Impacts of tropical forest modification on soil microbial community attributes and function in Southeast Asia

Samuel James Burgess Robinson

Thesis submitted for the degree of Doctor of Philosophy at Lancaster Environment Centre, Lancaster University, United Kingdom.

September 2020

Lancaster Environment Centre

For Mum and Dad

Di mana bumi dipijak, di situ langit dijunjung

~

On which soil we stand, is where we carry the weight of the sky

(Malaysian proverb)

Declaration

I herewith declare that this thesis is my own work, and that it has not been previously presented to obtain a degree in any form. 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 Prof Nick Ostle (Lancaster University), Dr Niall McNamara (UK Centre for Ecology & Hydrology, Lancaster) and Dr Rob Griffiths (UK Centre for Ecology & Hydrology, Bangor).

This thesis word length is 42,312, and therefore does not exceed the permitted maximum.

Samuel James Burgess Robinson,

Lancaster University, March 2020.

Abstract

Tropical forests are vital global reservoirs of biodiversity and carbon (C). Deforestation and degradation of these ecosystems greatly threatens their capacity to provide crucial ecosystem functions and services, by altering complex plant-soil interactions and biogeochemical cycles underpinned by soil microbes. Forest disturbance is accelerating in Southeast Asia, through widespread selective logging (SL) and forest conversion to oil palm plantation (OP). This has major implications for soil microbial communities and functions, although effects of tropical forest disturbance on belowground biodiversity and the resistance and resilience of soil microbial nutrient and C-cycling are unresolved. The potential to restore soil microbial communities and essential functions is also largely unknown. The aim of this thesis was to evaluate impacts of tropical forest modification (degradation, conversion and restoration) on soil microbial community attributes, and implications for ecosystem biogeochemical cycling. The rainforests of Borneo were used as a model study system, representing a hotspot of biodiversity and forest degradation. I conducted survey and experiments across land-use contrasts of old-growth (OG), SL and restored forest and OP. SL and OP significantly affected relative abundances of mycorrhizal fungal types, with implications for soil C storage. Mycelial productivity was not affected by SL but was negatively impacted by OP, indicating potential for SL forest rehabilitation but consequences for OP nutrient cycling and restoration. Logging gaps in SL forest significantly altered bacterial and fungal community structure, reducing mycorrhizal abundance and altering supply rates of key nutrients. Logging gaps may also supress microbial C cycling, implied by reduced soil respiration, although soil functioning appeared more resilient to drought than adjacent closed canopy forest. Prolonged increases in soil respiration in SL forest soils after rewetting highlight sensitivity of

tropical forest to future climate change perturbations. Overall, soil microbial communities did not recover with restoration of SL forest, suggesting current management practices select for different microbial taxa which may impede rehabilitation of ecosystem functions. Overall findings demonstrate human modification of tropical forest affects key soil microbial groups, with potential consequences for biogeochemical cycling and atmospheric C feedbacks at the landscape scale. This highlights the need to incorporate evaluation of belowground communities and function in predicting impacts of land-use and climate change, as well as effective ecosystem rehabilitation for biodiversity conservation and provision of essential ecosystem services by these vital, hyperdiverse environments.

Keywords: *old-growth • selective logging • oil palm • ecosystem restoration • resistance and resilience • carbon dioxide emissions*

Acknowledgements

This PhD was funded through the UK Natural Environment Research Council (NERC) Envision Doctoral Training Programme. The studies described in chapters 2-4 received additional support from the NERC Human Modified Tropical Forests programme (grant number NE/K016377/1) and Sime Darby Foundation funding to the SAFE project. These studies are contributions from the NERC Biodiversity and Land-use Impacts on Tropical Ecosystem Function (BALI) consortium. I express my gratitude to the Sabah Biodiversity Council (SaBC), Yayasan Sabah (Sabah Foundation), the Danum Valley and Maliau Basin Management Committees, and Glen Reynolds and the South East Asia Rainforest Research Partnership (SEARRP) for support and granting permission to access field sites (SaBC Access License no. JKM/MBS.1000-2/2 JLD.3 (173)). Thanks also to Laura Kruitbos and Unding Jami (BALI) for essential support in applications and undertaking of these studies.

I am extremely grateful to my supervisors Nick Ostle, Niall McNamara and Rob Griffiths for their help and guidance over the last four years, which includes (but is not limited to) supporting the development of the studies in this thesis. You have all taught me a great deal, from specific science methods to managing a research project, and about how to ask the right questions. Thank you for sharing your expertise and life experiences with me. Nick, you have been a great mentor and friend since the days of my Masters, and I appreciate all of the time and energy you've spent helping me at every stage on this learning journey.

I have also learnt a great deal from those I have collaborated with through the BALI project consortium and in Lancaster. In particular, Dr Noreen Majalap (Sabah Forest Research Centre, Malaysia), Dr Sabine Both (University of New England,

Australia), Prof Dave Johnson (University of Manchester, UK) and Dr Terhi Ruitta (University of Oxford, UK), who have helped my thinking and work expand into unexpected and exciting areas ever since those early days in the field. Special thanks also to Dr Yap Sau Wai (Yayasan Sabah) for support in the forest rehabilitation project proposal and study at INFAPRO. Thanks to Tim Goodall (UK Centre for Ecology and Hydrology, Wallingford) for the instruction (and patience!) in teaching me methods in soil DNA extraction and sequencing, and for providing bioinformatics steps (generation of raw sequence reads used in chapters 2, 3 and 5). Many thanks also to Dr Annette Ryan (Lancaster University) who has provided much needed support and teaching as a lab manager. I have been very lucky to have met and worked with you all, and hope to keep up the collaborations in the future.

I am especially grateful to my collaborator Daf Elias. Thank you for the invaluable discussion, teaching, field assistance, and most of all companionship over the last four years. The undertakings in this PhD would not have been possible without you, and I couldn't have asked for a better partner in soil.

It has been an immense privilege to have worked in these amazing, diverse environments. I'll never forget waking up to the sound of gibbons, watching the sunrise over the canopy, or the hum of the jungle (I might even miss the leeches). A big part of this privilege has been working with research assistants in Sabah. From you I learned a great deal about the forest (importantly how not to get lost, and when to run away from elephants) as well as life in Sabah. I am immensely grateful for the essential help in the field. Thank you in particular to Zul and Austin, for sticking with us for all that time. Jumpa lagi!

During this PhD there have been highs and lows, successes and challenges. There are a number of people in the LEC community that have helped to make this process rich and enjoyable. Friends I have made in my PhD office and beyond have become like family over the last few years, and provided a great source of support. A few special thanks to Rosanne (Peg Buddy), Mounir, James, Dee, Andy, Craig, Maria, Kasia, Abby, Radim, Katherine, Jens, Guy, Bobby, Natalie, Phil and Malika, for all being a part of this experience. Thanks also to Danny and the Tropical Group, who helped to set me on this path.

I am incredibly grateful to my parents and family for the constant encouragement and unending support, who I wouldn't have got here without.

Finally, to my Gabi. Thank you for everything, and for sharing in all of the ups, downs and adventures along the way. Here's to our next chapter.

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1 Introduction

1.1 The world's tropical forests: a global life support system under pressure

The world's forests provide vitally important ecosystem services, including the maintenance of global biodiversity, conservation of soil and water, provision of food, medicine and fuel, and regulation of the Earth's hydrological and biogeochemical cycles (Jenkins and Schaap, 2018). Tropical forests represent the most biologically rich and ecologically complex ecosystems on the planet (Laurance, 2007b). Although they constitute just 7 % of the Earth's land cover (Bradshaw et al., 2009), tropical forests support more than two-thirds of all known species (Dirzo and Raven, 2003; Laurance, 1999). This biodiversity is itself integral in supporting crucial ecosystem functions that sustain life on Earth (Dirzo and Raven, 2003). For example, tropical forests provide the world's largest terrestrial carbon (C) sink (approximately 50 %) (Malhi et al., 2004; Pan et al., 2011). Tropical forests therefore play a central role in global C cycling and mitigation of the effects of climate change by offsetting anthropogenic C emissions (Zarin, 2012; DeFries et al., 2002).

