot Code	DAN-05	SAF-04	-
Soil Type	Orthic Acrisol	Orthic Acrisol	Orthic Acrisol
Soil Texture	Sandy Clay Loam	Sandy Loam	Clay Loam
Mean Annual Rainfall	3052	2717	2717
Average Slope (degrees)	12 (1.1)	11 (2.73)	18 (0.93)
Altitude (m)	222 (2.92)	399 (3.48)	327 (1.17)
Mean Soil Moisture (%)	38.99 (0.05)	50.47 (0.14)	24.14 (0.79)
Mean Soil Temperature (°C)	24.93 (0.00)	24.32 (0.01)	25.45 (0.16)
Mean Air Temperature (°C)	24.38 (0.02)	23.96 (0.02)	25.15 (0.04)
Gravimetric Moisture Content (%)	0.30 (0.01)	0.36 (0.04)	0.22 (0.03)
Bulk Density (g/cm^3)	1.02 (0.03)	0.89 (0.10)	1.14 (0.06)
pH	5.88 (0.15)	4.45 (0.12)	4.66 (0.08)
C (%)	2.80 (0.36)	5.22 (1.65)	1.57 (0.35)
N (%)	0.24 (0.02)	0.29 (0.08)	0.19 (0.03)
C:N	11.40 (0.59)	17.60 (1.41)	7.99 (0.54)
Bray P (µg/g)	7.86 (1.61)	25.3 (6.95)	295.11 (162.01)
Ammonium (NH_4) (µg/4 cm^2/1 day)	2.40 (1.52)	13.23 (1.37)	1.18 (0.57)
Nitrate (NO_3) (µg/4 cm^2/1 day)	18.90 (2.62)	5.88 (2.16)	26.10 (5.09)
Field soil respiration (mg CO_2-C/m^2/hr)	239.80 (23.32)	416.88 (69.14)	64.46 (13.66)

***Table 5.2** – Soil nitrogen availability, richness and diversity of bacteria and fungi in response to D-RW treatments. Data represent means ± 1 SE in brackets.*

	OG Forest	**SL Forest**	**Oil Palm**
Control			
NH4 - rewet (μg/4 cm^2/14 days)	7.21 (4.50)	127.42 (8.22)	2.06 (1.09)
NO3 - rewet (μg/4 cm^2/14 days)	146.50 (29.49)	56.47 (23.80)	206.29 (26.70)
Bacterial richness	613 (59)	507 (66)	439 (142)
Bacterial Shannon diversity	5.90 (0.10)	5.66 (0.15)	4.97 (0.56)
Fungal richness	123 (5)	183 (22)	148 (32)
Fungal Shannon diversity	3.05 (0.18)	4.04 (0.14)	3.53 (0.54)
Low Intensity Drought (LID)			
$NH_{4\text{ - rewet}}$ (μg/4 cm^2/14 days)	2.40 (1.29)	30.81 (2.72)	1.46 (0.81)
$NO_{3\text{ - rewet}}$ (μg/4 cm^2/14 days)	164.32 (39.75)	40.98 (13.34)	206.10 (39.63)
Bacterial richness	294 (69)	140 (37)	350 (109)
Bacterial Shannon diversity	4.60 (0.33)	3.75 (0.35)	4.97 (0.43)
Fungal richness	117 (12)	132 (14)	118 (23)
Fungal Shannon diversity	2.76 (0.33)	3.41 (0.13)	3.08 (0.16)
High Intensity Drought (HID)			
$NH_{4\text{ - rewet}}$ (μg/4 cm^2/14 days)	3.86 (1.90)	17.74 (2.36)	1.17 (0.25)
$NO_{3\text{ - rewet}}$ (μg/4 cm^2/14 days)	240.70 (31.02)	72.97 (26.49)	263.51 (32.93)
Bacterial richness	338 (21)	197 (48)	192 (80)
Bacterial Shannon diversity	4.49 (0.18)	3.98 (0.29)	3.93 (0.29)
Fungal richness	111 (11)	128 (15)	117 (22)
Fungal Shannon diversity	2.90 (0.07)	3.26 (0.09)	3.26 (0.20)

5.4.2 Effects of drought intensity on microbial GHG production

Immediately prior to rewetting, the mean percentage of maximum WHC in LID and HID treatments was 46.17±1.2 % (SE) and 17.03±1.0 % (SE) respectively (Figure 5.1). The drought treatment influenced the magnitude of the % CO_2 flux change after rewetting but the effect varied according to land use as there was an interaction between drought treatment and land use (Figure 5.2, Table 5.3). % flux change of CO_2 was higher in HID relative to LID treatments across OG forest and OP soils but there was no difference between drought treatments in SL forest soils (Figure 5.2). When we replaced the term land use with measured soil properties, the % CO_2 flux change

was best explained by soil C:N ratio which solely explained more than 60 % of variation (Figure 5.3, Table 5.4).

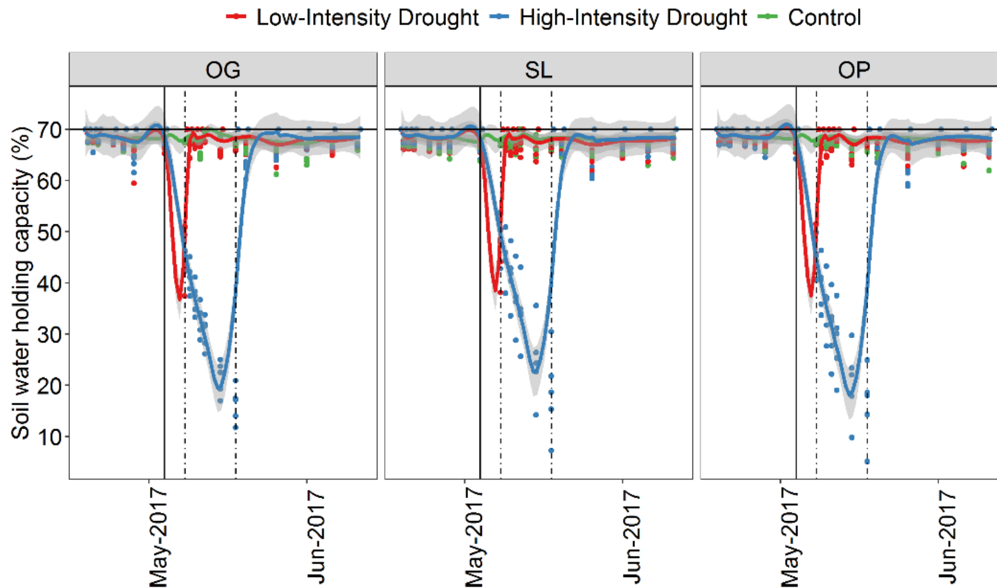

Figure 5.1 *- Soil water holding capacity (as a % of the maximum) during the experimental period. Lines represent fitted loess regression curves and grey shaded areas represent 95% confidence intervals. Solid vertical line represents the start of the drought period. Dashed vertical lines represent the time of rewetting, 4 and 14 days following drought. OG = OG forest, SL = SL forest.*

Drought treatments also influenced the cumulative CO_2 produced following rewetting although the treatment effect again varied between land uses (Figure 5.4, Table 5.3). Cumulative CO_2 emission was marginally higher in HID relative to LID treatments ($p = 0.06$) and significantly higher relative to the control treatment ($p = 0.03$) in OG forest soils. Cumulative CO_2 emission was significantly lower in HID relative to control treatment in SL forest soils ($p = 0.03$) but did not differ between LID and HID drought treatments ($p = 0.47$) (Figure 5.4). There was no difference in the cumulative CO_2 emission between treatments in OP soils (Figure 5.4). When we replaced the term land use with measured soil properties, variation in cumulative CO_2 emission was best explained by soil bulk density, $NH_{4\,-\,rewet}$ and pH (Table 5.4).

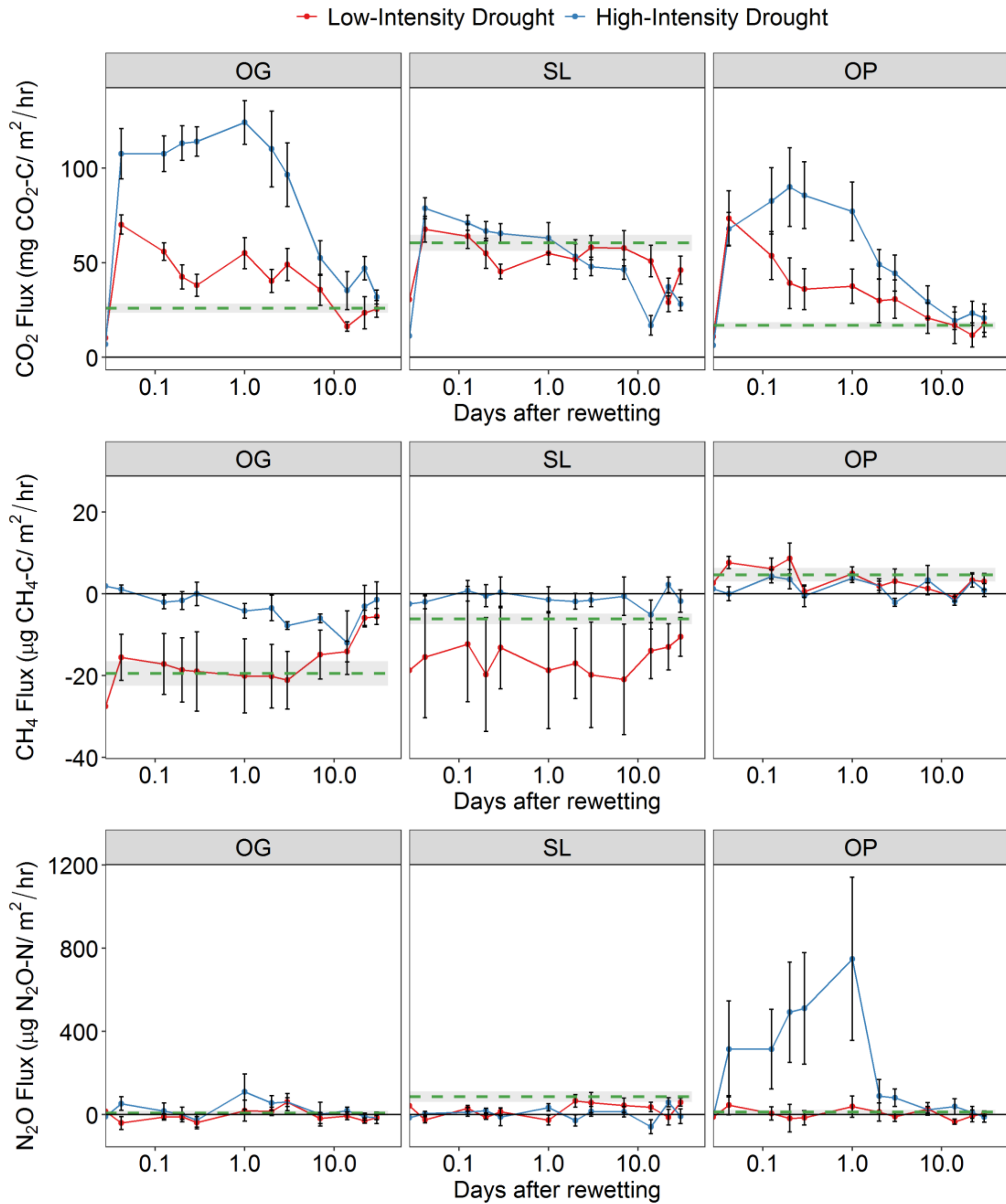

Figure 5.2 *- Soil CO_2, CH_4 and N_2O flux measured immediately prior to (T_0) and for 30 days after rewetting. Data points represent means. Vertical error bars represent ± 1 standard error. Green horizontal dashed line represent the mean flux from control soils measured at 6 time points over a 30 day period. The grey shaded area represents the 95% confidence interval. Note: X-axis are on a log scale.*

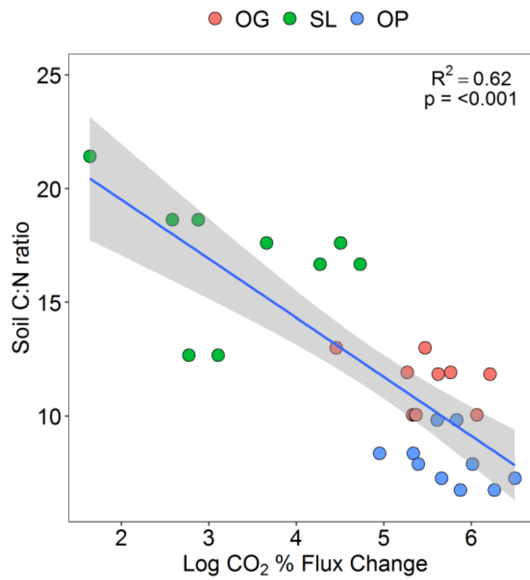

***Figure 5.3** - Relationship between soil C:N ratio and the % CO_2 flux change (log transformed) following rewetting. Grey shaded area represents the 95% confidence interval.*

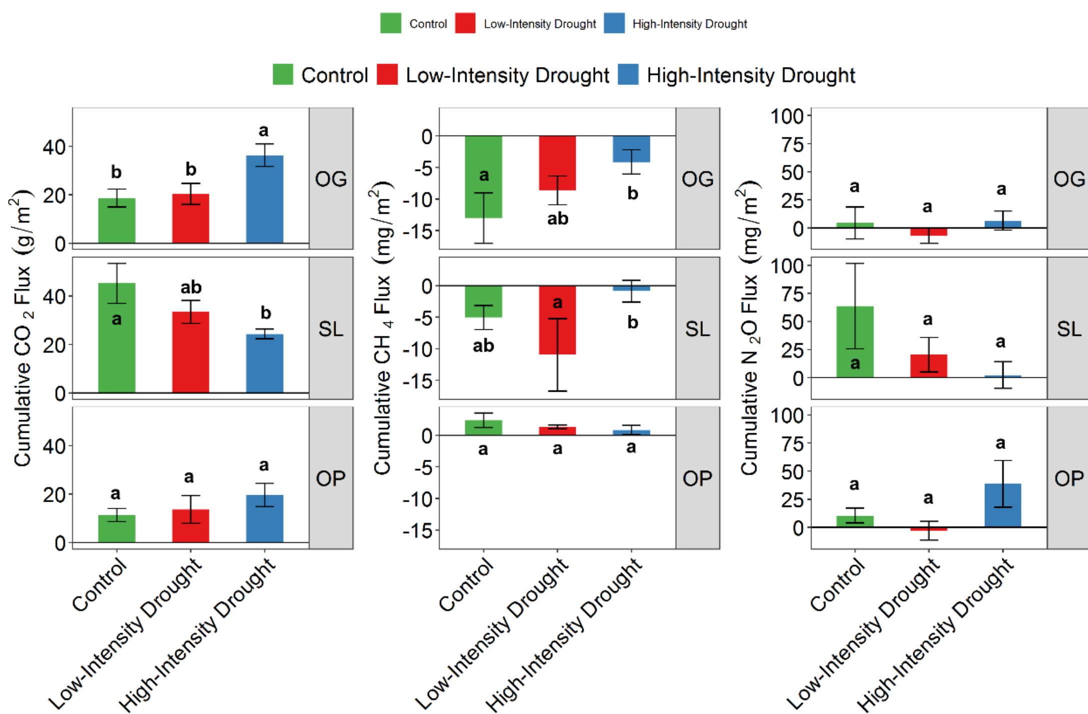

***Figure 5.4** - Cumulative CO_2, CH_4 and N_2O fluxes during the 30 day rewetting period estimated using linear interpolation between flux measurements. Bars represent means whilst error bars represent ± 1 standard error.*

***Table 5.3** - Two way ANOVA results for the effects of land use, drought treatment, and an interaction term on % CO_2 flux change and cumulative GHG emissions after rewetting. The relative importance of factors was calculated by partitioning R^2 using averaging over orders of regressors and is presented as decimal fractions which sum to the overall model R^2.*

Source of variation	Sum of Squares	df	Relative Importance	F	P - value	R^2
% CO_2 flux change						
Land Use	501054	2	0.58	23.18	<0.001	0.70
Treatment	326	1	0	0.03	0.864	
Treatment x Land Use	106967	2	0.12	4.95	0.016	
Error	259457	24				
Cumulative CO_2 emission						
Land Use	2875	2	0.31	12.13	<0.001	0.55
Treatment	142.5	2	0.01	0.6	0.554	
Treatment x Land Use	2138.1	4	0.23	4.51	0.005	
Error	4265.8	36				
Cumulative CH_4 emission						
Land Use	857.7	2	0.31	11.39	<0.001	0.51
Treatment	205.6	2	0.08	2.73	0.079	
Treatment x Land Use	327.8	4	0.12	2.18	0.091	
Error	1355.6	36				
Cumulative N_2O emission						
Land Use	6210	2	0.07	1.85	0.17	0.29
Treatment	5848	2	0.07	1.74	0.19	
Treatment x Land Use	12525	4	0.15	1.86	0.14	
Error	60449	36				

Cumulative CH_4 emission upon rewetting varied across land uses and were marginally different between treatments with no interaction between treatment and land use (Figure 5.4, Table 5.3). Variation in cumulative CH_4 emission was best explained by soil bulk density, pH and $NO_{3\text{-rewet}}$ (Table 5.4).

***Table 5.4** – Multiple linear regression results for the effects of soil properties and microbial community characteristics on % CO_2 flux change and cumulative GHG emissions after rewetting. The relative importance of factors was calculated by partitioning R^2 using averaging over orders of regressors and is presented as decimal fractions which sum to the overall model R^2. Continuous predictors were mean-centred and scaled by standard deviation to give standardised coefficients.*

Source of variation	Sum of Squares	df	Relative Importance	F	P - value	Standardised coefficients	R^2
% CO_2 flux change							
Treatment	0.08	1	0	0.12	0.73		
Soil C:N Ratio	28.4	1	0.64	45.89	<0.001	-1.01	0.64
Error	16.1	26					
Cumulative CO_2 Flux							
Treatment	621.6	2	0.05	4.94	0.012		0.75
Bulk density	1535.1	1	0.35	24.39	<0.001	-6.74	
Soil pH	460.3	1	0.03	7.31	0.010	3.62	
$NH_{4\text{ - rewet}}$	2107.9	1	0.32	33.49	<0.001	9.50	
Error	2391.9	38					
Cumulative CH_4 Flux							
Treatment	103.2	2	0.07	2.12	0.13		0.50
Bulk density	250.0	1	0.18	8.96	0.004	2.59	
Soil pH	313.4	1	0.14	12.96	<0.001	-2.76	
$NO_{3\text{ - rewet}}$	122.6	1	0.11	7.25	0.010	1.94	
Error	948.6	39					
Cumulative N_2O Flux							
Treatment	593.0	2	0.04	0.19	0.83		0.35
Bulk density	7258	1	0.05	4.53	0.04	17.34	
$NH_{4\text{ - rewet}}$	14515	1	0.18	9.06	0.005	24.60	
Bacterial Richness	4993	1	0.05	3.12	0.09	-20.69	
Bacteria NMDS1	4185	1	0.03	2.61	0.09	-19.83	
Error	51287	32					

Cumulative N_2O emission was not significantly influenced by either treatment or land use (Table 5.3). However, variation in cumulative N_2O emission was better explained by soil properties; $NH_{4\text{-rewet}}$ followed by soil bulk density, bacterial richness and community composition (Table 5.4). Drought treatment did influence the short term peak N_2O flux rates, although the effect varied according to land use (treatment x land use: $F_{4,36} = 4.11$, $p = 0.008$). There was no difference in peak N_2O flux rates between

treatments in either OG or SL forest soils but peak N_2O flux was higher in OP soils under HID relative to both LID ($p = 0.003$) and control ($p = <0.001$) treatments (Figure 5.2).

5.4.3 Microbial resistance and resilience to drought rewetting disturbance

There was no difference in the drought resistance of microbial activity to soil drying between sites, irrespective of the intensity of drying (Figure 5.5, Table 5.5). However, unsurprisingly resistance was strongly influenced by the intensity of drought, as CO_2 respiration immediately prior to rewetting was lower compared to pre-drought respiration in HID relative to LID treatments (Figure 5.5, Table 5.5). The resilience of microbial activity to D-RW differed significantly between land uses but was not influenced by drought intensity (Figure 5.5, Table 5.5). Soils from OG forest were significantly more resilient to D-RW than either SL forest ($p = 0.001$) or OP ($p = 0.035$) although there was no difference in microbial resilience between SL forest and OP ($p = 0.34$) (Figure 5.5, Table 5.5). Microbial resilience was best explained by variation in $NO_3^-{}_{rewet}$, bacterial and fungal community composition (Table 5.6). Bacterial richness and diversity across land uses declined in response to D-RW (Richness: $F_{2,32} = 6.05$, $p = 0.006$; Shannon Diversity: $F_{2,32} = 9.10$, $p = <0.001$) with higher richness and diversity in control soils relative to either LID (Richness: $p = 0.003$; Shannon Diversity: $p = 0.002$) or HID treatments (Richness: $p = 0.002$; Shannon Diversity: $p = <0.001$) (Table 5.2).

Figure 5.5 *- Resistance (A.) and resilience (B.) metrics calculated as described in Nimmo et al, (2015) of soil microbial communities measured using* CO_2 *respiration as a response function. Bars represent means whilst error bars represent ± 1 standard error. Lowercase letters denote whether parameters (resistance or resilience) were significantly different between land use (OG, SL and OP) for each drought intensity treatment derived from Tukey's HSD test. Significant differences (p <0.05) between plots are indicated when letters are different. Non – significant differences (P >0.05 between plots are indicated when letters are shared*

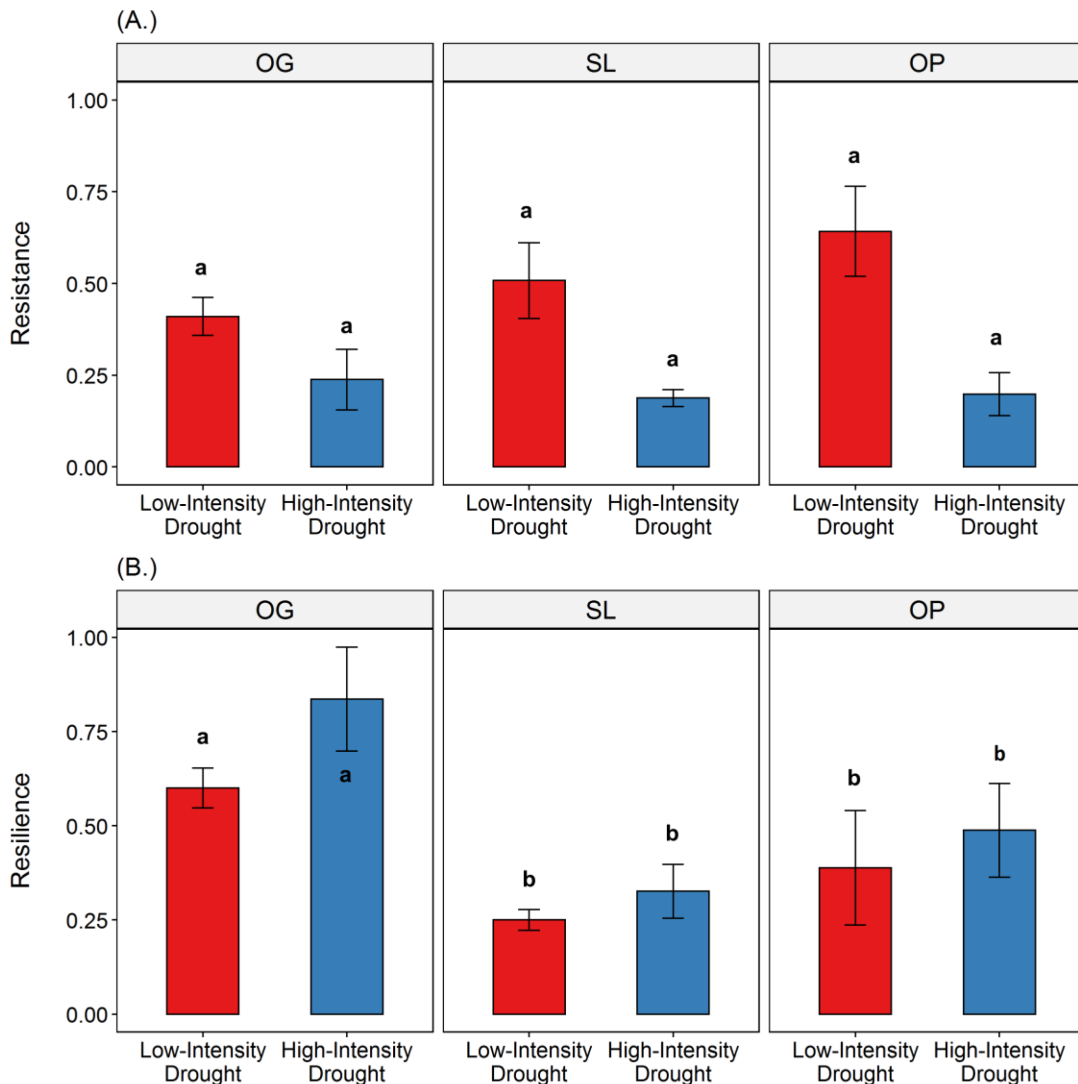

***Table 5.5** - Two way ANOVA results for the effects of land use, drought treatment, and an interaction term on microbial resistance and resilience indices. The relative importance of factors was calculated by partitioning R^2 using averaging over orders of regressors and is presented as decimal fractions which sum to the overall model R^2.*

Source of variation	Sum of Squares	df	Relative Importance	F	P - value	R^2
Resistance						
Land Use	0.05	2	0.03	0.76	0.477	0.52
Treatment	0.73	1	0.44	22.35	<0.001	
Treatment x Land Use	0.09	2	0.06	1.42	0.26	
Error	0.78	24				
Resilience						
Land Use	0.95	2	0.39	8.63	0.001	0.46
Treatment	0.14	1	0.06	2.56	0.122	
Treatment x Land Use	0.04	2	0.01	0.34	0.717	
Error	1.32	24				

Table 5.6 – *Multiple linear regression results for the effects of soil properties and microbial community characteristics on the microbial resilience index. Relative importance of predictors was calculated by partitioning R^2 and averaging over the orders of regressors, presented as decimal fractions which sum to the overall model R^2. Continuous predictors were mean centred and scaled by standard deviation to give standardised coefficients*

Source of variation	Sum of Squares	df	Relative Importance	F	P - value	Standardised Coefficients	R^2
Resilience							
Treatment	0.06	1	0.04	1.64	0.21		0.63
$NO_{3\text{ - rewet}}$	0.23	1	0.18	6.04	0.02	0.16	
Bacteria NMDS2	0.56	1	0.26	14.51	0.001	0.26	
Fungi NMDS1	0.59	1	0.15	15.14	<0.001	0.28	
Error	0.81	21					

Bacterial ($F_{2,40}$ = 4.47, p = <0.001, R^2 = 0.17) and fungal ($F_{2,43}$ = 6.77, p = <0.001, R^2 = 0.24) community composition from control treatments differed between land uses (Figure 5.6). After rewetting, the resilience of soil bacterial community composition varied between land uses as shown by a significant interaction between drought intensity and land use ($F_{2,43}$ = 1.62, p = <0.001, R^2 = 0.11). Bacterial community composition from OG and SL forest was different in LID (OG: $F_{1,9}$ = 3.06, p = 0.008, R^2 = 0.28, SL: $F_{1,9}$ = 4.20, p = 0.008, R^2 = 0.34) and HID (OG: $F_{1,9}$ = 2.96, p = 0.008, R^2 = 0.30, SL: $F_{1,9}$ = 4.14, p = 0.008, R^2 = 0.34) treatments relative to the control. In contrast, bacterial community composition in OP was not different between LID and control ($F_{1,9}$ = 1.42, p = 0.10, R^2 = 0.15) and only marginally different between HID and control treatments ($F_{1,9}$ = 1.77, p = 0.03, R^2 = 0.18). There was no difference in bacterial community composition between LID and HID treatments across land uses ($F_{1,28}$ = 0.66, p = 0.95, R^2 = 0.02). Soil fungal communities were also influenced by drought intensity across land uses as fungal community composition was different between control and drought treatments ($F_{2,43}$ = 1.42, p = 0.03, R^2 = 0.05) (Figure 5.6). However, the effect of D-RW treatment explained only a small amount of variance relative to community differences between land uses.

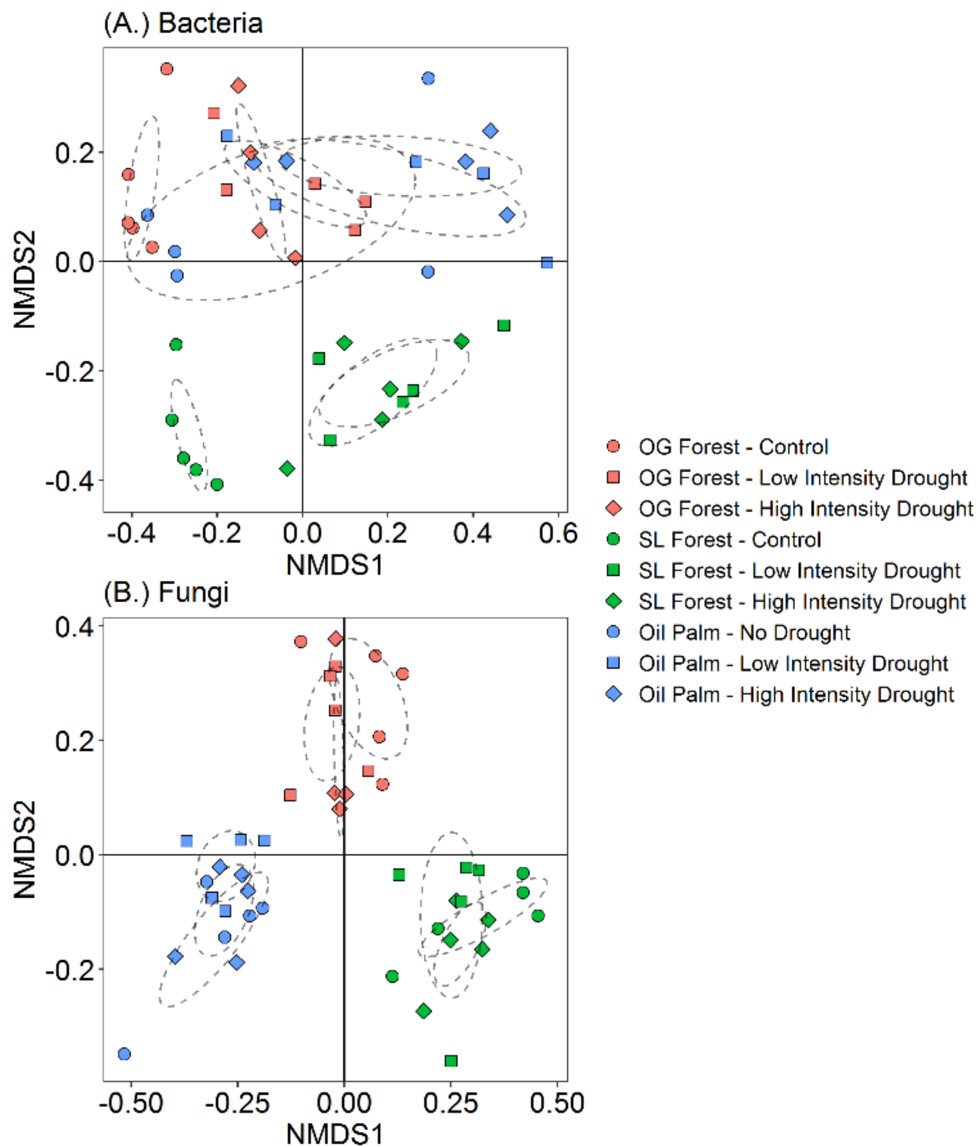

Figure 5.6 *- Non-metric multidimensional scaling (NMDS) ordinations of bacteria (A.) and fungal (B.) community composition measured from soils across no drought, low-intensity drought and high intensity drought treatments, 30 days after rewetting. Bacteria Stress score = 0.15, Fungal stress score = 0.16.*

Across land uses, bacterial communities that were subjected to a D-RW cycle (LID or HID) were characterised by a higher relative abundance (relative to control soils) of genera *Bacillus, Alicyclobacillus, Paenibaccilus, Clostridium, Coproccus, Ammoniphilus, Staphylococcus* and *Eschericia* (Figure 5.7). A higher relative abundance of *Bacillus* in D-RW soils was common across all 3 land uses whilst higher relative abundance of *Alicyclobacillus and Paenibaccilus* was common in D-RW soils from OG forest and OP.