Despite their fundamental importance, forests worldwide are under immense pressure due to human activity. The global extent of natural forest is rapidly diminishing, with the currently leading form of global land cover change is conversion of primary (undisturbed) forest (Keenan et al., 2015). The highest rates of loss are occurring in tropical regions (Hansen et al., 2013), most extreme in Southeast Asia (Laurance, 2007a), driven by the interactive effects of human land-use and climate change (Lambin et al., 2003; Malhi and Phillips, 2004). The most recent estimates indicate a loss of 5.5 million hectares of tropical forest cover per year, with a total loss

of 195 million hectares between 1990 and 2015 (Keenan et al., 2015). Besides forest clearance, remaining tropical forest has been extensively disturbed, and in 2012 there was already an estimated 500 million hectares of degraded forest across the tropical regions (International Timber Trade Organisation (ITTO), 2012). Causes of loss and degradation include logging, agricultural intensification, expansion of cattle pasture, hunting and urban development (Asner et al., 2009; Wilcove et al., 2013; de Sy et al., 2019), furthered by increased susceptibility of remaining fragmented forest to environmental disturbances such as fire (Malhi and Phillips, 2004). As a consequence, immense human-modified landscapes now dominate much of tropical regions (Gardner et al., 2009). These trends are only expected to continue, as increasing demand for food production and infrastructure rises alongside rapidly expanding populations in developing tropical countries (Laurance et al., 2014) in tandem with growing global demand for agricultural products produced in these regions (Corley, 2009).

Tropical deforestation and degradation represents a major ecological crisis (Laurance, 2007b; Gibson et al., 2011), with predicted biodiversity losses amounting to a global mass extinction event if tropical forest disturbance continues unchecked (Powers and Jetz, 2019; Alroy, 2017; Giam, 2017). Subsequently, reduced cover and quality of tropical forest negatively impacts on essential ecosystem functions (Ferraz et al., 2014), including C storage (Baccini et al., 2017; Berenguer et al., 2014), and has major consequences for large-scale soil emissions of other greenhouse gases such as methane (CH_4) (Han and Zhu, *forthcoming*). Furthermore, predicted future climate scenarios for tropical regions are likely to magnify effects of human disturbance on ecosystem functions, through increasing intensity and duration of drought events and temperatures extremes (Rifai et al., 2019; Coelho and Goddard, 2009).

1.2 The forests of Southeast Asia: a hotspot of biodiversity and degradation

The forests of Southeast Asia are uniquely biologically rich, owing to a complex combination of distinctive biogeographical factors, and harbour the greatest levels of diversity in the world for several groups of faunal and floral taxa (Sheldon et al., 2015; Hughes, 2017; Woodruff, 2010). The island of Borneo in particular is a recognised global biodiversity and evolutionary hotspot (Myers et al., 2000; de Bruyn et al., 2014), with extremely high botanical and animal endemism (approximately 37 % of vascular plants, 28 % of overall plants and vertebrates) (Raes et al., 2009; Runting et al., 2015; Roos et al., 2004). Bornean rainforests have a characteristically highly abundance of trees of the Dipterocarpaceae family, which are (often mono-) dominant in the forest canopy (Whitmore, 1984). These are now known to be the largest tropical trees in the world, the tallest reaching over 100 metres (Gagen, 2019). Due to the unique rapid growth and morphological traits of the Dipterocarpaceae, the rainforests of Borneo are capable of storing more C than even Amazonian forests (Banin et al., 2014), supporting their role as a vital and irreplaceable global C sink (Qie et al., 2017).

The most rapid forest losses in Southeast Asia are occurring on the island of Borneo (Bryan et al., 2013). Here, the combined effects of industrial timber extraction and expansion of monoculture plantations for the production of palm oil has resulted in a reduction of more than 30 % of forest cover (approximately 18.7 Mha) since the early 1970s, while more than 70 % of the remaining forest has been degraded through selective logging (Gaveau et al., 2014; Gaveau et al., 2016) (Fig. 1.1).

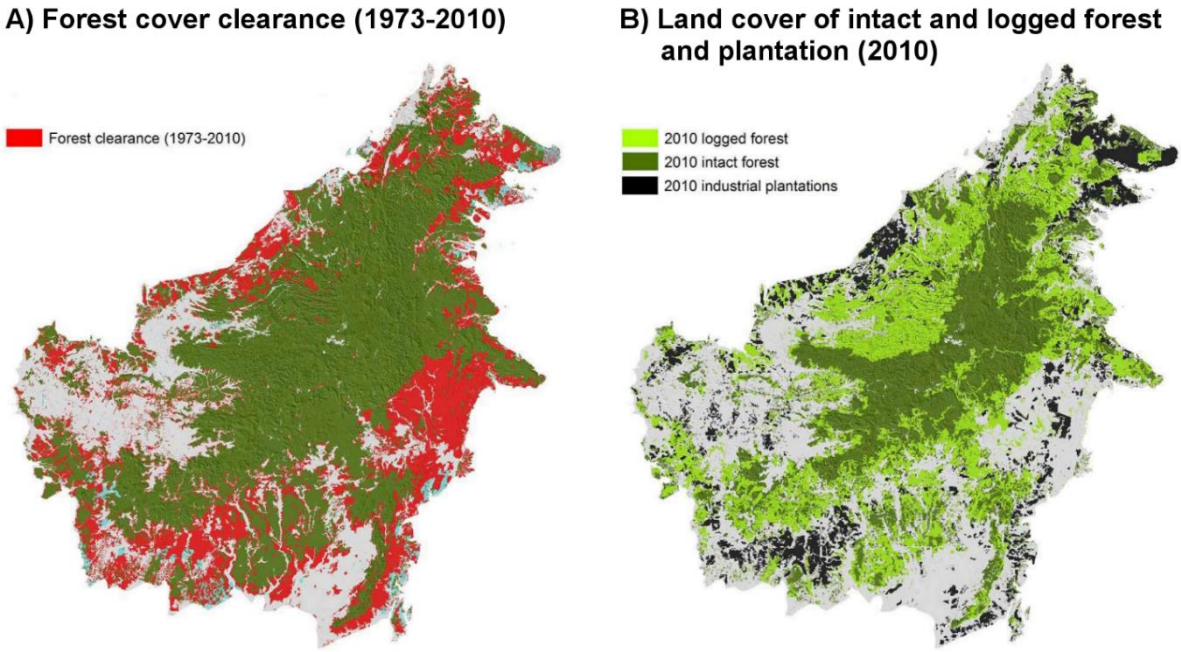

Figure 1.1 *Land-cover maps for island of Borneo derived from LANDSAT data illustrating A) forest cover loss between 1973 and 2010 due to the combined effects of timber harvesting and expansion of industrial plantations, and B) recent land-cover classification for intact old-growth and selectively-logged forest and monoculture oil palm plantation in 2010. Modified from Gaveau et. al. (2014).*

Between 1980 and 2000, more wood was harvested from Borneo than from the Amazon and Africa combined (Curran et al., 2004). The state of Sabah in Northern Malaysian Borneo represents the fastest rates of deforestation in the world, with only 8% of Sabah's current land area now covered by intact forest (Bryan et al., 2013; Gaveau et al., 2014). Although legal protection from logging has in some areas been granted to

protect remaining intact old-growth forests in Sabah (Hazebroek et al., 2004; Marsh and Greer, 1992), these conservation areas are small in number and relative scale (Reynolds et al., 2011). The landscape is now a mosaic of fragmented and degraded selectively-logged forest (SL), interspersed with isolated patches of intact old-growth forest (OG) and expansive monoculture oil palm plantations (OP) (Gaveau et al., 2014) (Fig. 1.2).

Figure 1.2 *The major land cover types across the human-modified landscapes of Borneo: remaining intact old-growth rainforest (A), characteristically dominated by trees of the Dipterocarpaceae (B & C); extensively degraded selectively-logged forest (D & E); expansive monoculture oil palm plantations (F & G). All photographs were taken by the author in the Malaysian state of Sabah. Photographs were taken in the Maliau Basin (A) and Danum Valley (B) Conservation Areas, Kalabakan Forest Reserve (B & C), and Menggaris Oil Palm Estate, Benta Wawasan Sdn. Bdh. (F & G).*

The practice of selective logging involves the removal of individual large trees rather than clearing forest entirely, and is widely used across the tropics (Asner et al., 2009). On Borneo, dipterocarp species (Fig. 1.2 B & C) are targeted during selective logging for their high commercial value as a timber product (Gaveau et al., 2014). Although forest is not clear-felled by this method, an opening of the canopy through removing large individuals, and creation of logging landings and skid trails for extractive machinery can have significant effects on forest ecosystems (Fig. 1.3).