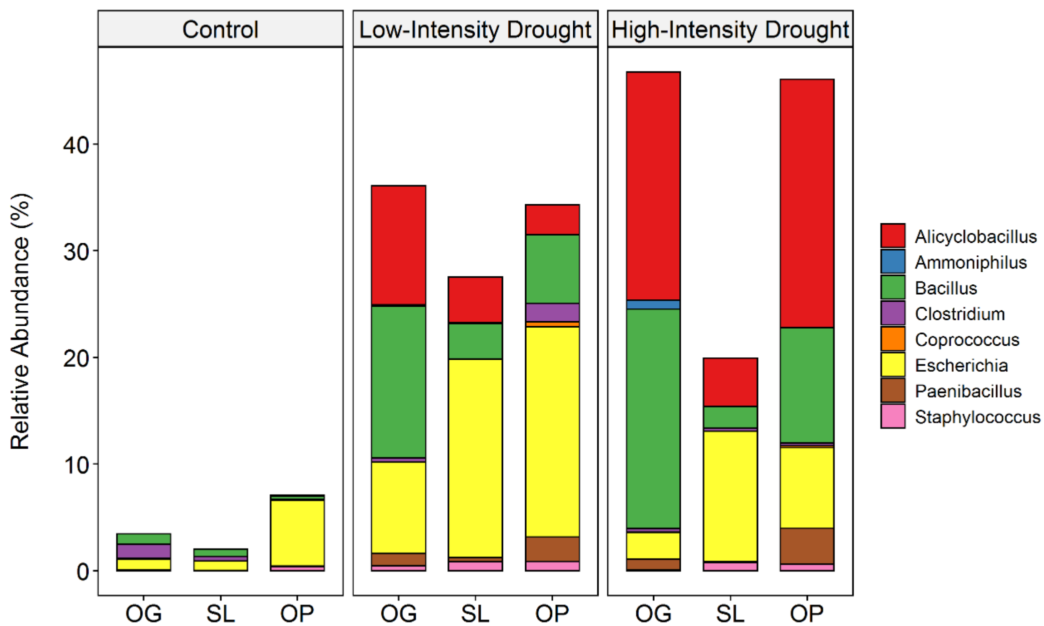

Figure 5.7 *- Relative abundance of bacterial genera, identified using Random Forest classification that best grouped samples into control and drought treatments.*

5.5 Discussion

Microbial respiration from incubated cores was highly correlated to field measurements demonstrating that by retaining soil structure, field differences in microbial activity between land uses were preserved (Appendix 4: Figure 8.7). Differences between field and laboratory CO_2 respiration also revealed that the heterotrophic component of soil respiration was lower in OG and SL forest (11.3-12.9 %) relative to oil palm (32.5 %). This suggests that the autotrophic contribution to soil respiration was higher in forested sites with respect to oil palm possibly due to greater root density. We predicted that drying intensity would be positively associated with peak and cumulative GHG emissions upon soil rewetting across OG, SL forest and OP soils (hypothesis 1). Our findings only partially supported this hypothesis as we found that emission responses to the intensity of drought varied between GHG's and that the CO_2 response was site specific (Figure 5.2, Table 5.3 Figure 5.4). Drought intensity was positively related to the % CO_2 flux change and cumulative CO_2 emissions upon rewetting of OG forest and OP soils. This response in OG forest and OP soils is consistent with the dynamics observed in studies of temperate ecosystems, which imposed different levels of drought duration or intensity (Navarro-García et al., 2012; Sun et al., 2018). The increased % CO_2 flux change and cumulative CO_2 emission may reflect progressively enhanced mineralisation of soil organic matter, due to aggregate disruption increasing C availability and turnover of dead microbial biomass with increasing drought intensity (Schimel, 2018; Wu and Brookes, 2005). In contrast, the % CO_2 flux change upon rewetting in SL forest soils was not influenced by the intensity of drought and cumulative CO_2 emissions were reduced relative to the moist control soils (LID: -28.3±10.1 %, HID: -47.0±4.5 %) (Figure 5.2, Figure 5.4). The difference in rewetting flux dynamics between sites is likely due to variation in soil

texture. OG forest and OP soils were clay rich relative to SL forest soils. Clay rich soils can maintain large pools of stable organic matter (OM) that can fuel large respiration pulses upon rewetting whilst coarser soils show weaker rewetting pulses (Schimel, 2018). Flux rates also remained depressed 30 days post rewetting. This suggests decreased bioavailable soil organic C (SOC) to fuel microbial respiration and may also be due to soil hydrophobicity induced by drying (Goebel et al., 2005; Goebel et al., 2007). SL forest soil had lower pH, higher SOC and C:N ratios than OG forest or OP soils (

Table **5.1**) and these soil properties have been associated with soil hydrophobicity (Goebel et al., 2011; Mataix-Solera et al., 2007). The interpretation of microbial drought-rewetting responses across heterogeneous ecosystems such as tropical forests, can be strongly influenced by the selection of sites to represent each ecosystem or land use. We found that the % CO_2 flux change upon soil rewetting across land uses and D-RW treatments was strongly negatively correlated with soil C:N ratios (Figure 5.3). This likely reflects that more labile substrates stimulate increased CO_2 fluxes upon rewetting and suggest that microbial respiratory responses to D-RW across heterogeneous tropical land uses may be generalized by accounting for differences in key soil properties. However, drought treatments were simplified proxies for drought under field conditions. Droughts in Bornean tropical forests are operationally defined as successive months <100m rainfall (Walsh and Newbery, 1999) rather than short periods of zero rainfall as imposed in this experiment. However, Danum Valley, (the OG forest site) experiences ~220 rain days per annum with no distinct dry season (Walsh and Newbery, 1999). Therefore, a 14 day continuous period with no

precipitation (the most intense drought treatment) represents an infrequent but not unrealistic event.

Very little is known of the microbial CH_4 response to soil rewetting, especially in tropical soils. In partial agreement with hypothesis 1, drought intensity marginally influenced cumulative CH_4 consumption from OG and SL forest soils as net CH_4 uptake was lower in HID relative to LID and control treatments (Figure 5.2, Figure 5.4). This suggests that rewetting following intense drought reduced soil O_2, possibly due to greater soil structural disruption from dessication and modifying soil porosity to promote methanogenesis over methanotrophy (Dutaur and Verchot, 2007). Soil drying may have also suppressed the activity of methanotrophs by pushing methanotrophy outside of the optimum range of soil moisture (Reay et al., 2001). Drought intensity had no effect on the CH_4 flux from OP soils. However, in agreement with hypothesis 1a, OP was a minor net source of CH_4, related to greater soil bulk density and nitrate availability. This agrees with a synthesis which found a negative ~~positive~~ relationship between soil N and CH_4 uptake (Liu and Greaver, 2009).

In addition to altered C dynamics, drought can also lead to the accumulation of inorganic N in soils, due to limited diffusion of N bearing soluble substrates (Homyak et al., 2017; Leitner et al., 2017). As N_2O is driven primarily by soil water filled pore space and substrate availability (Butterbach-Bahl et al., 2013; van Lent et al., 2015), we hypothesized that drying intensity would be positively related to N_2O emissions upon rewetting (fueled by a flush of inorganic N) and that emissions would be greatest from OP soils, due to increased N availability (Hypothesis 1 and 1b). Our findings did not support these hypotheses as there was no difference in cumulative N_2O emissions between drought treatments or land uses (Figure 5.4, Table 5.3). This is in contrast to both a laboratory and field study of tropical forests, which have shown substantial N_2O pulses upon rewetting of dried soils (Drewer et al., 2020; van Haren et al., 2005). We did observe a large, short term rewetting pulse of N_2O from OP soils but only

from those assigned to HID treatments, whilst emissions from LID treatment did not differ from the moist control (Figure 5.2). This is likely due to past fertilization as N_2O emissions from tropical agricultural land uses are driven strongly by N application rates (van Lent et al., 2015) and conversion from forest to OP leads to increased N_2O emissions (Fowler et al., 2011). Although our soil sampling targeted only the inter row areas of oil palm plantations and avoided the fertilized palm circle, there was substantial variability in N_2O flux between replicates. This suggests spatial heterogeneity within plantation management zones, due to variable aboveground C inputs and fertilizer application practices (Carron et al., 2015) may be important factors driving “hot moments” of N_2O (Wagner-Riddle et al., 2020). Low intensity D-RW did not stimulate any significant N_2O production in oil palm. This suggests minimal physical disruption of soil aggregates upon rewetting, which can expose previously protected organic matter or some resistance of oil palm microbial communities to osmotic shock and subsequent nutrient release (Schimel, 2018).

It has been shown that different precipitation histories can explain the abundance of drought tolerant and sensitive microbial taxa (Evans and Wallenstein, 2014; Meisner et al., 2018). We therefore hypothesized that oil palm microbial activity and community composition would be more resistant and resilient to D-RW relative to OG and SL forest microbial communities due to legacy effects of a drier and less buffered soil moisture environment (Appendix 4: Figure 8.6) (Hypothesis 2) (Luskin and Potts, 2011b; Meijide et al., 2018). Our findings did not fully support hypothesis 2 as resistance of microbial activity did not differ between land uses and resilience was higher in OG forest relative to SL forest and OP (Figure 5.5). This agrees with a previous study which also found that OG forest had higher functional resilience than either SL forest or OP (Brearley, 2015). This hints that soil microbial communities

from OG tropical forests might have a greater capacity to withstand future climatic perturbations. However, in partial agreement with hypothesis 2 we found that bacterial community composition in OP was unaffected by LID and only marginally affected by HID treatments. In contrast, bacterial communities from both OG and SL forest were strongly modified by D-RW, irrespective of the intensity of drought (Figure 5.6). This agrees with a previous study that showed changes to microbial community composition persisting several weeks after rewetting (Meisner et al., 2018). The relative resilience of oil palm microbial community composition suggests that soil moisture history in oil palm may have selected for species or traits within species that confer tolerance to desiccation (Bouskill et al., 2013; Evans and Wallenstein, 2012; Luskin and Potts, 2011a). However, we caution that the variability in oil palm microbial community composition between replicates was far higher than from forests. In agreement with previous studies, fungal communities across land uses were far more tolerant to D-RW than bacterial communities (Figure 5.6) (Barnard et al., 2013; de Vries et al., 2018).

We also found that gram-positive bacilliform bacteria (*Bacillus* sp., *Alicyclobacillus* sp., *Paenibacillus* sp.) markedly increased in relative abundance with progressively higher drought intensity (Figure 5.7) and that the resilience of microbial activity was best explained by bacterial and fungal community composition (Table 5.6). These findings suggest that microbial traits may influence the microbial response to D-RW as *Bacillus* sp., *Alicyclobacillus* sp. and *Paenibacillus* sp. form highly resistant endospores and can tolerate minimal water potentials (Setlow, 2006; Vardharajula et al., 2011). It also agrees with previous studies that have shown increases in the

abundance of rare taxa following rewetting that become dominant members of rewetted communities (Aanderud et al., 2015).

5.6 Conclusions

Our findings suggest that under controlled temperature conditions, interactions between drought intensity and land use may drive the response of soil-atmosphere GHG exchange across tropical forest and oil palm landscapes. More intense drought increased CO_2 emissions in OG forest and OP, reduced CH_4 uptake from forest soils and drove short term “hot moments” in N_2O from OP soils upon rewetting. This has implications for the ecosystem C balance under predicted future hydrological regimes, if replicated under field conditions. However, soil properties may be useful as general predictors of microbial GHG responses to D-RW across contrasting tropical land uses with the C:N ratio strongly associated to the magnitude of the rewetting CO_2 flush. OG forest microbial communities appeared most functionally resilient to D-RW, although the impacts on bacterial community composition were persistent. Therefore, legacy effects of D-RW may persist in soil microbial communities, selecting for traits and life history strategies that could influence the future resilience and functioning of soil microbial communities.

5.7 Acknowledgements

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6 General Discussion

6.1 Microbial ecology in a changing world

Soil microbial communities are the engine that drives ecosystem functions in terrestrial ecosystems (Graham et al., 2016). Technological advances over the last decade have revealed the extraordinary diversity of soil microbial communities across an array of terrestrial environments. However, comparatively few studies have examined tropical ecosystems, which are experiencing rapid land use and environmental change, due to human activities. Land use change can modify tropical soil microbial communities and potentially influence rates of biogeochemical cycling (Kroeger et al., 2020; Rodrigues et al., 2013). However, microbial ecological understanding is still very limited in tropical ecosystems.

This thesis aimed to enhance understanding of the environmental drivers and biotic interactions shaping soil microbial communities across human modified tropical forests in Borneo, and explore the effects of land use change on soil microbial functioning and resilience. A survey across intact and degraded tropical forest addressed the effects of forest disturbance on functional groups of soil microbial communities and their association with soil properties and tree community metrics. *In situ* invertebrate suppression treatments elucidated the important role that invertebrate-microbial interactions play in mediating microbial community structure and activity in tropical forest. Finally, controlled laboratory incubations provided new insights into the microbial contribution to litter decomposition, the functional dissimilarity of microbial communities across tropical land uses and the functional resilience of microbial communities to altered precipitation regimes. The findings

outlined in this thesis expand our knowledge of the abiotic and biotic controls on the distribution of soil microbes in tropical forests, highlight the functional dissimilarity of microbial decomposer communities across land uses and provide insights into the resilience of microbial communities to future climate extremes. The key findings in this thesis contribute to an improved understanding of above-belowground interactions in tropical ecosystems and have wider implications for large scale ecosystem processes, such as soil carbon storage and nutrient recycling. The findings also emphasize key uncertainties, which should steer future research priorities in tropical microbial ecology.

6.2 Controls on soil microbial communities in tropical forest

The enormous microbial diversity in soils presents major challenges to modelling microbial systems and to explaining patterns of microbial community variation across space and time (Louca et al., 2018; Nesme et al., 2016). Identifying local and regional scale drivers across tropical forests is especially challenging, due to their extremely high biodiversity and structural complexity (Townsend et al., 2008). Moreover, human modification of tropical forests increases forest heterogeneity (Blonder et al., 2018; Ordway and Asner, 2020). Because of this complexity the principal controls on microbial community turnover across tropical forests is still poorly characterised. Chapter 2 sought to identify the effects of forest degradation on functional groups of soil microbial communities and explain community variation in relation to tree communities and soil properties across intact and degraded tropical forest plots. The results showed that selective logging strongly shifted EcM fungal community structure and reduced their relative abundance, which was linked to the standing biomass of host trees (Dipterocarpaceae and Fagaceae). Although previous studies have shown shifts in EcM community structure (McGuire et al., 2015), this is the first

study to show a substantial decline in the relative abundance of EcM fungi in SE Asian tropical forests. These findings add to the understudied field of mycorrhizal ecology in the lowland tropics and raise further questions as to whether mycorrhizae may dictate the efficacy of conservation efforts including tree species reintroduction programmes and influence soil carbon storage.

Mycorrhizal abundance and distribution may have important implications for regional forest recovery and the success of active forest restoration efforts. If sufficient EcM inoculum remains in forest soils and in the absence of seed bank depletion or seed dispersal limitation, reestablishment of canopy forming dipterocarp trees during forest recovery may not be impaired. However, the regional loss of specific EcM taxa in logged forests (and in surrounding agricultural plantations) may impede the recovery of old growth forest taxa, particularly if EcM taxa have specificity for tree hosts (Essene et al., 2017). It also has important implications for active forest restoration across the region such as enrichment planting schemes in previously logged forests (e.g. Sow-A-Seed INIKEA reforestation project and Face the Future: INFAPRO. Sabah Malaysia) and national commitments toward natural forest regeneration on degraded and abandoned agricultural lands (Kemppinen et al., 2020; Lewis et al., 2019).

Shifts in mycorrhizal communities can also have significant consequences for ecosystem C cycling and storage with EcM dominated ecosystems associated with higher soil C stocks per unit of N, independent of climatic variation (Averill et al., 2014; Wurzburger and Brookshire, 2017). This is an important observation as globally soil contains more carbon than the atmosphere and vegetation combined and therefore shifts in the mycorrhizal status of ecosystems may have significant implications for

the global C cycle. Although I did not measure soil C stocks, the findings presented in chapter 2 suggest that selective logging of dipterocarp trees could shift logged SE Asian tropical forests from EcM dominance toward more AM fungal dominated ecosystems, with significant potential impacts on C stocks in disturbed SE Asian tropical forest soils. Although findings from chapter 2 did not show an increase in the relative abundance of AM fungal taxa, there was a clear negative relationship between the presence of EcM host tree species and AM fungal relative abundance.

However, it is important to acknowledge the limitations of this survey. OG and SL forest plots were not co-located and therefore physical proximity could confound observed differences in microbial communities between forest types. Unfortunately, very little OG forest remains at the landscape scale in Sabah, Malaysia and research permits only allowed for sampling in specific areas. Therefore, a paired site approach was not possible. Nonetheless, using sites from the pantropical Global Ecosystems Monitoring (GEM) intensive carbon plot network (http://gem.tropicalforests.ox.ac.uk/) conferred the unique advantage of access to an extensive dataset of tree community attributes. The ITS2 primers used in this study have relatively low resolution for AM fungi and preferentially amplify Glomeraceae (Lekberg et al., 2018). Specific primers targeting AM fungi, combined with root and rhizosphere sampling could be applied, which may reveal differences in the abundance and community composition, potentially obscured by primer and sampling bias in this study. High throughput sequencing is not suited to measuring absolute microbial abundance and the PLFA biomarkers applied cannot distinguish between the biomass of different mycorrhizal groups. Biomarkers such as chitin, ergosterol and the neutral lipid fatty acid 16:1ω5c could be applied to quantify the biomass of EcM and AM fungi and assess absolute change in abundance across human modified

tropical forests (Wallander et al., 2013). These data would give more confidence to the inferences made from observed differences in mycorrhizal relative abundance between OG and SL forest.

6.3 Invertebrate – microbial interactions in tropical forest

Interactions between invertebrates and soil microbes are an important part of the detritus based food chain in soils and facilitates energy transfer between trophic levels of ecosystems (Benbow et al., 2019). However, the nature of invertebrate-microbial interactions and the contribution to soil biogeochemical cycles remains unclear, particularly in tropical ecosystems. Chapter 3 sought to explore the role of two key soil invertebrates (ants and termites), considered ecosystem engineers in tropical forest, to mediate microbial community composition and function. The results from chapter 3 demonstrated that ant activity regulated fungal mycelial production as hyphal abundance increased under ant suppression. This is significant as soil mycelium are a key component of terrestrial C and nutrient cycles (Cairney, 2012; Finlay, 2008) and contribute to the accumulation of soil organic matter (Wallander et al., 2013). For example, in EcM dominated ecosystems, more than half of newly formed SOM was attributed to extraradical hyphae (Frey, 2019). Termites also influenced the distribution of wood decay fungi and the relative abundance of lignin degrading bacteria. This finding is important as deadwood decomposition is a key component of the C balance in tropical forests (Pfeifer et al., 2015) and many termites are specialist wood eaters. These findings highlight that complex ecological interactions operate between ants, termites and specialist microorganisms and suggest that forest disturbance may disrupt trophic interactions to influence ecosystem level processes. Further studies should investigate how these interactions scale up to influence communities and ecosystem level processes across disturbed tropical forests.

Previous studies in temperate ecosystems have demonstrated that invertebrate-microbe interactions can mediate increases in soil microbial decomposition and carbon loss from soils under projected global change scenarios (Crowther et al., 2015). As selective logging of SE Asian tropical forests strongly modifies the functional structure of ant communities by promoting generalist vs specialist species and reduces termite abundance (Luke et al., 2014), the findings presented in chapter 3 suggest that microbial responses to future global change may differ between OG and SL tropical forests driven by differences in invertebrate-microbe interactions. For example, increases in microbial decomposition rates and soil C loss under increased temperature could be regulated by the level of top-down control on fungal grazers by ants. This has implications for ecosystem biogeochemical cycling and therefore the abundance and activity of key invertebrates should be considered as a driver of microbial community structure, distribution and potential function in tropical forests. Although we cannot disentangle whether the observed microbial responses are directly because of a reduction in ant and termite abundance or indirectly through their effect on the soil environment, these are the first reported data demonstrating invertebrate-microbial interactions at the field scale in tropical forests. Using microbial ecological networks, it was also found that ant and termite suppression led to the reorganisation of microbial networks that were more connected, less modular and potentially more vulnerable to disruption. Although the biological interpretation of microbial networks is still in its infancy, these findings raise intriguing questions regarding the role of invertebrate-microbe interactions in mediating microbial resilience to disturbance.

Although invertebrate suppression treatments were very effective at reducing activity of target species, the chemical compounds used may also have directly influenced microbial communities (Lo, 2010), thus confounding interpretation of invertebrate

influence on microbial communities. However, the dosage applied was low and incorporated into baits specific to the target organisms. Moreover, whilst aromatic degrading bacteria did increase in relative abundance, the magnitude of increase differed between invertebrate suppression treatments, suggesting some biological influence. The approach used to classify fungi into functional groups and assign putative functions to bacteria is also dependent on the quality of the annotation of reference databases. To ensure that erroneous classifications were not included, only those taxa annotated with high confidence were retained. However, a significant proportion of taxa were thus excluded, which highlights the need to improve reference databases through enhanced understanding of the ecological roles of described and undescribed taxa.

6.4 Functional equivalence and dissimilarity of tropical soil microbial communities

Microbial populations readily adapt to alterations in their abiotic environment, yet the functional implications of these shifts in microbial ecology are still poorly understood and characterised (Allison et al., 2013; Graham et al., 2016; Graham et al., 2014; Kaiser et al., 2014; Martiny et al., 2015; Nemergut et al., 2014). In tropical forests, litter decomposition is one of the most important ecosystem functions as they often grow on highly weathered soils with a large proportion of available nutrients tied up in the living biomass (Attiwill and Adams, 1993; Sayer and Tanner, 2010). Although litter quality and climate largely regulate rates of litter decomposition (Bradford et al., 2016), previous studies in tropical forests have suggested that decomposer communities may play an important role in explaining site specific variation in litter decomposition rates (Powers et al., 2009). Findings in chapter 4 showed that under controlled climatic conditions, litter chemistry explained the majority of variation in

litter decomposition rates; yet inclusion of measures describing microbial abundance and community richness significantly increased explanatory power. This demonstrates that knowledge of underlying microbial communities may enhance our ability to predict ecosystem process rates. Therefore, improvements to ecosystem process and global change models may be achieved by continued efforts to integrate measures of microbial community structure, richness and abundance (Graham et al., 2014; Hararuk et al., 2015; Treseder et al., 2012; Wieder et al., 2014).

The findings also revealed differences in the functional ability of microbial communities across OG forest, SL forest and oil palm plantations to degrade an array of litter mixtures. Despite comparable microbial abundance, OG forest communities retained greater functional ability as they degraded all litters most quickly, whilst heavily logged forest communities were the least functionally able. This was suggestive of functional dissimilarity between decomposer communities. Functional dissimilarity is thought to be most relevant for physiologically and phylogenetically "narrow" soil microbial processes (i.e. production of N_2O, methanogenesis or the mineralization of recalcitrant organic pollutants) rather than broad scale processes such as organic matter decomposition (Bakken et al., 2012; Girvan et al., 2005; Jia and Whalen, 2020; Schimel and Schaeffer, 2012). These findings suggest that microbial community structure can be consequential even for broad ecosystem processes and that forest disturbance may have a long term impact on soil microbial function. This has implications for rates of forest soil carbon and nutrient cycling as reduced decomposition rates in heavily logged forests could slow nutrient turnover and increase soil C stocks.

Microbial communities from moderately logged forest, with the most chemically recalcitrant litter also appeared to exhibit specific adaptations or functional specialisation as native litter decomposed faster when combined with native soil (The so called home-field advantage). This is consistent with findings suggesting that home-field advantage effects are stronger in low quality litter environments such as forests (Veen et al., 2015). Understanding this local scale variation is important as decomposition processes have direct feedbacks on plant growth and performance. It also highlights that to fully understand plant-soil feedback effects in tropical forests with respect to ecosystem function, interactions between plants, plant litter and local decomposer communities must be considered. Taken together these findings add to the growing body of evidence suggesting that the impact of small scale variation in decomposer communities may be much more important for driving decomposition than previously assumed (Bradford et al., 2016; Bradford et al., 2017; Fanin et al., 2014). A more complete understanding of this local scale complexity is the first step towards the design and validation of fine scale models that capture fundamental microbial mechanisms. These may then be scaled up to the ecosystem scale and ultimately incorporated into global climate models (Todd-Brown et al., 2012).

Although laboratory incubations offer the advantage of controlling for external factors to test specific hypotheses, the extent to which they represent *in situ* activity is unclear. For example, soil mesofauna and macrofauna are important for the physical breakdown and redistribution of organic matter, with faunal exclusion reducing litter decomposition rates by 24 % in a Bornean tropical forest (Both et al., 2017). Fauna are not present in *ex situ* incubations and therefore litter decomposition may proceed differently to under *in situ* conditions. Moreover, the influence of local variation in forest floor microclimate may also interact with microbial processes (Blonder et al.,

2018). Interpreting effects of land use in soil incubations from single sites is also highly dependent on the selection of representative areas within each land use for sampling. These are inherent limitations of the incubation approach and therefore highly replicated *in situ* litterbag experiments with co-located measures of local scale environmental factors are necessary to validate these findings. Resilience of tropical soil microbial communities to future climate extremes

Over the next few decades, tropical regions will experience increases in temperature, rapid increases in atmospheric CO_2 concentrations, and significant alterations in the timing and amount of rainfall (Anderson, 2011; Dai, 2013; Diffenbaugh and Scherer, 2011; Kumagai et al., 2013; Mora et al., 2013). However, there are major uncertainties in the response of tropical ecosystems to this future global environmental change (Bastos et al., 2020; Bonal et al., 2016). As tropical ecosystems exchange more CO_2 with the atmosphere than any other biome (Beer et al., 2010), the limited knowledge of tropical ecosystem responses to altered climate represents a major barrier to accurate predictions of the earth's future climate. The findings in chapter 5 showed that the magnitude of soil CO_2 efflux, in response to rewetting after different intensities of drought was land use specific, linked to differences in key soil properties. This is significant as linking heterotrophic CO_2 production upon rewetting to easily measured soil properties facilitates biogeochemical modelling to predict climate change responses at the wider landscape scale. More intense drought did increase cumulative soil CO_2 emissions under OG forest and oil palm soils, which suggests that increased drought duration may acts as a positive feedback for the rewetting soil CO_2 flux in these land uses. This could be linked to a larger nutrient pulse from disruption of soil aggregates or lysis of microbial cell walls. However, longer drought periods also suppress microbial metabolic activity and therefore long

term experiments are necessary to determine the net GHG balance under different rainfall regimes. The net CH_4 balance varied between forests (net CH_4 uptake) and oil palm (net CH_4 emission) with uptake being reduced upon soil rewetting from forest soils. However, fluxes were small and of minimal importance in terms of global warming potential. N_2O efflux appeared to interact with drought intensity in oil palm soils with higher but short lived fluxes following rewetting after high intensity drought. This may have significant implications for future biosphere-atmosphere GHG exchange from oil palm plantations. As palm oil plantations are the most rapidly growing land use in SE Asia (Gaveau et al., 2016) and N_2O is a potent GHG, this represents a major uncertainty in the terrestrial GHG balance.

Findings in chapter 5 also suggested that OG forest microbial communities were more metabolically resilient to drought-rewetting cycles than those from SL forest or OP plantations as heterotrophic respiration returned close to pre-drought levels after 30 days. This suggests that OG forests might be more resilient to future drought dynamics and raises further questions regarding the longer term legacy effects of drought-rewetting on microbial activity. The response of soil decomposition processes to changes in moisture has regional and global implications for soil C cycling. These findings highlight the importance of considering interactions between tropical land use and drought intensity, as drivers of short term microbial SOM decomposition dynamics upon rewetting.

Although intact soil cores were assayed to maintain soil physical structure, laboratory incubations represent a simplified system. Under *in situ* conditions, rhizodeposition from plant roots may fuel increased heterotrophic respiration upon rewetting. Moreover, soil trace gas fluxes (CH_4 and N_2O) are not only driven by abiotic

conditions but can also be influenced by tree species identity, whilst tree stems can act as conduits for trace gases (Welch et al., 2019). CH_4 and N_2O can also be produced and consumed within deeper soil layers, far below the depth to which we cored to. The drought treatments (4 or 14 days without rainfall) were also simplified and not comparable to ecological droughts under field conditions. In tropical forests, droughts are defined as longer periods (several months) with below average rainfall rather than short periods of zero precipitation (Walsh and Newbery, 1999). We also conducted our incubation at a standard temperature. However, soil surface microclimate varies between OG forest, SL forest and oil palm plantations (Hardwick et al., 2015). Moreover, interpreting effects of land use in soil incubations from single sites is highly dependent on the selection of representative areas within each land use for sampling. Therefore, field scale measurements across land use and precipitation gradients are necessary to infer changes to the net GHG balance of tropical ecosystems under different rainfall regimes.

6.5 Implications for tropical C cycling under future environmental change

The knowledge gained from this thesis suggests that selective logging of tropical forests, through modification of tree, invertebrate and microbial community composition could impact on forest C cycling. For example, Chapter 2 demonstrated that reduced abundance of EcM associating dipterocarp trees in SL forest was associated with declines in the abundance of EcM fungi. This suggests that soil C storage may be lower in SL relative to OG forest as EcM fungi are major conduits of belowground C transport, with greater ecosystem EcM dominance associated with higher soil C stocks (Averill et al., 2014). However, logging may also reduce rates of soil organic matter turnover and increase soil C stocks, due to changes in the activity

of key invertebrates (ants and termites), modifying rates of microbial organic matter decomposition. Selective logging may increase ant activity at moderate logging intensity (Luke et al., 2014). Increased ant activity in SL forest may slow rates of fungal decomposition relative to OG forest as findings in Chapter 3 demonstrated that ants suppress soil fungal growth – key decomposers of organic matter in forests. Termites are key agents of decomposition in tropical forests and logging reduces termite abundance (two thirds reduction in the study area) and their contribution to decomposition processes (Ewers et al., 2015). Findings in chapter 3 also showed that suppressed termite activity increased abundance and altered the distribution of microbial wood degrading taxa, suggesting that specialist microbial decomposers may compensate for the loss of termite function in SL forests and maintain decomposition rates. However, more general microbial decomposer communities appeared to have impaired functional abilities in SL relative to OG forest as findings in chapter 4 indicated reduced ability of SL forest communities to decompose diverse litter mixtures from forests and oil palm plantations. This agrees with the finding of Ewers et al, 2015 that showed a 15 % decrease in litter decomposition rates in SL relative to OG forest. Taken together the findings from Chapters 2-4 suggest that the overall impact of selective logging on soil C cycling is determined by the balance between changes to mycorrhiza mediated belowground C transport and alterations to rates of decomposition processes, driven by invertebrate – microbial interactions.