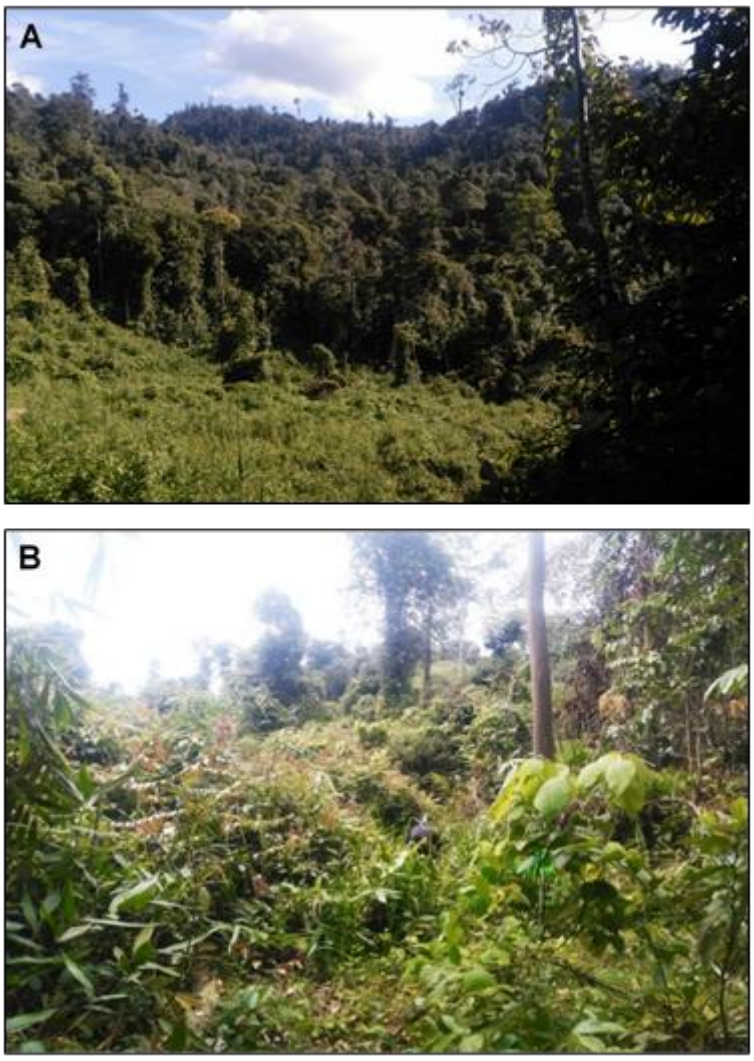

Figure 1.3 *Examples of human-made canopy gaps in selectively logged forest in Sabah, Borneo, created through removal of large individual trees of the Dipterocarpaceae, and opening of logging landings and skid trails for extractive machinery. These can be highly variable is scale and vegetation characteristics, as shown.*

This disturbance modifies vegetation structure, community characteristics and plant inputs due to removal of species and alterations in plant functional niches (Muscolo et al., 2014), which can affect interrelated microclimate, soil conditions, nutrient- and C-cycling (Marthews et al., 2008; Hartmann et al., 2013; Scharenbroch and Bockheim, 2007; 2008a; Saner et al., 2009). Subsequently, the majority of remaining forest cover on Borneo is a highly heterogeneous environment, comprising a tremendously variable matrix of closed-canopy forest and human-made canopy gaps of various sizes and stages of natural regeneration (Ellis et al., 2016; Bossel and Krieger, 1991).

1.2.1 *Rehabilitation of degraded forest and ecosystem functions*

There is now an increased pressure on the remaining Bornean rainforest to provide essential ecosystem functions. Despite the unique capability of Bornean dipterocarp rainforest to store C (Banin et al., 2014), this extensive degradation by selective logging significantly threatens its capacity as a crucial global C sink (Qie et al., 2017; Asner et al., 2018; Ferraz et al., 2018). Ecological restoration of degraded forest ecosystems through large-scale rehabilitation projects is becoming a widely adopted approach across the tropics, attempting to recover coupled biodiversity and ecosystem services (Aronson and Alexander, 2013; Benayas et al., 2009; Brancalion et al., 2013). However, success of restoration programmes is often limited by lack of context-specific knowledge of the ecology of planted tree species and plant-soil interactions (Rodrigues et al., 2009). On Borneo, forest rehabilitation interventions mainly take the form of enrichment planting, where removed indigenous dipterocarp species are reintroduced back into SL forest, with an aim to restore floristic composition to that of intact OG forest (Daisuke et al., 2013). In Sabah alone, *c*. 44,000 hectares of degraded forest are currently under active restoration through co-funded collaborations between international corporations, the government of Sabah and the Yayasan Sabah

Foundation, primarily to offset carbon emissions associated with industrial practices (Reynolds et al., 2011; Face the Future, 2007).

1.3 Soil microbial diversity and function: the unseen biogeochemical engine

Recent advances in molecular techniques, such as high-throughput and next-generation sequencing (NGS), have provided novel insights into the incredible diversity of soil microbiota that has previously been impossible due to the sheer number of taxa and limitations in cultivability (Schloss and Handelsman, 2006; Barriuso et al., 2011; Soliman et al., 2017; Caspermeyer, 2017; Nema, 2019). One gram of soil may, for example, contain up to 5×10^4 bacterial species (Roesch et al., 2007; Curtis et al., 2002), with the number of individual bacteria estimated at the giga-scale (Raynaud and Nunan, 2014; Horner-Devine et al., 2003). As such, soil microbiota represent a significant contribution to the Earth's overall genetic diversity (Whitman et al., 1998). Although the impacts of tropical land-use change on aboveground (plant and animal) biodiversity has been a significant research focus during the past decades (Gibson et al., 2011; Laurance, 1999), we are now only just beginning to understand the effects for belowground soil microbial communities and their associated functions (Rodrigues et al., 2013; Tripathi et al., 2016; Lee-Cruz et al., 2013; Kerfahi et al., 2014).

Soil microbes underpin vital biogeochemical cycles, affecting C and nutrient flows through entire ecosystems (Trivedi et al., 2016; Schimel and Schaeffer, 2012; Wardle et al., 2004). Soil microorganisms function as crucial 'gatekeepers' determining the relative accumulation or release of soil C and N pools through soil-atmosphere exchange (Malik et al., 2018; Kuypers et al., 2018), maintaining soil as a global reservoir of C which holds double the amount of C in the atmosphere, and more than the atmosphere and plants combined (Singh et al., 2010). These functions are driven by complex plant-soil interactions, involving reciprocal feedbacks between aboveground

vegetation and belowground soil microbial communities (van der Heijden et al., 2008; van Der Putten et al., 2013; Cortois et al., 2016; Bever et al., 2010; Wardle et al., 2004). Soil microbes are well recognised as key regulators of plant primary productivity, diversity and community structure through their influence on plant growth and survival (van der Heijden et al., 2008). In turn, soil microbial communities are mutually influenced by plants via inputs from litter and roots altering soil biotic and abiotic conditions (Bever et al., 2010; van Der Putten et al., 2013; Cortois et al., 2016).