The response of forest C cycling to future global environmental change may also differ between OG and SL tropical forests. For example, increases in microbial decomposition rates and soil C loss, driven by increased air temperatures could be suppressed in SL forests by greater top-down control on fungal grazers by ants. Furthermore, higher termite activity in OG relative to SL forest has been shown to

mitigate the effects of drought in tropical forest (Ashton et al., 2019) and could therefore maintain rates of ecosystem processes such as litter decomposition. This may also explain findings in Chapter 5 showing that OG forest microbial communities had greater functional resilience to experimental drought – rewetting cycles relative to communities from SL forest or oil palm plantations. Although invertebrate abundance is much lower in oil palm plantations relative to forests, the effects of drought on soil C stocks in deforested landscapes such as oil palm plantations is likely to be smaller than in tropical forests as large quantities of soil C are lost following forest conversion (Guillaume et al., 2015). Moreover, microbial communities were more resilient in terms of their community composition (Chapter 5) and rates of litter decomposition have been found to recover rapidly after drought periods (Eycott et al., 2019).

6.6 Conclusions

This thesis sought to investigate the impacts of selective logging and tropical land use change on soil microbial community composition, function and resilience to future climatic extremes and examine the abiotic and biotic factors structuring microbial assemblages across complex, tropical forest ecosystems. EcM fungal communities were distinct in OG and SL forest and their relative abundance was strongly reduced in SL forests. This is the first time that a reduction in relative abundance has been measured and has wider implications for forest recovery, restoration strategies and ecosystem soil C storage. In OG forest, ants mediated fungal hyphal production whilst termites exerted top down control on lignin degrading fungi and bacteria. These findings suggest that invertebrate-microbial interactions play an important role in the regulation of soil biogeochemical cycles in OG tropical forest and that invertebrate abundance may mediate shifts in microbial function across SL forests. Soil microbial decomposers from OG forest retained greater functional breadth as they decomposed a

range of contrasting litter mixtures faster relative to communities from SL forest and oil palm plantation. This suggests that microbial communities across tropical ecosystems are not functionally equivalent and highlights the importance of efforts to integrate microbial ecology into ecosystem models to predict global change effects. Microbial responses to varying intensities of drought-rewetting stress were land use specific with CO_2 efflux driven by variation in soil properties and N_2O efflux driven by N availability. However, OG forest microbial communities appeared more resilient to drought-rewetting relative to those from SL forest and oil palm. This has implications for regional predictions of biosphere-atmosphere GHG exchange in response to intensified and more frequent drought events, as predicted due to anthropogenic climate change in the tropics. OG forests are irreplaceable for sustaining aboveground tropical biodiversity. Taken together, the findings in this thesis suggest that OG tropical forests may also be vital for the maintenance of soil microbial diversity, function and resilience to future global environmental change.

6.7 Future work

The findings from the work described in this thesis have raised a number of potential opportunities for future research.

- Findings from chapter 2 showed a particularly strong effect of selective logging on mycorrhizal communities and abundance. The abundance and taxonomy of mycorrhizal inocula present in soils may dictate the success of forest restoration efforts using enrichment planting of dipterocarp species and the reforestation of abandoned agricultural lands. Therefore, in this context, further studies should focus on elucidating the nature of mycorrhizal-host tree relationships across a wide range of tree species used in enrichment planting

schemes and determine whether the extent and taxonomy of EcM fungal colonisation confers benefits in terms of dipterocarp tree seedling survival, establishment and vegetative growth. The relationship between EcM colonization and soil C stocks under different tree species could also be investigated. As most remaining intact forest across Borneo is now under legal protection, forest restoration efforts are crucial for wider landscape scale conservation of biodiversity and the continued provision of essential ecosystem services.

- Results reported in chapter 3 were the first to demonstrate *in situ* that ants and termites influence the activity and abundance of key microbial functional groups in OG tropical forest. As selective logging of forests alters the functional diversity of ants and termites, further work should examine the nature of invertebrate-microbial interactions in the context of ecosystem functionality across human modified tropical forests. For example, logging reduces the abundance of wood feeding termites. Therefore it is important to understand to what extent soil microbial decomposers can occupy this functional niche and how this influences deadwood decomposition rates in logged forest.
- Litter decomposition assays performed in chapter 4 demonstrated that taxonomically distinct microbial communities across the dominant tropical land uses in Borneo may be functionally dissimilar, even for broad scale ecosystem processes. More research efforts are thus required to link microbial diversity patterns to measured ecosystem functions, particularly in understudied tropical ecosystems. Describing communities in terms of their metabolic functions of interest through shotgun metagenomic sequencing and

adopting a functional trait based framework could reduce the complexity of microbial systems and may prove to be valuable in the search for general patterns in microbial ecology.

- Findings in chapter 5 suggest that microbial responses to different intensities of drought-rewetting cycles may differ across tropical land uses. This highlights the major uncertainties in the potential response of tropical landscapes to future global environmental change. Large scale *in situ* ecological manipulations of global change factors, such as temperature and precipitation are required across a range of natural and disturbed tropical land uses. This would allow for the investigation of interactions between land use and global change factors and how this mediates the response of tropical ecosystems.

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8 Appendices

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Appendix 1 - Impacts of selective logging on tropical forest soil microbial communities

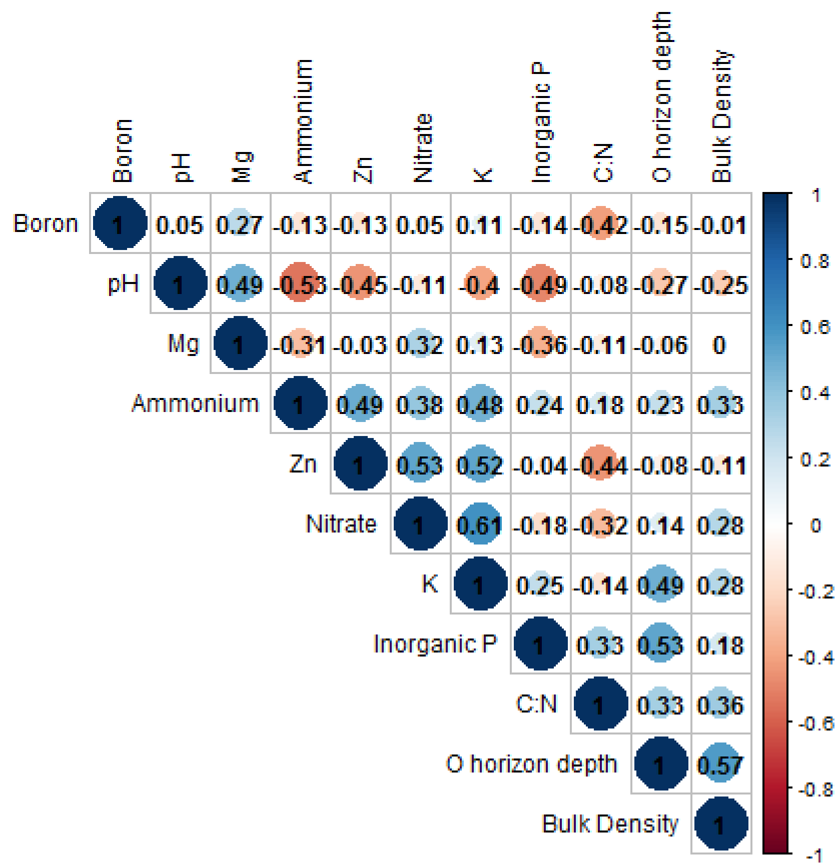

Figure 8.1 *- Correlogram of selected soil properties. Those parameters with a correlation coefficient of < ±0.7 were retained for further analyses. Positive correlation coefficients are shown in blue whilst negative correlation coefficients are shown in red.*

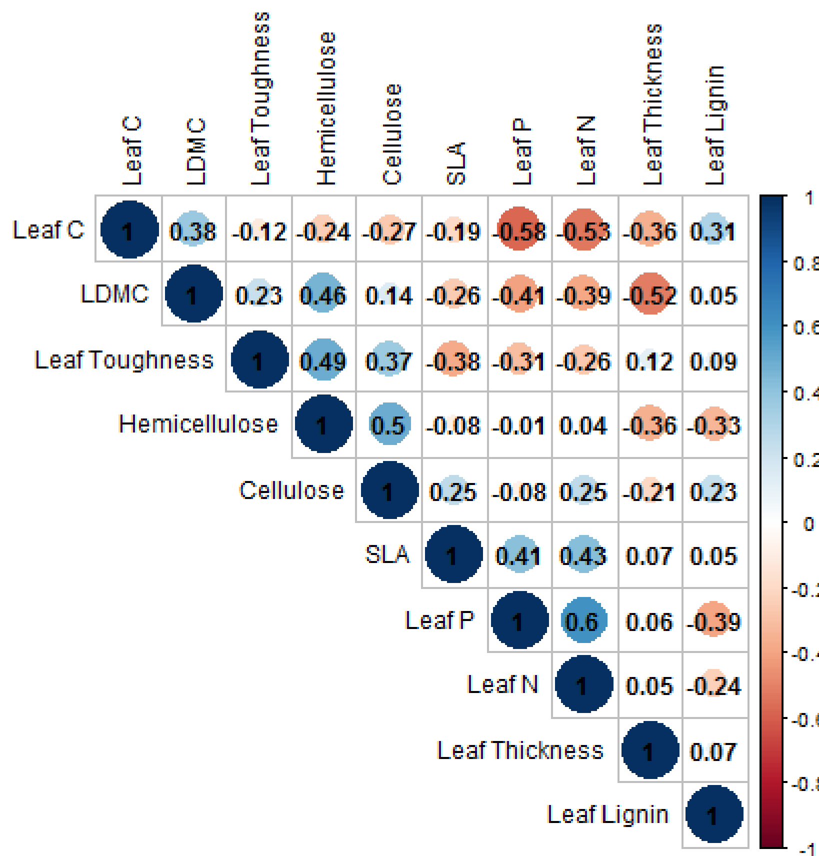

***Figure 8.2** – Correlogram of selected CWM traits. Those parameters with a correlation coefficient of < ±0.7 were retained for further analyses. LDMC = leaf dry matter content, SLA = specific leaf area. Positive correlation coefficients are shown in blue whilst negative correlation coefficients are shown in red.*

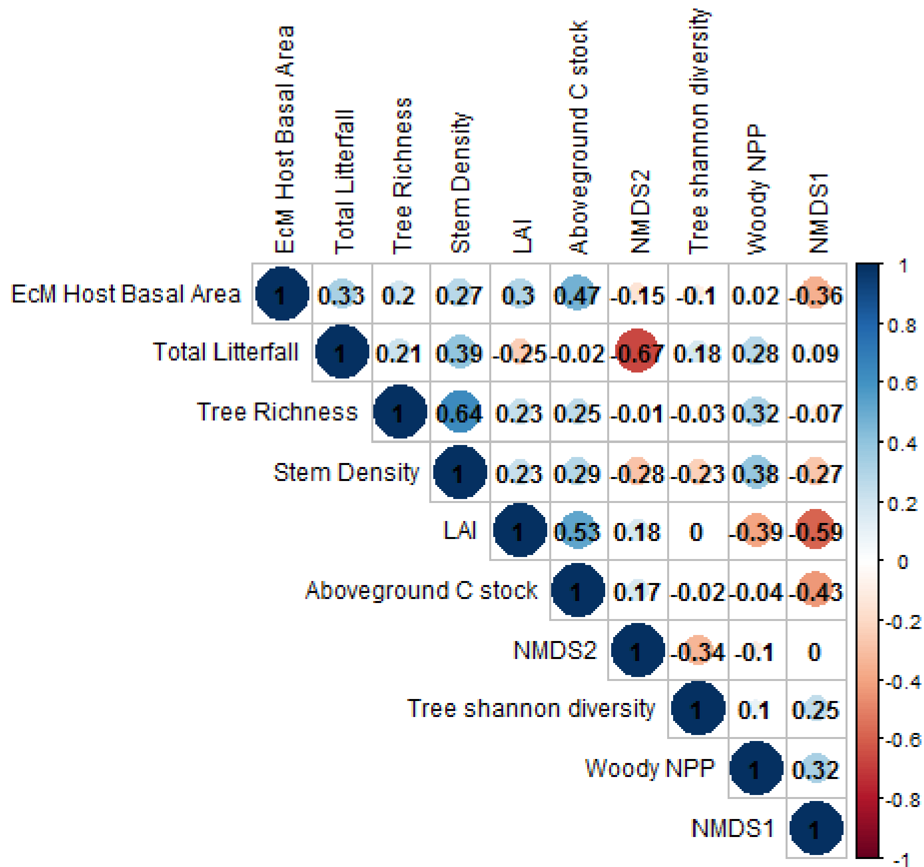

Figure 8.3 *- Correlogram of selected tree community characteristics. Those parameters with a correlation coefficient of < ±0.7 were retained for further analyses. LAI = leaf area index. NMDS1 & 2 = axis scores from ordination of tree community composition. Positive correlation coefficients are shown in blue whilst negative correlation coefficients are shown in red*

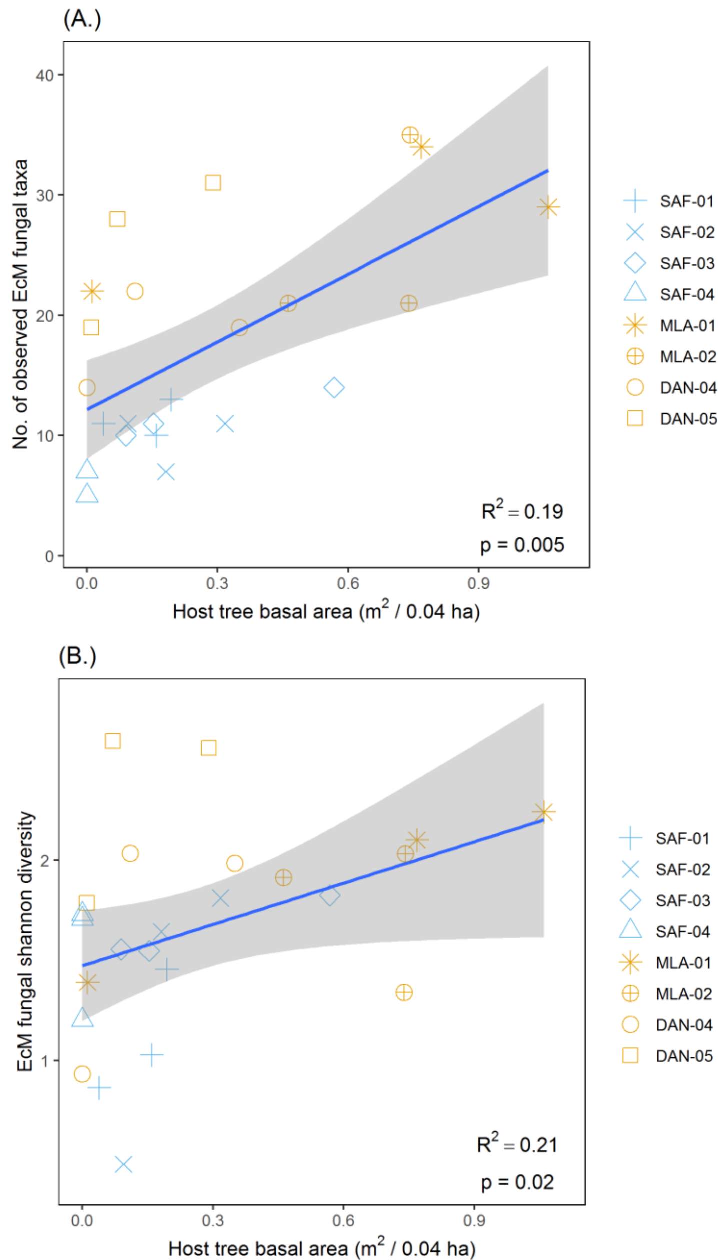

***Figure 8.4** - Correlations between ectomycorrhizal fungal species richness (A.), ectomycorrhizal Shannon diversity (B.) and the basal area of potential EcM host trees across old-growth (OG) and selectively logged (SL) plots. Statistics represent results from linear mixed effects models with plot as a random term. R^2 represents the marginal R^2 and p-values were calculated using F tests implementing the Satterthwaite denominator degrees of freedom approximation.*