Specific processes mediated by soil microbiota, largely bacteria and fungi, include: soil formation and stabilisation (Rillig et al., 2015; Wilson et al., 2009; Rillig and Mummey, 2006); decomposition of soil organic matter (SOM) (e.g. from plant litter) whereby organic compounds are broken down and transformed or mineralised into the form of bioavailable inorganic nutrients (Schimel and Bennett, 2004; van der Heijden et al., 2008); mining and mobilisation of nutrients from mineral soils (Landeweert et al., 2001); contributions to SOM through production and turnover of microbial biomass (Liang et al., 2019; Kyaschenko et al., 2017; Wallander et al., 2013); N-cycling processes (ammonification, nitrification and de-nitrification) (Schimel and Bennett, 2004); CH_4-cycling processes (methanogenesis and methane oxidation) (Aronson et al., 2013); soil emissions of carbon dioxide (CO_2) through microbial respiration for energy production, required for growth and activity (Auffret et al., 2016). These mechanisms are driven both by free-living soil microbes, and microbiota forming mutualistic plant-root associations. Such symbioses result from several hundred million years of coevolution between plants and microbes (Brundrett, 2002; Humphreys et al., 2010; Redecker et al., 2000), and play specific key roles in functioning of ecosystems. Throughout tropical, temperate and boreal biomes, N-fixing bacteria of the rhizobia form partnerships with some vascular (typically leguminous) plants by root nodulation,

overcoming plant N deficiencies through their ability to convert atmospheric dinitrogen (N_2) into plant-available forms (Nasto et al., 2014; Vitousek et al., 2002). Mycorrhizae are ubiquitous associations between certain fungi and the majority (approximately 80%) of terrestrial plants. In exchange for plant-derived photosynthates required for growth and survival, mycorrhizal fungi supply their hosts with key limiting nutrients such as phosphorus (P) and N. This is achieved through establishment of often extensive hyphal networks (mycelium) able to reach distant nutrient pools, and release nutrients from otherwise non-bioavailable sources through extracellular enzyme production (Smith and Read, 2008; Lambers et al., 2008; Itoo and Reshi, 2013). As such, mycorrhizal fungi provide a 'functional link' between plants and the soil (Wurzburger and Clemmensen, 2018), ultimately influencing nutrient dynamics over multiple trophic levels (Maxwell Stevens et al., 2018). As much as 200 m of fungal hyphae can be found in one gram of soil (Leake et al., 2004) and the mycelium of actively-foraging fungi itself provides a soil C sink, while mycelial turnover can in some cases lead to accumulation of SOM (Wallander et al., 2013). The characteristics of mycorrhizal communities may determine soil C dynamics and storage potential at the ecosystem scale (Averill et al., 2014; Dickie et al., 2014; Orwin et al., 2011; Zak et al., 2019).

Resistant, resilient, redundant? Impacts of forest disturbance on soil microbial communities and function in Southeast Asia

An understanding of the resistance (ability to remain unchanged) and resilience (ability to recover after change) of soil microbial communities and functions to environmental perturbation is of central importance for predicting impacts of global change on ecosystem processes. Considerable questions remain about the potential for land-use disturbances to alter microbial community diversity and structure, and whether or not these shifts correspond to changes in function as resultant communities may

support similar soil processes (i.e. functional redundancy) (Allison and Martiny, 2008; Griffiths and Philippot, 2013; Shade et al., 2012). Some studies have shown land use change to have profound and long-lasting effects on microbial community attributes and functions across multiple biomes (Fraterrigo et al., 2006; Bonner et al., 2019; Fichtner et al., 2014; Rodrigues et al., 2013), while other evidence suggests high levels of functional redundancy and community plasticity owing to the extreme diversity of soil microbiota (Nannipieri et al., 2017; Grządziel, 2017).

A handful of recent studies have begun to elucidate the impacts of forest clearance and degradation in Southeast Asia on soil microbial diversity and community structure. While bacterial and protistan communities appear to be broadly resilient to forest ecosystem perturbations (Tripathi et al., 2016; Lee-Cruz et al., 2013), strong effects of both forest conversion to OP and logging disturbance on fungal community attributes have been highlighted (Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015). Observed impacts, including significant reductions in ectomycorrhizal (EcM) fungal abundance and diversity in OG versus SL forest (Elias et al., 2019), may relate to alteration in aboveground communities as selectively removed dipterocarp trees are known to be an obligate EcM-associating family (Brearley, 2012). Recent studies show that even in extremely heterogeneous and hyper-diverse tropical forests, patterns in soil microbial community composition may relate to the phylogenetic and taxonomic structure of aboveground vegetation – although fungal assemblages may be more sensitive than bacteria (Barberán et al., 2015).

Shifts in plant functional traits and net primary productivity (NPP) with increasing disturbance intensity have recently been identified in Bornean rainforest (Riutta et al., 2018; Both et al., 2019). However, there has been little overall exploration

of the functional implications of alterations in soil microbial communities in disturbed Southeast Asian forest (Both et al., 2017). The factors governing microbial functioning in tropical forests as a whole represents a significant knowledge gap (Camenzind et al., 2018). For example, we do not yet know the impacts of observed shifts in foraging fungal community attributes on fungal productivity, despite the central importance of the soil mycelium in biogeochemical cycling as extensively studied in boreal and temperate systems (Ekblad et al., 2013). Moreover, the limited number of studies of soil microbial communities to date have mainly adopted a broad land-use classification approach for comparative analysis between OG and SL forest and/or industrial plantation. However, SL forests are highly heterogeneous and more local impacts of disturbance, e.g. by creation of selective-logging canopy gaps, is unknown. Soil organic C pools and emissions through soil respiration are known to be highly sensitive to both land-use and climate changes, by altering soil abiotic and biotic conditions and temperature which may accelerate decompositional processes (Nazaries et al., 2015; Auffret et al., 2016). A single *in situ* study undertaken in logged-over Bornean forest in recent years found soil respiration to be lower in human made canopy gaps relative to surrounding closed canopy forest (Saner et al., 2012). However, the relative contributions to C emissions by heterotrophic soil microbial versus autotrophic plant processes, and roles of microclimatic conditions and soil microbial community composition is unclear. Furthermore, knowledge of responses of altered soil microbial communities in heterogeneous SL forest to future climate scenarios is greatly lacking. Specifically, there is an urgent need to understand the resistance and resilience of soil microbial functions to drought events, the frequency and intensity of which are predicted to increase as the main impacts of climate change in Southeast Asia (Rifai et al., 2019). Due to the extensive cover of current SL forest on Borneo, an unpicking of

these mechanisms is of vital importance for understanding effects of forest disturbance on soil C cycling now and in the future. Finally, although large-scale forest rehabilitation projects on Borneo appear to have had significant successes in promoting C sequestration by trees (Face the Future, 2020), the wider consequences of restoration interventions on broader ecosystem biodiversity and functions is little understood, and remains a subject of contention (Cerullo et al., 2019). Understanding of coupled above- and below-ground processes during restoration and effects on microbial communities and function is still required (Perumal et al., 2016), necessary for evaluating recovery of vital biogeochemical cycles.

1.4 Thesis aims and objectives

The overarching aim of this thesis is to address current knowledge gaps regarding the impacts of human modification of tropical forests (degradation, conversion and restoration) on soil microbial community attributes and functioning, and evaluate implications for ecosystem biogeochemical cycling. Using the highly biodiverse and heavily altered rainforest of Sabah, Borneo, as a study system, this thesis is structured around the following specific research questions:

1) How does selective logging and conversion of forest to oil palm affect active soil fungal community attributes and mycelial productivity?
2) How do logging gaps affect soil bacterial and fungal community attributes and nutrient cycling?
3) How do logging gaps affect the resistance and resilience of soil microbial carbon cycling to drought?
4) Does active ecological restoration of degraded forest recover soil microbial community attributes and function?

2 Soil fungal community characteristics and mycelial production across a tropical forest disturbance gradient

2.1 Abstract

The rainforests of Southeast Asia are a global hotspot of biodiversity and forest degradation. Selective logging and forest conversion to oil palm plantation has major implications for biogeochemical cycling and carbon (C) storage that are underpinned by plant-soil interactions. Soil fungi are key regulators of C and mineral nutrient flows between above- and below-ground organisms, yet understanding of fungal community-productivity relationships in hyper-diverse tropical forests is lacking. Recent studies suggest sensitivity of soil fungal communities to land-use change, although impacts on fungal productivity remain unresolved. To address this gap, we installed hyphal in-growth bags for six months in old-growth (OG), selectively-logged (SL) forest and oil palm plantation (OP) in Bornean lowland rainforest. Mycelial (actively foraging) fungal communities were characterised by ITS amplicon sequencing, and mycelial production estimated by measurement of fungal hyphae. Mycelial fungal community compositions were similar in OG and SL forest, whereas OP had significantly different communities of saprotrophic, mycorrhizal, and pathogenic fungi. In particular, mycorrhizal relative abundance and diversity and mycelial production was reduced. However, due to restricted sampling replication in OP, effects associated with site could not be excluded. In forest plots (OG & SL), we further explored the broader drivers of mycelial fungal communities using tree community, structure and productivity data, and soil and environmental properties. Forest mycelial community dissimilarities were related to soil and vegetation characteristics. Mycelial production was independent of fungal community or vegetation attributes but positively related to soil inorganic P concentrations (although tenuously). Changes in relative abundances of mycorrhizal

types were also found with selective logging, which may have implications for C storage capacity in these forests, while an apparent retention of mycorrhizal mycelium in SL forest may act as a reservoir of inoculum that could aid forest restoration. Our results show that conversion of rainforest to OP has significant consequences for fungal diversity-productivity relationships with implications for nutrient and C dynamics and restoration over large spatial scales.

2.2 Introduction

Tropical forests represent the most biodiverse terrestrial ecosystems on the planet (Myers et al., 2000) and provide a globally important C sink (Pan et al., 2011). Increasingly rapid reductions in forest cover through land-use change threatens the capacity of tropical forest to support biodiversity (Powers and Jetz, 2019; Hansen et al., 2013) and store C (Baccini et al., 2017). Significant forest degradation is occurring in Southeast Asia, with highest rates in Borneo (Bryan et al., 2013). Since the early 1970s, expansion of industrial oil palm (OP) plantation has resulted in the loss of >30 % of forest cover (18.7 Mha of old-growth forest), while more than 70 % of the remaining forest has been degraded through selective logging for extraction of commercially valuable timber (Gaveau et al., 2014; Gaveau et al., 2016).

Ecosystem functions and biogeochemical cycles are underpinned by complex plant-soil interactions, mediated through reciprocal feedbacks between aboveground vegetation and belowground soil microbial communities (van der Heijden et al., 2008; Cortois et al., 2016; van Der Putten et al., 2013; Bever et al., 2010; Wardle et al., 2004). Changes in soil properties associated with forest disturbance have been shown to have significant and long-lasting effects on microbial community assemblages and diversity across multiple biomes (Hartmann et al., 2013; McGuire et al., 2015). However, despite the importance of plant-soil microbe interactions, understanding of relationships between above-below-ground communities alongside soil properties in tropical ecosystems remains limited (Barberán et al., 2015; Elias et al., 2019; Mueller et al., 2016). A small number of recent studies have highlighted the sensitivity of soil fungal communities to land-use change in Southeast Asia, including effects of logging and forest conversion to oil palm plantation on community structure and diversity (Kerfahi

et al., 2014; McGuire et al., 2015), although the direct impacts on functioning of fungal communities are unclear.

The mycelium produced by actively foraging soil fungi is a key component of carbon (C) and mineral nutrient cycles in terrestrial ecosystems (Cairney, 2012; Finlay, 2008; Johnson et al., 2002). The extraradical mycelia of mycorrhizal fungi act as direct pathways for the reciprocal exchange of mineral nutrients from soils and photosynthetic C between plants and fungal symbionts. This mutualistic association benefits the host plant through increased surface area for the absorption of mineral nutrients from soil, in exchange for plant-derived photosynthates required for fungal growth and survival (Smith and Read, 2008; Itoo and Reshi, 2013; Chen et al., 2016). Plant productivity is enhanced through this mutually beneficial partnership (Wurzburger and Clemmensen, 2018; Lambers et al., 2008; Nasto et al., 2014), in turn leading to greater belowground C allocation by plants (Orwin et al., 2011) and C supply to the wider soil microbiome (Nottingham et al., 2013; Drigo et al., 2012). Recent research has evidenced nutrient transfer between plants of the same or even different species through common mycelial networks (CMNs), that physically connect two or more individual plants and can support interplant exchanges over long distances (Babikova et al., 2013; Bever et al., 2010; Gorzelak et al., 2015; Barto et al., 2012). While this process can influence plant survival and growth, it may also support establishment of young trees by providing existing infrastructure for seedlings to access (Nara, 2006; Gorzelak et al., 2015). While fungal hyphal structures themselves provide a C sink, they may also contribute to soil organic matter accumulation through mycelial turnover (Wallander et al., 2013) and protection of organic substrates through effects on soil aggregation (Rillig et al., 2015; Wilson et al., 2009). Although the precise role of mycelial production and activity in soil C dynamics is contentious and remains an area of active research (Zak et al., 2019),

recent studies have highlighted links between mycorrhizal community structure and soil C storage. For example, dominance of ectomycorrhizal (EcM) versus arbuscular mycorrhizal (AM) fungi may influence soil C accumulation potentially through competition with saprotrophic fungi for resources required for the decomposition of organic matter (Averill et al., 2014).

Mycelial production is regulated by a range of abiotic and biotic factors such as soil mineral nutrient availability (Ekblad et al., 2013; Hagerberg et al., 2003; Potila et al., 2009; Nilsson and Wallander, 2003), soil moisture (Majdi et al., 2008), climate (Bakker et al., 2015), phenological/seasonal changes in belowground C allocation (Ekblad et al., 2013) and direct grazing by soil mesofauna which may inhibit or stimulate mycelial production (Ek et al., 1994; Setälä et al., 1999). Plant and fungal community structure themselves are also critical for determining mycelial growth and turnover (Clemmensen et al., 2015), as shifts in vegetation and mycelial fungal communities related to forest management have been linked to patterns in mycelial production (Hagenbo et al., 2018). However, quantification of mycelial production rates has largely been confined to boreal and temperate biomes, mostly focussing on EcM-dominated systems in Scandinavia (Ekblad et al., 2013).

The lowland rainforests of Borneo are characterised by the high abundance and canopy dominance of tree species belonging to the obligate EcM-associating Dipterocarpaceae family (Whitmore, 1984; Brearley, 2012; Taylor and Alexander, 2005), with dipterocarp community assemblages potentially mediated by their mycorrhizal partners (Essene et al., 2017). Overall, the majority of tree species in these hyper-diverse forests also associate with AM fungi as in most tropical forests (McGuire et al., 2008). Dipterocarps are also directly targeted through selective logging due to

their commercial value as timber (Appanah and Turnbull, 1998), making way for establishment of other tropical tree species that are likely to be AM-forming (McGuire et al., 2008). A recent study highlighted the effects of such tree community alterations on net primary productivity (NPP) allocation (Riutta et al., 2018), with shifts from canopy NPP to woody NPP fractions in logged forest in Bornean lowland dipterocarp rainforest. Corresponding shifts in tree functional traits have also been reported, indicating traits associated with carbon capture and growth to be more pronounced in selectively logged (SL) forest compared to structural and persistence traits in old-growth (OG) forest (Both et al., 2019). These alterations to aboveground productivity patterns and plant functional traits along with modified soil properties due to logging may have strong implications for soil mycelial fungal community characteristics (i.e. the structure and diversity of actively foraging soil fungi) and their productivity, although these relationships to date have not been investigated.

The overarching aim of this study was to evaluate the impact of selective logging and forest conversion to oil palm plantation on mycelial fungal community characteristics and productivity, and explore the role of soil and vegetation properties as drivers of mycelial fungal community composition and productivity in tropical lowland dipterocarp rainforest. This study was constructed to address the following hypotheses:

> H1. Mycelial fungal community attributes (composition and alpha diversity) and mycelial production will differ between OG and SL forest and OP, with corresponding differences in soil and environmental properties, tree community composition and functional characteristics between land-use types.

H2. Across OG and SL forest, mycelial fungal community attributes and production will be explained by soil and environmental properties, tree community composition and functional characteristics.

H3. Across OG and SL forest, mycelial fungal community attributes will correlate with rates of mycelial production.

2.3 Methods

2.3.1 Study sites

This study was carried out in the Malaysian state of Sabah, northern Borneo. This region is characterised by moist tropical climate and is considered mainly a-seasonal (average daily temperature 27 ˚C, annual precipitation 2,600 - 2,700 mm) although may experience irregular inter-annual dry periods which with an average total of ~1.4 months per year (Walsh and Newbery, 1999; Kumagai and Porporato, 2012). Sampling was conducted in a total of nine 1 ha plots across OG and SL lowland dipterocarp rainforest and OP (Fig. 2.1).