***Table 8.1** - Putative ectomycorrhizal (EcM) host tree species used to calculate total EcM host basal area.*

Species	Family
Dipterocarpus caudiferus	Dipterocarpaceae
Dryobalanops lanceolata	Dipterocarpaceae
Parashorea malaanonan	Dipterocarpaceae
Parashorea tomentella	Dipterocarpaceae
Shorea angustifolia	Dipterocarpaceae
Shorea argentifolia	Dipterocarpaceae
Shorea beccariana	Dipterocarpaceae
Shorea dasyphylla	Dipterocarpaceae
Shorea faguetiana	Dipterocarpaceae
Shorea fallax	Dipterocarpaceae
Shorea gibbosa	Dipterocarpaceae
Shorea guiso	Dipterocarpaceae
Shorea guiso	Dipterocarpaceae
Shorea johorensis	Dipterocarpaceae
Shorea leprosula	Dipterocarpaceae
Shorea leptoderma	Dipterocarpaceae
Shorea macroptera	Dipterocarpaceae
Shorea ovalis	Dipterocarpaceae
Shorea ovata	Dipterocarpaceae
Shorea parvifolia	Dipterocarpaceae
Shorea pauciflora	Dipterocarpaceae
Shorea symingtonii	Dipterocarpaceae
Shorea xanthophylla	Dipterocarpaceae
Vatica dulitensis	Dipterocarpaceae
Vatica odorata	Dipterocarpaceae
Castanopsis hypophoenicea	Fagaceae
Lithocarpus conocarpus	Fagaceae
Lithocarpus echinifer	Fagaceae
Lithocarpus gracilis	Fagaceae
Quercus merrillii	Fagaceae
Trigonobalanus verticillata	Fagaceae

Table 8.2 *- Fungal taxa assigned to the arbuscular mycorrhizal fungi ecological guild following annotation using FunGuild. All sequences taxonomically identified as phylum Glomeromycota without lower classification were also included.*

Phylum	Class	Order	Family	Genus
Glomeromycota	Archaeosporomycetes	Archaeosporales	Ambisporaceae	Ambispora
Glomeromycota	Glomeromycetes	Diversisporales	Acaulosporaceae	Acaulospora
Glomeromycota	Glomeromycetes	Diversisporales	Diversisporaceae	Redeckera
Glomeromycota	Glomeromycetes	Gigasporales	Gigasporaceae	Gigaspora
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	Dominikia
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	Funneliformis
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	Glomus
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	Kamienskia
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	Rhizophagus

***Table 8.3** - Fungal taxa assigned to the Ectomycorrhizal fungal ecological guild following annotation using FunGuild.*

Phylum	Class	Order	Family	Genus
Ascomycota	Dothideomycetes	Dothideomycetes	Gloniaceae	Cenococcum
Ascomycota	Eurotiomycetes	Eurotiales	Elaphomycetaceae	Elaphomyces
Ascomycota	Pezizomycetes	Pezizales	Pezizaceae	Delastria
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	Chloridium
Basidiomycota	Agaricomycetes	Agaricales	Amanitaceae	Amanita
Basidiomycota	Agaricomycetes	Agaricales	Cortinariaceae	Cortinarius
Basidiomycota	Agaricomycetes	Agaricales	Hydnangiaceae	Durianella
Basidiomycota	Agaricomycetes	Agaricales	Hydnangiaceae	Laccaria
Basidiomycota	Agaricomycetes	Agaricales	Hymenogastraceae	Anamika
Basidiomycota	Agaricomycetes	Agaricales	Hymenogastraceae	Hebeloma
Basidiomycota	Agaricomycetes	Agaricales	Inocybaceae	Inocybe
Basidiomycota	Agaricomycetes	Atheliales	Atheliaceae	Piloderma
Basidiomycota	Agaricomycetes	Boletales	Boletaceae	Mycoamaranthus
Basidiomycota	Agaricomycetes	Boletales	Boletaceae	Phylloporus
Basidiomycota	Agaricomycetes	Boletales	Boletaceae	Pulveroboletus
Basidiomycota	Agaricomycetes	Boletales	Boletaceae	Tylopilus
Basidiomycota	Agaricomycetes	Boletales	Sclerodermataceae	Scleroderma
Basidiomycota	Agaricomycetes	Cantharellales	Cantharellaceae	Cantharellus
Basidiomycota	Agaricomycetes	Cantharellales	Cantharellaceae	Craterellus
Basidiomycota	Agaricomycetes	Cantharellales	Clavulinaceae	Clavulina
Basidiomycota	Agaricomycetes	Cantharellales	Hydnaceae	Hydnum
Basidiomycota	Agaricomycetes	Hysterangiales	Hysterangiaceae	Hysterangium
Basidiomycota	Agaricomycetes	Russulales	Russulaceae	Lactarius
Basidiomycota	Agaricomycetes	Russulales	Russulaceae	Lactifluus
Basidiomycota	Agaricomycetes	Russulales	Russulaceae	Russula
Basidiomycota	Agaricomycetes	Sebacinales	Sebacinaceae	Helvellosebacina
Basidiomycota	Agaricomycetes	Thelephorales	Bankeraceae	Sarcodon
Basidiomycota	Agaricomycetes	Thelephorales	Thelephoraceae	Tomentella
Basidiomycota	Agaricomycetes	Thelephorales	Thelephoraceae	Tomentellopsis
Mucoromycota	Endogonomycetes	Endogonales	Endogonaceae	Endogone

***Table 8.4** – Fungal taxa assigned to the saprotrophic ecological guild following annotation using FunGuild*

Phylum	Class	Order	Family	Genus
Ascomycota	Archaeorhizomycetes	Archaeorhizomycetales	Archaeorhizomycetaceae	Archaeorhizomyces
Ascomycota	Ascomycota_cls_Inc. Sed.	Ascomycota_ord_Inc. Sed.	Ascomycota_fam_Inc. Sed.	Tetracladium
Ascomycota	Ascomycota_cls_Inc. Sed.	Ascomycota_ord_Inc. Sed.	Ascomycota_fam_Inc. Sed.	Virgaria
Ascomycota	Ascomycota_cls_Inc. Sed.	Ascomycota_ord_Inc. Sed.	Ascomycota_fam_Inc. Sed.	Xylomyces
Ascomycota	Dothideomycetes	Capnodiales	Capnodiaceae	Antennariella
Ascomycota	Dothideomycetes	Capnodiales	Capnodiaceae	Capnodium
Ascomycota	Dothideomycetes	Capnodiales	Capnodiaceae	Leptoxyphium
Ascomycota	Dothideomycetes	Capnodiales	Capnodiaceae	NA
Ascomycota	Dothideomycetes	Dothideomycetes_ord_Inc. Sed.	Dothideomycetes_fam_Inc. Sed.	Paramicrothyrium
Ascomycota	Dothideomycetes	Dothideomycetidae_ord_Inc. Sed.	Eremomycetaceae	Eremomyces
Ascomycota	Dothideomycetes	Hysteriales	Hysteriaceae	Rhytidhysteron
Ascomycota	Dothideomycetes	Jahnulales	Aliquandostipitaceae	Jahnula
Ascomycota	Dothideomycetes	Pleosporales	Corynesporascaceae	Corynespora
Ascomycota	Dothideomycetes	Pleosporales	Cucurbitariaceae	Pyrenochaeta
Ascomycota	Dothideomycetes	Pleosporales	Didymosphaeriaceae	Alloconiothyrium
Ascomycota	Dothideomycetes	Pleosporales	Didymosphaeriaceae	Montagnula
Ascomycota	Dothideomycetes	Pleosporales	Didymosphaeriaceae	Paraconiothyrium
Ascomycota	Dothideomycetes	Pleosporales	Didymosphaeriaceae	Paraphaeosphaeria
Ascomycota	Dothideomycetes	Pleosporales	Leptosphaeriaceae	Plenodomus
Ascomycota	Dothideomycetes	Pleosporales	Lophiostomataceae	Lophiostoma
Ascomycota	Dothideomycetes	Pleosporales	Lophiotremataceae	Lophiotrema
Ascomycota	Dothideomycetes	Pleosporales	Melanommataceae	Pseudotrichia
Ascomycota	Dothideomycetes	Pleosporales	Morosphaeriaceae	Acrocalymma
Ascomycota	Dothideomycetes	Pleosporales	Phaeosphaeriaceae	Phaeosphaeria
Ascomycota	Dothideomycetes	Pleosporales	Pleomassariaceae	Tumularia
Ascomycota	Dothideomycetes	Pleosporales	Sporormiaceae	NA
Ascomycota	Dothideomycetes	Pleosporales	Sporormiaceae	Preussia
Ascomycota	Dothideomycetes	Pleosporales	Teichosporaceae	NA
Ascomycota	Dothideomycetes	Pleosporales	Teichosporaceae	Teichospora
Ascomycota	Dothideomycetes	Pleosporales	Thyridariaceae	NA
Ascomycota	Dothideomycetes	Pleosporales	Thyridariaceae	Roussoella
Ascomycota	Dothideomycetes	Tubeufiales	Tubeufiaceae	Tubeufia
Ascomycota	Dothideomycetes	Venturiales	Sympoventuriaceae	NA
Ascomycota	Dothideomycetes	Venturiales	Sympoventuriaceae	Ochroconis
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	Cladophialophora
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	Fonsecaea
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	Rhinocladiella
Ascomycota	Eurotiomycetes	Eurotiales	Trichocomaceae	Rasamsonia
Ascomycota	Eurotiomycetes	Eurotiales	Trichocomaceae	Talaromyces
Ascomycota	Eurotiomycetes	Onygenales	Onygenaceae	Arachnotheca
Ascomycota	Eurotiomycetes	Onygenales	Onygenaceae	NA
Ascomycota	Geoglossomycetes	Geoglossales	Geoglossaceae	Geoglossum
Ascomycota	Geoglossomycetes	Geoglossales	Geoglossaceae	Leucoglossum
Ascomycota	Lecanoromycetes	Ostropales	Stictidaceae	Cryptodiscus
Ascomycota	Leotiomycetes	Helotiales	Dermateaceae	Corniculariella
Ascomycota	Leotiomycetes	Helotiales	Helotiaceae	Crocicreas
Ascomycota	Leotiomycetes	Helotiales	Helotiaceae	Idriella
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Catenulifera
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Cistella
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Hyaloscypha
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	NA
Ascomycota	Leotiomycetes	Helotiales	Leotiaceae	Alatospora

Table 8.4 *- Continued*

Ascomycota	Leotiomycetes	Helotiales	Rutstroemiaceae	NA
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Leotiomycetes_fam_Inc. Sed.	Lauriomyces
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Leotiomycetes_fam_Inc. Sed.	Leohumicola
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Leotiomycetes_fam_Inc. Sed.	Scytalidium
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Pseudeurotiaceae	Gymnostellatospora
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Pseudeurotiaceae	NA
Ascomycota	Leotiomycetes	Leotiomycetes_ord_Inc. Sed.	Pseudeurotiaceae	Pseudeurotium
Ascomycota	Pezizomycetes	Pezizales	Ascobolaceae	NA
Ascomycota	Pezizomycetes	Pezizales	Pyronemataceae	Scutellinia
Ascomycota	Pezizomycetes	Pezizales	Sarcoscyphaceae	Cookeina
Ascomycota	Pezizomycetes	Pezizales	Sarcosomataceae	Trichaleurina
Ascomycota	Sordariomycetes	Boliniales	Boliniaceae	Endoxyla
Ascomycota	Sordariomycetes	Calosphaeriales	Calosphaeriaceae	Jattaea
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	Codinaea
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	NA
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	Pyrigemmula
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	Sporoschisma
Ascomycota	Sordariomycetes	Chaetosphaeriales	Chaetosphaeriaceae	Thozetella
Ascomycota	Sordariomycetes	Diaporthales	Melanconidaceae	Prosthecium
Ascomycota	Sordariomycetes	Hypocreales	Bionectriaceae	Verrucostoma
Ascomycota	Sordariomycetes	Hypocreales	Hypocreales_fam_Inc. Sed.	Myxocephala
Ascomycota	Sordariomycetes	Hypocreales	Hypocreales_fam_Inc. Sed.	Sarocladium
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Gliocephalotrichum
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Gliocladiopsis
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Mariannaea
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Stephanonectria
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Thelonectria
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	NA
Ascomycota	Sordariomycetes	Microascales	Microascaceae	Pseudallescheria
Ascomycota	Sordariomycetes	Microascales	Microascaceae	Scedosporium
Ascomycota	Sordariomycetes	Myrmecridiales	Myrmecridiaceae	Myrmecridium
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	Humicola
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	Zopfiella
Ascomycota	Sordariomycetes	Sordariales	Sordariaceae	Sordaria
Ascomycota	Sordariomycetes	Sordariales	Sordariales_fam_Inc. Sed.	Lunulospora
Ascomycota	Sordariomycetes	Sordariomycetes_ord_Inc. Sed.	Sordariomycetes_fam_Inc. Sed.	Barbatosphaeria
Ascomycota	Sordariomycetes	Sordariomycetes_ord_Inc. Sed.	Sordariomycetes_fam_Inc. Sed.	Conlarium
Ascomycota	Sordariomycetes	Sordariomycetes_ord_Inc. Sed.	Sordariomycetes_fam_Inc. Sed.	Xylomelasma
Ascomycota	Sordariomycetes	Sordariomycetidae_ord_Inc. Sed.	Amplistromataceae	Amplistroma
Ascomycota	Sordariomycetes	Trichosphaeriales	Trichosphaeriaceae	Nigrospora
Ascomycota	Sordariomycetes	Xylariales	Apiosporaceae	Arthrinium
Ascomycota	Sordariomycetes	Xylariales	Apiosporaceae	NA
Ascomycota	Sordariomycetes	Xylariales	Beltraniaceae	Beltraniella
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Biscogniauxia
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Camillea
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Emarcea
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Hypoxylon
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Lopadostoma
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Muscodor
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Nemania
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Nodulisporium
Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	Obolarina
Ascomycota	Sordariomycetes	Xylariales	Xylariales_fam_Inc. Sed.	Hansfordia
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Agaricus