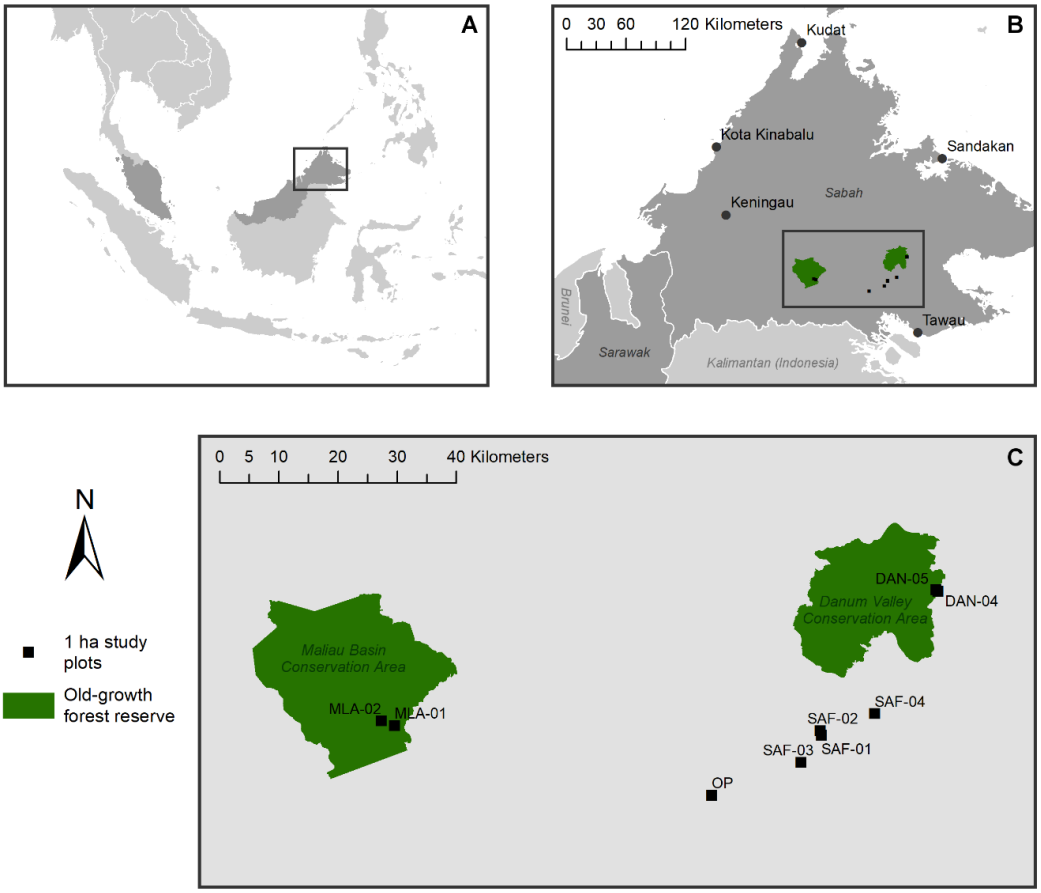

Figure 2.1 *Map of nine sampling locations A) in northern Malaysian Borneo B) in the state of Sabah, C) with four 1 ha study plots situated within old-growth forest (DAN-04, DAN-05, MLA-01 and MLA-02), four in selectively-logged forest (SAF-01, SAF-02, SAF-03, SAF-04) and one in oil palm plantation (OP).*

Four plots were distributed across OG forest: two plots were situated in the Danum Valley Conservation Area (DVCA) (4.951°, 117.796° and 4.953°, 117.793°), and two in the Maliau Basin Conservation Area (MBCA) (4.747°, 116.970° and 4.754°, 116.950°), coded as DAN-04, DAN-05, MLA-01 and MLA-02 respectively in the ForestPlots database. These reserves have undergone little or no anthropogenic disturbance with legal protection from logging granted in 1976 and 1981, respectively (Marsh and Greer, 1992; Hazebroek et al., 2004). Four plots were located in SL forest in the Kalabakan Forest Reserve (SAF-01: 4.732°, 117.619°; SAF-02: 4.739°, 117.617°; SAF-03: 4.691°, 117.588° and SAF-04: 4.765°, 117.700°) and one in OP

(4.641°, 117.452°; Benta Wawasan Sdn. Bdh.), in established research sites within the large-scale forest fragmentation study Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al., 2011). Two SL plots had been selectively logged twice and two four times, with forests undergoing timber extraction first during the mid-1970s (approximately 113 m^3 ha^{-1} timber removed), followed by up to three more rounds between 1990 and 2008 (approximately 37-66 m^3 ha^{-1} cumulative timber removed) (Fisher et al., 2011; Riutta et al., 2018). The OP plot was located in a stand aged approximately seven years at the time of sampling, where fertiliser applications were roughly two applications of 3-4 kg bags $palm^{-1}$ $year^{-1}$ (comprising a mixture of diammonium phosphate, potassium chloride, ammonium sulphate, magnesium sulphate and borax pentahydrate) prior to this study (J. Drewer, personal communication). All plots in OG and SL forest were previously established as part of the Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/) for the long-term evaluation of forest carbon cycling and productivity since 2011 (Malhi et al., 2015; Riutta et al., 2018), and have recently been characterised for tree community assemblage, plant traits, soil microbial communities and soil physicochemical properties (Both et al., 2019; Elias et al., 2019).

2.3.2 Sampling design

Three 20 × 20 m subplots were randomly chosen per 1 ha plot for assessing mycelial community attributes and productivity. Ten hyphal in-growth bags were installed per subplot at a randomly chosen location. Bags were buried at 50 cm intervals along two parallel transects (5 bags per transect) spaced 1 m apart to ensure adequate sample recovery and account for spatial variability in fungal community composition and mycelial production.

2.3.3 Hyphal in-growth bags

Hyphal in-growth bags were constructed from two 5 cm × 5 cm squares of fine pore-size nylon mesh (Plastok, UK) sealed with a soldering iron. A mesh size of 41 µm was chosen to allow access to fungal hyphae, but prevent infiltration of plant roots (Wallander et al., 2013; Fisher et al., 2013). Bags were filled with 25 g oven-dried, heat-sterilised quartz sand (150 ˚C for 24 hours). In-growth bags were installed between April-May 2016 by burying vertically at the soil surface covering a depth of approximately 0-5 cm. This was chosen to include the organic layer and interface between organic and mineral horizons to maximise fungal in-growth (Lindahl et al., 2007; Wallander et al., 2013). As there is no distinct growing season in this region, in-growth bags were harvested after a period of 6 months to allow fungal colonisation under relatively stable seasonal conditions. Bags were frozen in a field laboratory upon collection, and transported on ice to Lancaster University where they were stored at -20 ˚C prior to analysis. Bags were examined and discarded where there was clear damage or root ingress. Due to low recovery of undamaged bags, three in-growth bags were used per subplot to account for local variation in mycelial colonisation (with the exception of five composite samples: one bulked from two in-growth bags, and four from one bag due to high damage or loss rates in some subplots). Bags were opened in the laboratory and sand was carefully bulked per subplot and hand-mixed, providing 27 composite samples (three per 1 ha plot) for quantification of mycelial abundance and molecular analysis of fungal communities. Only one 1 ha plot was established in the OP site, due to logistical challenges and as spatial variation in this land-use type was expected to be low. As such the three composite OP samples were treated as independent replicates, each representing an individual plot-level sample for all analyses.

2.3.4 Hyphal extraction and estimation of mycelial productivity

Hyphae were extracted from sand using an adapted floatation method (Bakker et al., 2015). 5 g subsamples were transferred into 50 ml sample tubes, then filled up to 30 ml with 4M KCl solution. This extractant was used to ensure floatation of all hyphae and avoid clumping and sinking of fungal filaments, which may be hydrophilic or hydrophobic (Ekblad et al., 2013), preventing adequate seperation from sand particles (as found in prior labortory tests using distlled water). Tubes were vortexed at full speed for 1 minute, left to stand for 30 seconds to allow hyphal material to reach the surface of the solution, and 25 ml was decanted into a clean sample tube, avoiding the transfer of sand particles. This process was repeated once more on the same sand subsample. The extract was transferred into a sample pot and made up to 100 ml by rinsing the sample tube twice with 25 ml distilled water. Hyphal material was prepared for measurement using the membrane filtration technique (Hanssen et al., 1974). The extract was evenly mixed using a sample mixer at 700 rev min^{-1}, and 10 ml aliquots were transferred in two steps using a 5 ml pipette during mixing into a 15 ml glass filtration tube mounted on a nitrocellulose filter membrane (Merck Millipore, USA; 1.2 µm pore size, 25 mm diameter). The suspension was filtered with a vacuum pump, and hyphae were stained in the tube using Lactophenol cotton blue under a fume hood for 20 minutes. The filter membrane was then rinsed with distilled water until filtrate ran clear, and left to air dry overnight. Filter membranes were mounted onto microscope slides with immersion oil for transparency and sealed under a coverslip.

Hyphae on filter membranes were photographed at high resolution (4080 × 3072 pixels) using a microscope-mounted camera at x 100 magnification (Olympus BX51, Olympus DP71), allowing identification of hyphal structures with diameters ≥ 1 µm. Photographs were used for hyphal measurement to maximise membrane coverage

and capture of within-sample variation not possible through direct microscope observation at higher magnification. Twenty-five photographs (each covering an area of approximately 1.53 mm^2) were taken per membrane along four crossing transects positioned at 45 ˚ to each other, as described by Boddington et. al (1999). Hyphal length was estimated from photographs using the gridline intersect method (Tennant, 1975). A regular grid with grid size 50 × 50 µm was digitally placed on top of each photograph using ImageJ (Shen et al., 2016; Schneider et al., 2012). Image contrast and brightness were altered as necessary to improve visualisation of hyphae. All intersections between hyphae and gridlines were counted, and total hyphal length was calculated using Tennant's formula. The total hyphal length in each subsample was estimated using hyphal length per area in photographs and area of membrane used for filtration. 10 g of fresh sand from each composite sample was oven-dried at 105 ˚C to constant weight to calculate moisture content for standardisation of hyphal length estimations. Hyphal length was then calculated in mm g^{-1} dry sand for statistical analysis of mycelial production.

2.3.5 Soil, environmental and vegetation characteristics

Soil physicochemical data for corresponding subplots were obtained from an existing dataset (Elias et al., 2018). Briefly, five soil samples were collected within each subplot (3 cm diameter gouge auger) March-April 2015. Organic soil layer depth was measured before separation from underlying mineral soil. Organic layer soil samples were bulked per subplot and analysed for organic layer pH, total C, total N, total P, inorganic P and texture (% sand, silt and clay). pH in water was measured on fresh soils using a pH meter (1:2.5 soil to deionised water) after shaking overnight at 100 rev m^{-1} on an orbital shaker and standing for 30 min (Landon, 1984). The remaining soils were air-dried at 40 °C to constant weight and passed through a 2 mm sieve. Subsamples for total C and

N analysis were dried at 65 °C for 48 hours and milled to a fine powder with a pestle and mortar. Total soil C and N contents were determined by dry combustion at 900°C using an Elementar Vario Max CN analyser (Elementar Analysensysteme, Hanau, Germany). Samples were digested using sulphuric acid-hydrogen peroxide (Allen, 1989) for soil total P. Inorganic P was extracted using a Bray No. 1 extractant (Bray and Kurtz, 1945). P contents of extracts and digests were determined using the molybdenum-blue method (Anderson and Ingram, 1993), read at 880 nm on a spectrophotometer (HITACHI-UV-VIS, Japan). Soil texture was measured by the pipette method (Miller and Miller, 1987). Soil bulk density was determined from one additional sample taken per subplot using a 7.5 cm diameter volumetric, dried at 105 °C for 24 hours after removal of roots and stones (Emmett et al., 2008). Soil moisture content (top 12 cm), temperature (10 cm depth) and air temperature (20 cm above soil surface) values for corresponding subplots were accessed from datasets of continuous sampling of GEM plots, as described in Marthews et al. (2014). Slope measurements were taken upon in-growth bag harvesting using a clinometer at each subplot corner and centre, and values were averaged at the subplot level. Altitude was recording using a GPS in each subplot centre. Forest structural characteristics (stem density, basal area, and mean and maximum diameter of stems at breast height (DBH) ≥ 10 cm, pioneer tree proportion of basal area, and Leaf Area Index (LAI)) and tree productivity metrics (canopy net primary production (NPP), woody NPP, root NPP, total NPP) for corresponding subplots were also accessed from GEM plot datasets, using temporally-averaged data collected between 2011-2016 (Riutta et al., 2018; Marthews et al., 2014). Tree taxonomic community datasets were constructed at the 1 ha plot level from a previous survey undertaken July-December 2015, where all individual trees DBH ≥ 10

cm within three 20 × 20 m subplots were taxonomically identified (Both et al., 2019). Dipterocarp basal area was derived from tree community data at the plot level.

Molecular analysis of mycelial fungal communities and data pre-processing

DNA was extracted from 0.2 g sand from in-growth bags using the PowerSoil® DNA Isolation Kit and protocol (MoBio Laboratories). 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). Fungi were targeted by amplifying the ITS2 region using primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). Although the capability of detecting AM fungi using ITS primers is debated (Hart et al., 2015), recent studies have shown that patterns in diversity and community composition can be adequately identified within sample types such as soil (Berruti et al., 2017; Lekberg et al., 2018). 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 52 °C; annealing times were 30 seconds with extension at 72 °C for 30 seconds; cycle numbers were 25; a final extension of 10 minutes at 72 °C was included. Amplicon sizes were determined using an Agilent 2200 TapeStation system, samples were normalised using SequalPrep Normalization Plate Kit (Thermo Fisher Scientific) and pooled. The pooled library was quantified using a Qubit dsDNA HS kit (Thermo Fisher Scientific) prior to sequencing with an Illumina MiSeq using V3 600 cycle reagents at a concentration of 8 pM with a 5% PhiX Illumina control library. The sequencing run produced in excess of 18 million reads passing filter. Sequences were processed in R using DADA2 to quality filter, merge, de-noise and assign taxonomies (Callahan et al., 2016). Sequence 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. *mergePairs* and *removeBimeraDenovo* functions were used at default settings to merge forward and reverse reads and remove chimeric sequences. The amplicon sequence variants (ASVs) were subject to taxonomic assignment using *assignTaxonomy* and the training database UNITE version 7.2 (UNITE Community, 2017).

Fungal functional guild classifications were assigned to ASVs using the FUNGuild annotation tool (Nguyen et al., 2016). Only ASVs with unambiguous (non-multiple) classifications of "probable" or "highly-probable" confidence rankings were considered for analysis. These were used for calculating relative abundances of fungal guilds and sub-setting saprotrophic, mycorrhizal and pathogenic fungal datasets for assessment of diversity and community dissimilarity. Sequencing data were pre-processed (steps described below) and alpha diversity indices (ASV richness, Shannon index) and fungal guild relative abundances calculated in R version 3.5.1 (R Core Team, 2013) using the *phyloseq* package (Mcmurdie and Holmes 2013). Only ASVs assigned to the kingdom of Fungi were retained for downstream analysis (99.34 % of total reads), and all singleton ASVs were removed. Sub-setting by fungal guilds was conducted on the full unrarefied dataset to maximise the number of ASV reads available for analysis of functional groups. Sample sequencing depth was normalised for each group by rarefying to the minimum read counts of 4881, 151, 75 and 67 per sample for overall, saprotrophic, mycorrhizal and pathogenic fungal groups respectively. Analyses of diversity metrics and community dissimilarities were repeated using unrarefied and

whole-sample only rarefied datasets (before sub-setting fungal groups), which showed broadly consistent results.

2.3.6 Statistical analyses

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2013) and significance was considered at the $p \leq 0.05$ level. For univariate analyses, linear mixed effects regression models (LMMs) were constructed in the *lme4* R package (Bates et al., 2015). This included testing (H1) the effect of land-use type on relative abundances of mycelial fungal guilds and alpha diversity, mycelial production and soil, environmental and vegetation characteristics, and (H2 & H3) relationships between these variables across OG and SL plots. Post-hoc pairwise comparisons were conducted with the *emmeans* R package (Lenth et al., 2019) with Bonferroni correction to identify statistically different variable means between OG, SL and OP land-use types. To control for potential within-plot pseudoreplication, plot ID was included as a random intercept term. Significance was evaluated using the Satterthwaite degrees of freedom approximation (Luke, 2017). Normality of model residuals were evaluated using Shapiro-Wilk tests, and variables were log- and exponentially- transformed where necessary to improve model fit. Kruskal-Wallis tests were conducted when residual normality could not be satisfactorily achieved using data averaged at the plot level.