Table 8.4 *- Continued*

Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Coprinus
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Cystolepiota
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Echinoderma
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Leucoagaricus
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Leucocoprinus
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Macrolepiota
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Melanophyllum
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Micropsalliota
Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	NA
Basidiomycota	Agaricomycetes	Agaricales	Agaricales_fam_Inc. Sed.	Acanthocorticium
Basidiomycota	Agaricomycetes	Agaricales	Bolbitiaceae	Conocybe
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavaria
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Ramariopsis
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Scytinopogon
Basidiomycota	Agaricomycetes	Agaricales	Cortinariaceae	Gymnopilus
Basidiomycota	Agaricomycetes	Agaricales	Crepidotaceae	Crepidotus
Basidiomycota	Agaricomycetes	Agaricales	Entolomataceae	Clitopilus
Basidiomycota	Agaricomycetes	Agaricales	Lycoperdaceae	Bovista
Basidiomycota	Agaricomycetes	Agaricales	Lycoperdaceae	Calvatia
Basidiomycota	Agaricomycetes	Agaricales	Lycoperdaceae	Lycoperdon
Basidiomycota	Agaricomycetes	Agaricales	Lycoperdaceae	NA
Basidiomycota	Agaricomycetes	Agaricales	Lyophyllaceae	Termitomyces
Basidiomycota	Agaricomycetes	Agaricales	Pleurotaceae	Hohenbuehelia
Basidiomycota	Agaricomycetes	Agaricales	Psathyrellaceae	Coprinellus
Basidiomycota	Agaricomycetes	Agaricales	Psathyrellaceae	Coprinopsis
Basidiomycota	Agaricomycetes	Agaricales	Psathyrellaceae	NA
Basidiomycota	Agaricomycetes	Agaricales	Psathyrellaceae	Psathyrella
Basidiomycota	Agaricomycetes	Agaricales	Stephanosporaceae	Lindtneria
Basidiomycota	Agaricomycetes	Agaricales	Stephanosporaceae	NA
Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	Deconica
Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	Hypholoma
Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	Psilocybe
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Dermoloma
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Gamundia
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Gerronema
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Hydropus
Basidiomycota	Agaricomycetes	Auriculariales	Hyaloriaceae	Protomerulius
Basidiomycota	Agaricomycetes	Auriculariales	Hyaloriaceae	Pseudohydnum
Basidiomycota	Agaricomycetes	Boletales	Coniophoraceae	Coniophora
Basidiomycota	Agaricomycetes	Boletales	Coniophoraceae	Gyrodontium
Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	Phlebia
Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	Schizopora
Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	Scopuloides
Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	Subulicystidium
Basidiomycota	Agaricomycetes	Geastrales	Geastraceae	Geastrum
Basidiomycota	Agaricomycetes	Geastrales	Geastraceae	Nidulariopsis
Basidiomycota	Agaricomycetes	Hymenochaetales	Hymenochaetaceae	Hymenochaete
Basidiomycota	Agaricomycetes	Hymenochaetales	Hymenochaetaceae	Inonotus
Basidiomycota	Agaricomycetes	Hymenochaetales	Hymenochaetales_fam_Inc. Sed.	Resinicium
Basidiomycota	Agaricomycetes	Phallales	Phallaceae	NA
Basidiomycota	Agaricomycetes	Phallales	Phallaceae	Phallus
Basidiomycota	Agaricomycetes	Polyporales	Coriolaceae	NA

***Table 8.4** - Continued*

Basidiomycota	Agaricomycetes	Polyporales	Coriolaceae	Rigidoporus
Basidiomycota	Agaricomycetes	Polyporales	Coriolaceae	Tinctoporellus
Basidiomycota	Agaricomycetes	Polyporales	Phanerochaetaceae	Hyphodermella
Basidiomycota	Agaricomycetes	Polyporales	Phanerochaetaceae	Phanerochaete
Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	Abundisporus
Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	NA
Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	Perenniporia
Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	Physisporinus
Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	Trichaptum
Basidiomycota	Agaricomycetes	Polyporales	Polyporales_fam_Inc. Sed.	Junghuhnia
Basidiomycota	Agaricomycetes	Polyporales	Schizoporaceae	Xylodon
Basidiomycota	Agaricomycetes	Polyporales	Xenasmataceae	Xenasmatella
Basidiomycota	Agaricomycetes	Russulales	Lachnocladiaceae	Scytinostroma
Basidiomycota	Agaricomycetes	Trechisporales	Hydnodontaceae	Luellia
Basidiomycota	Agaricomycetes	Trechisporales	Hydnodontaceae	Trechispora
Basidiomycota	Geminibasidiomycetes	Geminibasidiales	Geminibasidiaceae	Geminibasidium
Chytridiomycota	Rhizophydiomycetes	Rhizophydiales	Kappamycetaceae	Kappamyces
Chytridiomycota	Rhizophydiomycetes	Rhizophydiales	Terramycetaceae	Boothiomyces
Mucoromycota	Mucoromycetes	Mucorales	Mucoraceae	Mucor
Mucoromycota	Umbelopsidomycetes	Umbelopsidales	Umbelopsidaceae	Umbelopsis

***Table 8.5** - Fungal taxa assigned to the pathogenic ecological guild following annotation using FunGuild*

Phylum	**Class**	**Order**	**Family**	**Genus**
Ascomycota	Dothideomycetes	Botryosphaeriales	Botryosphaeriaceae	Endomelanconiopsis
Ascomycota	Dothideomycetes	Botryosphaeriales	Botryosphaeriaceae	Lasiodiplodia
Ascomycota	Dothideomycetes	Botryosphaeriales	Botryosphaeriaceae	Neofusicoccum
Ascomycota	Dothideomycetes	Capnodiales	Dissoconiaceae	Ramichloridium
Ascomycota	Dothideomycetes	Capnodiales	Mycosphaerellaceae	Mycosphaerella
Ascomycota	Dothideomycetes	Capnodiales	Mycosphaerellaceae	Pseudocercospora
Ascomycota	Dothideomycetes	Capnodiales	Mycosphaerellaceae	Readeriella
Ascomycota	Dothideomycetes	Capnodiales	Teratosphaeriaceae	Devriesia
Ascomycota	Dothideomycetes	Pleosporales	Didymellaceae	Ascochyta
Ascomycota	Dothideomycetes	Pleosporales	Leptosphaeriaceae	Leptosphaeria
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Edenia
Ascomycota	Dothideomycetes	Pleosporales	Pleosporales_fam_Inc. Sed.	Nigrograna
Ascomycota	Dothideomycetes	Pleosporales	Trematosphaeriaceae	Falciformispora
Ascomycota	Eurotiomycetes	Chaetothyriales	Chaetothyriales_fam_Inc. Sed.	Strelitziana
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	Veronaea
Ascomycota	Eurotiomycetes	Coryneliales	Coryneliaceae	Caliciopsis
Ascomycota	Eurotiomycetes	Onygenales	Nannizziopsiaceae	Nannizziopsis
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Hyphodiscus
Ascomycota	Leotiomycetes	Helotiales	Sclerotiniaceae	NA
Ascomycota	Leotiomycetes	Rhytismatales	Rhytismataceae	Coccomyces
Ascomycota	Leotiomycetes	Rhytismatales	Rhytismataceae	Lophodermium
Ascomycota	Sordariomycetes	Diaporthales	Diaporthales_fam_Inc. Sed.	Auratiopycnidiella
Ascomycota	Sordariomycetes	Diaporthales	Schizoparmaceae	Coniella
Ascomycota	Sordariomycetes	Glomerellales	Plectosphaerellaceae	Musicillium

Table 8.5 - *Continued*

Ascomycota	Sordariomycetes	Glomerellales	Plectosphaerellaceae	Plectosphaerella
Ascomycota	Sordariomycetes	Hypocreales	Bionectriaceae	Clonostachys
Ascomycota	Sordariomycetes	Hypocreales	Bionectriaceae	Nectriopsis
Ascomycota	Sordariomycetes	Hypocreales	Clavicipitaceae	Metarhizium
Ascomycota	Sordariomycetes	Hypocreales	Clavicipitaceae	Pochonia
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Beauveria
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Lecanicillium
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Simplicillium
Ascomycota	Sordariomycetes	Hypocreales	Hypocreaceae	Cladobotryum
Ascomycota	Sordariomycetes	Hypocreales	Hypocreaceae	Sphaerostilbella
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Calonectria
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Curvicladiella
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Cylindrocladiella
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Volutella
Ascomycota	Sordariomycetes	Hypocreales	Ophiocordycipitaceae	Hirsutella
Ascomycota	Sordariomycetes	Hypocreales	Ophiocordycipitaceae	Polycephalomyces
Ascomycota	Sordariomycetes	Hypocreales	Ophiocordycipitaceae	Purpureocillium
Ascomycota	Sordariomycetes	Magnaporthales	Magnaporthaceae	Mycoleptodiscus
Ascomycota	Sordariomycetes	Ophiostomatales	Ophiostomataceae	Hawksworthiomyces
Ascomycota	Sordariomycetes	Ophiostomatales	Ophiostomataceae	Ophiostoma
Ascomycota	Sordariomycetes	Ophiostomatales	Ophiostomataceae	NA
Ascomycota	Sordariomycetes	Togniniales	Togniniaceae	Phaeoacremonium
Ascomycota	Sordariomycetes	Xylariales	Sporocadaceae	Pestalotiopsis
Ascomycota	Sordariomycetes	Xylariales	Sporocadaceae	Seiridium
Ascomycota	Sordariomycetes	Xylariales	Xylariales_fam_Inc. Sed.	Castanediella
Basidiomycota	Agaricomycetes	Cantharellales	Ceratobasidiaceae	Thanatephorus
Basidiomycota	Exobasidiomycetes	Exobasidiales	Brachybasidiaceae	Meira
Basidiomycota	Exobasidiomycetes	Microstromatales	Microstromatales_fam_Inc. Sed.	Sympodiomycopsis
Basidiomycota	Microbotryomycetes	Microbotryomycetes_ord_Inc. Sed.	Microbotryomycetes_fam_Inc. Sed.	Colacogloea
Basidiomycota	Tremellomycetes	Tremellales	Syzygosporaceae	Syzygospora
Basidiomycota	Tremellomycetes	Tremellales	Tremellaceae	Tremella
Basidiomycota	Tremellomycetes	Trichosporonales	Trichosporonaceae	Trichosporon
Chytridiomycota	Spizellomycetes	Spizellomycetales	Spizellomycetaceae	Spizellomyces

Appendix 2 - Ants and termites regulate microbial community structure and function in tropical forest

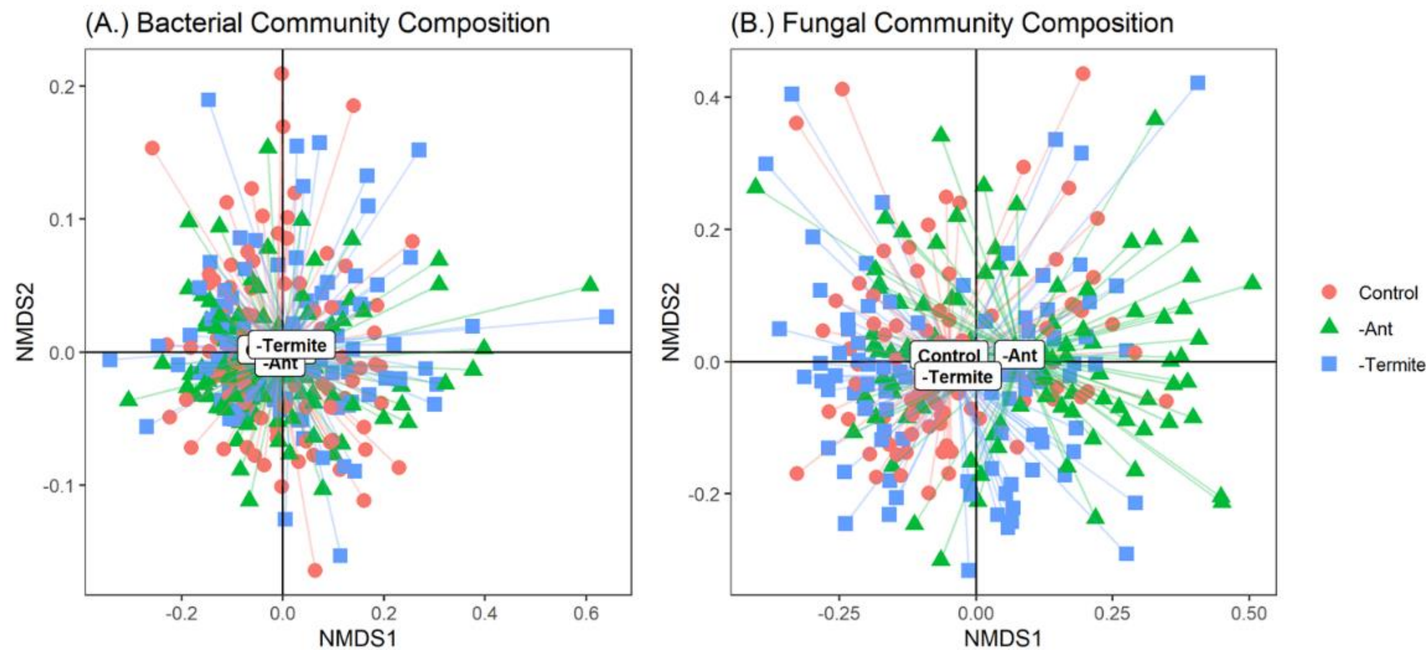

Figure 8.5 *- Non-metric multidimensional scaling (NMDS) ordinations of square-root transformed Bray-Curtis dissimilarities of bacterial and fungal community composition across control, ant and termite suppression treatments. These were calculated using the metaMDS function in the vegan R package A: NMDS Stress = 0.12, B: NMDS Stress = 0.22.*

Appendix 3 - Soil microbial community and litter quality controls on decomposition across a tropical forest disturbance gradient

***Table 8.6** - Chemical properties of non-autoclaved litter mixtures taken from old growth (OG) forest, moderate logged (ML) forest, heavily logged (HL) forest and oil palm plantation. Data are means (n=5) ± 1 standard error. Superscript letters denote whether parameters were significantly different between land uses from pairwise Tukey's HSD test. Significant differences (p <0.05) between land uses are indicated when letters are different. Non – significant differences (P >0.05 between land-uses are indicated when letters are shared. Solubles = soluble cell content. H + P = Hemicellulose & Proteins. L + R = Lignin & recalcitrants. L:N Ratio = Lignin:N Ratio.*

	OG Forest	**ML Forest**	**HL Forest**	**Oil Palm**
C (%)	^{a}45.47 (0.26)	^{a}45.13 (0.35)	^{b}42.36 (0.24)	^{b}41.65 (0.55)
N (%)	^{a}1.56 (0.03)	^{b}1.06 (0.07)	^{a}1.67 (0.05)	^{a}1.93 (0.19)
P (µg/g)	^{a}0.58 (0.03)	^{b}0.32 (0.01)	^{a}0.60 (0.03)	^{c}0.97 (0.05)
K (µg/g)	^{a}4.09 (0.30)	^{a}3.25 (1.56)	^{a}4.05 (0.34)	^{a}3.77 (0.16)
Ca (µg/g)	^{a}12.08 (0.74)	^{b}7.53 (0.42)	^{a}12.71 (0.46)	^{b}6.58 (0.46)
Mg (µg/g)	^{a}3.52 (0.25)	^{b}1.77 (0.06)	^{c}2.48 (0.07)	^{bc}2.05 (0.13)
Al (µg/g)	^{a}4473.87 (1111.84)	^{a}2639.24 (1279.61)	^{a}4047.22 (1038.77)	^{a}3991.15 (1253.12)
Solubles (%)	^{a}40.02 (0.37)	^{a}38.90 (0.77)	^{a}38.05 (0.67)	^{b}26.81 (0.87)
H + P (%)	^{a}8.84 (0.28)	^{b}7.65 (0.28)	^{c}10.49 (0.18)	^{d}16.75 (0.21)
Cellulose (%)	^{a}21.50 (0.29)	^{a}23.08 (0.54)	^{a}23.62 (0.71)	^{b}30.66 (0.61)
L + R (%)	^{a}29.58 (0.50)	^{a}30.32 (0.48)	^{b}27.79 (0.70)	^{b}25.73 (0.58)
C:N Ratio	^{a}29.21 (0.63)	^{b}43.27 (2.87)	^{a}25.47 (0.70)	^{a}22.81 (3.18)
L:N Ratio	^{a}19.00 (0.45)	^{b}29.12 (2.16)	^{a}16.74 (0.81)	^{a}14.09 (2.01)

Table 8.7 *- Linear regression models with litter mass loss of each litter type after 398 d as the dependent variable and axis scores 1 and 2 from principal co-ordinates analysis (PCoA) of initial bacteria, fungal and saprotrophic fungal community composition and principal components analysis (PCA) of PLFA's as independent variables.*

Litter Type	Source of variation	df	Sum of Squares	F	P - value	R^2
OG Litter	Bacteria - PCoA 1	1	55.55	0.24	0.28	0.08
	Bacteria - PCoA 2	1	9.11	0.2	0.66	
	residuals	17	764.42			
	Fungi - PCoA 1	1	35.1	0.75	0.4	0.05
	Fungi - PCoA 2	1	2.22	0.05	0.83	
	residuals	17	791.77			
	Saprotrophic Fungi - PCoA 1	1	10.11	0.23	0.64	0.08
	Saprotrophic Fungi - PCoA 2	1	58.53	1.31	0.27	
	residuals	17	760.45			
	PLFA PC1	1	6.21	0.17	0.68	0.26
	PLFA PC2	1	208.31	5.76	0.03	
	residuals	17	614.57			
ML Litter	Bacteria - PCoA 1	1	126.28	4.82	0.04	0.32
	Bacteria - PCoA 2	1	86.55	3.3	0.09	
	residuals	17	445.5			
	Fungi - PCoA 1	1	2.59	0.1	0.75	0.34
	Fungi - PCoA 2	1	219.91	8.58	0.009	
	residuals	17	435.83			
	Saprotrophic Fungi - PCoA 1	1	125.18	5.34	0.03	0.39
	Saprotrophic Fungi - PCoA 2	1	134.32	5.73	0.03	
	residuals	17	398.83			
	PLFA PC1	1	139.63	4.7	0.04	0.23
	PLFA PC2	1	13.48	0.45	0.51	
	residuals	17	505.22			
HL Litter	Bacteria - PCoA 1	1	46.35	0.88	0.36	0.1
	Bacteria - PCoA 2	1	48.56	0.93	0.35	
	residuals	17	891.89			
	Fungi - PCoA 1	1	10.55	0.21	0.65	0.15
	Fungi - PCoA 2	1	133.63	2.7	0.12	
	residuals	17	842.62			
	Saprotrophic Fungi - PCoA 1	1	35.6	0.73	0.4	0.16
	Saprotrophic Fungi - PCoA 2	1	123.8	2.54	0.13	
	residuals	17	827.39			
	PLFA PC1	1	237.03	5.9	0.03	0.31
	PLFA PC2	1	67.17	1.67	0.21	
	residuals	17	682.6			

***Table 8.7** – Continued*

OP Litter	Bacteria - PCoA 1	1	12.06	0.38	0.55	0.28
	Bacteria - PCoA 2	1	171.5	5.34	0.04	
	residuals	15	481.5			
	Fungi - PCoA 1	1	81.6	3.22	0.09	0.43
	Fungi - PCoA 2	1	257.21	10.14	0.006	
	residuals	15	380.16			
	Saprotrophic Fungi - PCoA 1	1	33.67	0.87	0.37	0.14
	Saprotrophic Fungi - PCoA 2	1	59.8	1.54	0.23	
	residuals	15	580.97			
	PLFA PC1	1	270.22	11.68	0.004	0.48
	PLFA PC2	1	128.23	5.54	0.03	
	residuals	15	347.1			

Appendix 4 - Drought intensity and land use regulates the resistance and resilience of tropical soil microbial communities to drought

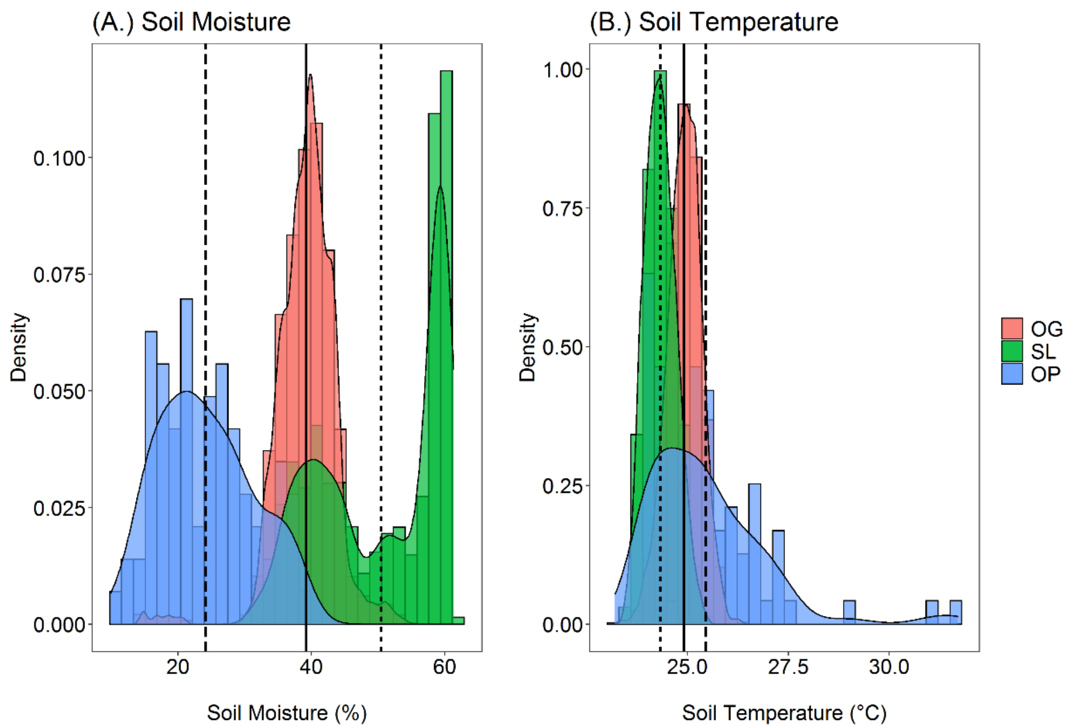

Figure 8.6 *– Histograms of soil moisture and temperature measured during November 2016 and April 2017 in OG forest, SL forest and oil palm plantation (OP). Vertical lines represents mean moisture and temperature for each land use. Dashed = Oil palm plantation, solid = OG forest, dotted = SL forest.*

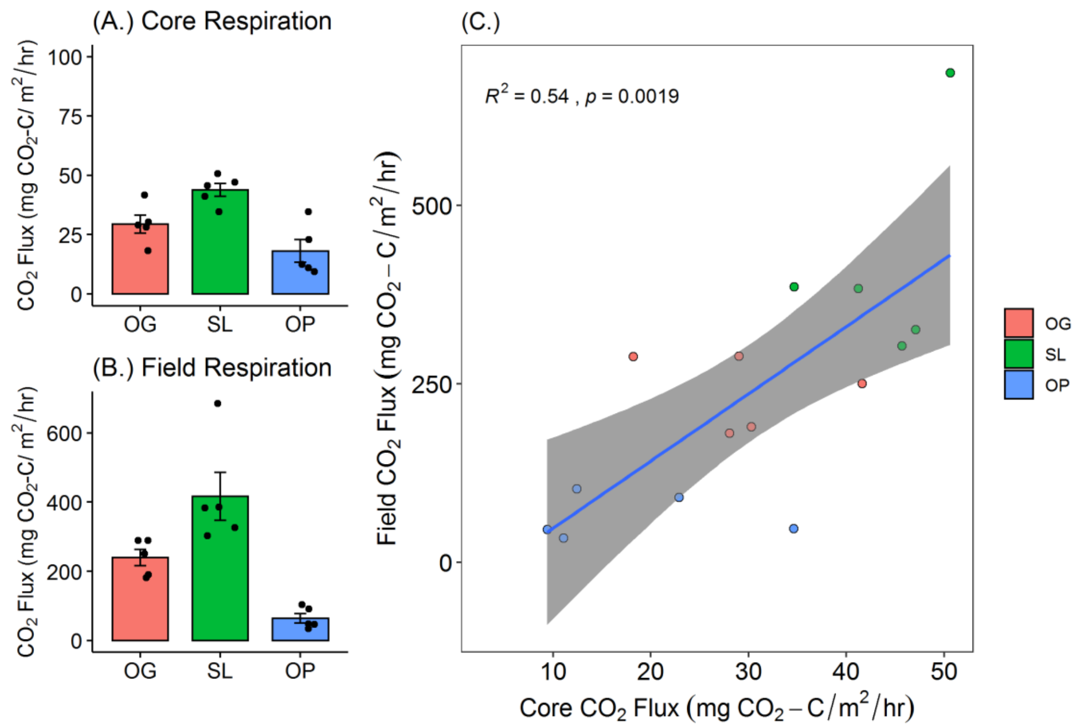

Figure 8.7 *– CO_2 flux measured on soil cores in microcosms after stabilizing at 25 °C prior to drought (A.) and in situ prior to soil sampling using an infrared gas analyser (B.). (C.) The correlation between CO_2 fluxes measured in situ and within soil microcosms. Grey shaded envelope represents the 95% confidence interval for the slope of the regression line.*

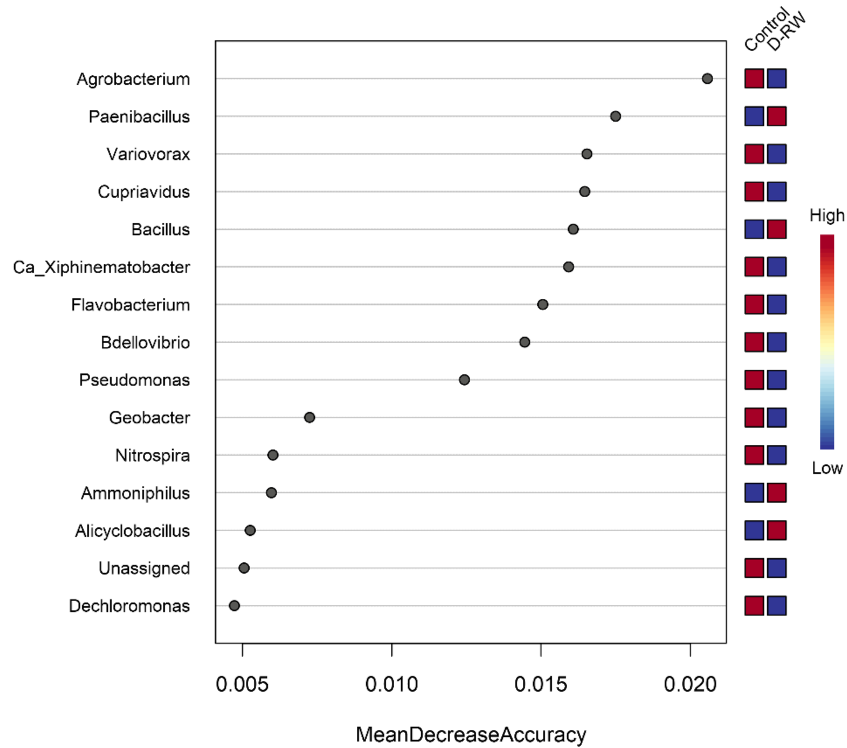

Figure 8.8 *- Mean Decrease Accuracy plot expressing how much classification accuracy the old growth (OG) forest random forest model loses by excluding each bacterial genera. The more the accuracy suffers, the more important the variable is for the successful classification of samples from OG forest soils to control or drought – rewetted groups. Only the top 15 genera are presented.*

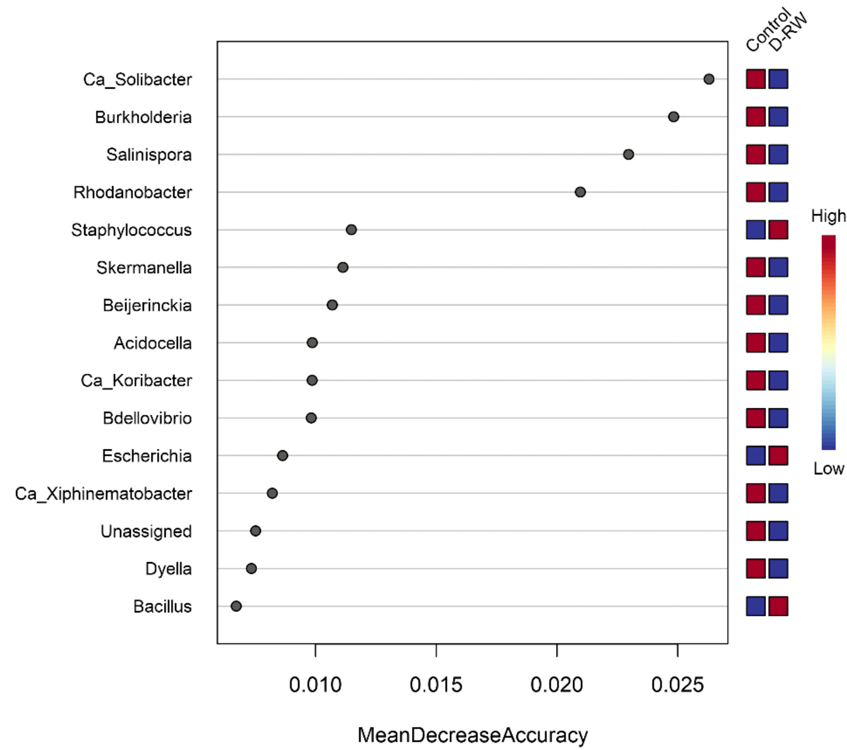

Figure 8.9 *- Mean Decrease Accuracy plot expressing how much classification accuracy the selectively logged (SL) forest random forest model loses by excluding each bacterial genera. The more the accuracy suffers, the more important the variable is for the successful classification of samples from SL forest soils to control or drought – rewetted groups. Only the top 15 genera are presented.*

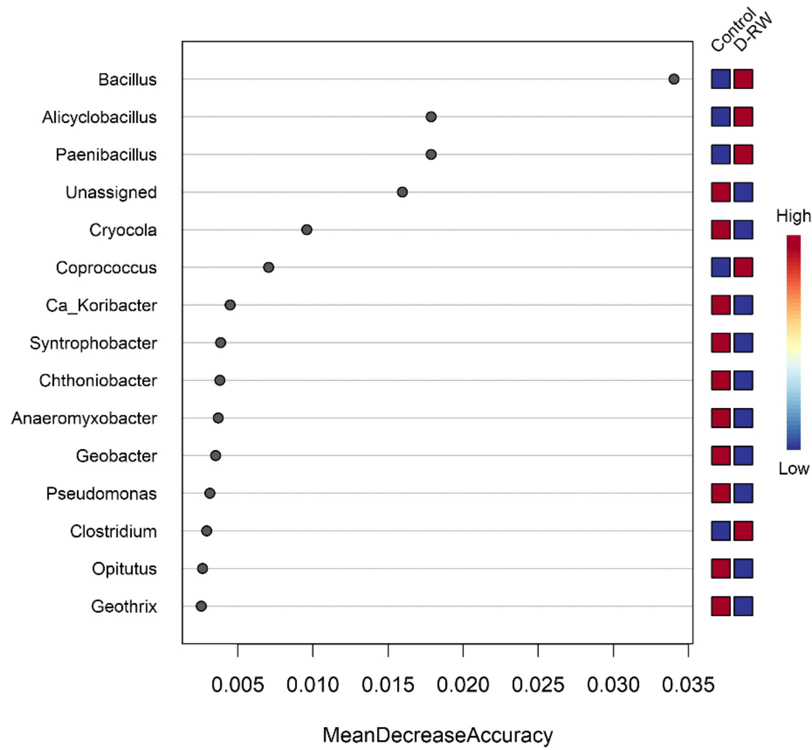

Figure 8.10 *- Mean Decrease Accuracy plot expressing how much classification accuracy the oil palm (OP) random forest model loses by excluding each bacterial genera. The more the accuracy suffers, the more important the variable is for the successful classification of samples from oil palm soils into control or drought – rewetted groups. Only the top 15 genera are presented.*