Mycelial fungal community compositions across all land-use types were visualised with PCoA using Bray-Curtis dissimilarities via the *phyloseq*, *vegan* (Oksanen et al., 2019) and *ggplot2* (Wickham, 2016) packages. To test differences in fungal community compositions between OG, SL and OP (H1), Bray-Curtis community dissimilarities were calculated from data averaged at the plot level (n = 11) using the merge_samples function in *phyloseq*. Differences between land-use types were tested

with PERMANOVA using the adonis *vegan* function, and statistically different groups were identified using the pairwise.adonis function in the *pairwiseAdonis* R package (Martinez Arbizu, 2019) controlling for the False Discovery Rate (FDR). All permutational tests were run with 9,999 permutations with the exception of pairwise multiple comparisons, where full enumeration was used. Indicator analyses were conducted to identify specific fungal taxa associated with different land-use types using the *labsdv* R package (Roberts, 2016; Dufrêne and Legendre, 1997). Differences in tree community composition between OG and SL forest (H1) were tested with PERMANOVA using Bray-Curtis community dissimilarities calculated from plot-level community data. Hellinger-transformation was applied to all community data prior to multivariate analyses (Legendre and Borcard, 2018) to control for the effect of rare taxa. Homogeneity of multivariate dispersion across land-use types (an assumption of PERMANOVA) for fungal and tree community dissimilarities was evaluated using the betadisper *vegan* function for overall and pairwise tests (FDR-corrected).

Relationships between mycelial fungal community compositions and soil, environmental and vegetation characteristics (H2) across forest (OG and SL) plots were evaluated using distance-based redundancy analysis (db-RDA). Tree community composition was included in analysis as represented by the first three PCoA axes, explaining most of the variation (60.39 % cumulative eigenvalues). Prior to analysis, highly correlated variables within 1) soil and environmental and 2) vegetation groups were identified with correlograms using the *corrplot* R package (Wei and Simko, 2017). Variables correlated with Pearson's $r > \approx 0.7$ were removed. Soil and environmental variables were treated as one group as soil characteristics were considered to be of primary ecological importance, while driven by environmental factors. The best predictors of fungal Bray-Curtis dissimilarities were identified through forward-

selection using the criteria of adjusted R^2 and significance level of $p < 0.05$ (Blanchet et al., 2008) with the ordiR2step *vegan* function. Here Bray-Curtis dissimilarities were calculated at the subplot level and permutational tests were restricted by plot ID to control for the nested sampling design using the *permute* R package (Simpson et al., 2019). Variation in fungal community dissimilarities was partitioned by soil and environmental and vegetation components using the varpart function, and significance of components and individual predictors was tested with partial db-RDA in *vegan*. Relationships between mycelial fungal and vegetation communities (H2) were tested using plot-level Bray-Curtis dissimilarities with Mantel tests (Spearman's rank correlation) in *vegan.* Relationships between mycelial fungal community compositions and mycelial production (H3) were tested with PERMANOVA using Bray-Curtis dissimilarities and the same permutational scheme described above.

2.4 Results

Overall, 3565 fungal ASVs from 10 phyla (Fig. 2.1) and 374 genera were detected across all samples of OG forest, SL forest and OP.

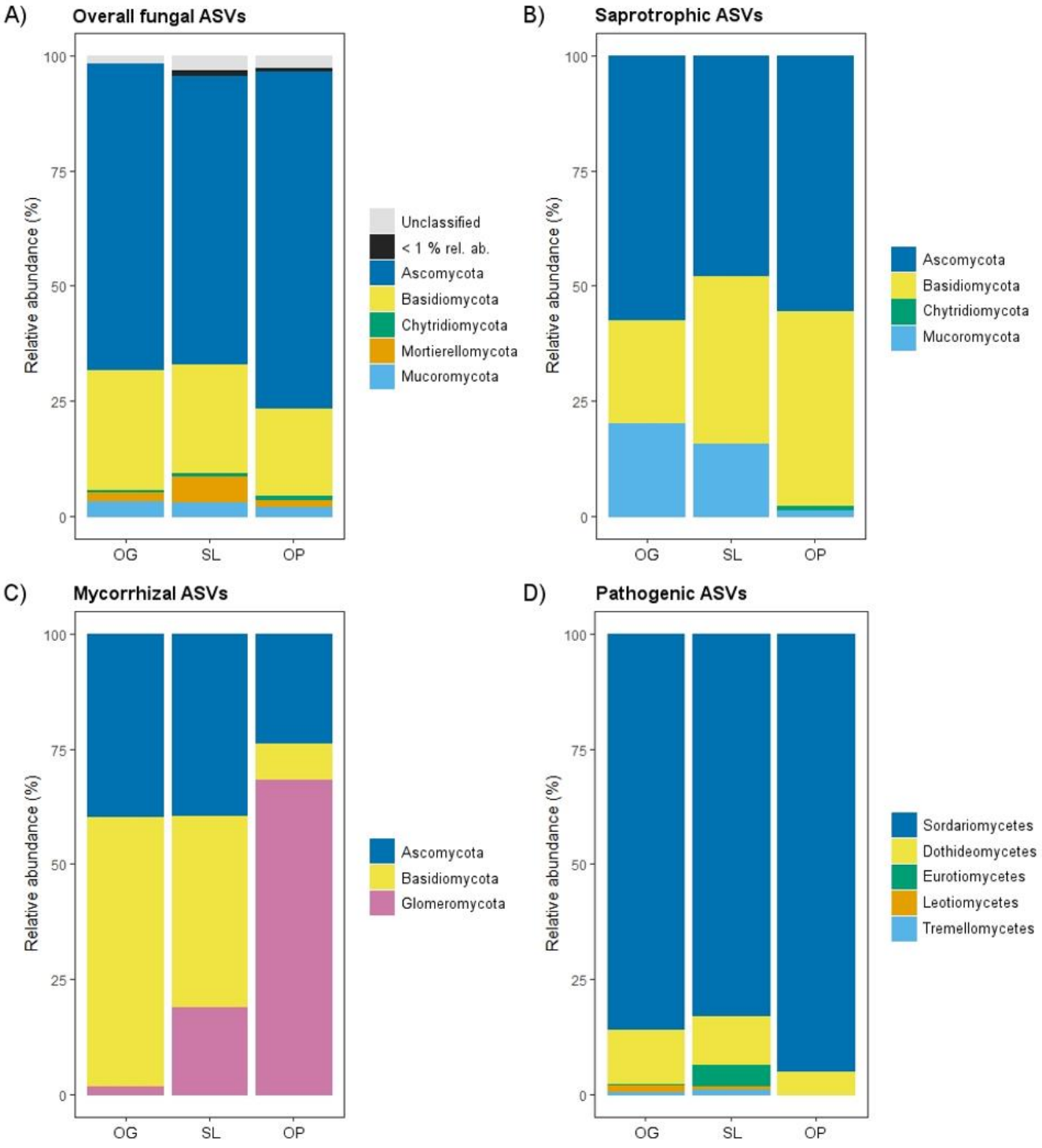

Figure 2.2 *Relative abundance of mycelial fungal phyla as a percentage of total Amplicon Sequence Variants (ASVs) in old-growth (OG) and selectively logged (SL) forest and oil palm plantation (OP) for A) overall, B) saprotrophic, C) mycorrhizal fungal groups. Phyla with < 1% relative abundance across all forest land-use types are represented as one group for overall fungi. C) Relative abundances of classes of mycelial pathogenic fungi. Phyla are not shown for this fungal group as reads were dominated by one phylum (Ascomycota: 98.76 % in OG, 100 % in SL and 99.38 in OP) with the remaining reads comprising taxa of the Basidiomycota.*

Of the ASVs that were assigned fungal functional guilds, the majority of reads comprised saprotrophic (39.9 %), followed by mycorrhizal (27.0 %: 83.1 % of which EcM; 16.7 % AM; 0.2 % ericoid mycorrhizal (ErM)), pathogenic (21.0 %: 51.4 % of which animal pathogenic; 48.6 % plant pathogenic), parasitic (7.1 %), endophytic (2.2 %), lichenised (2.0 %) and epiphytic (0.7 %) fungi.

2.4.1 Impact of land-use type on mycelial fungal community attributes, mycelial productivity and soil, environmental and vegetation characteristics

Land-use type significantly affected community dissimilarities for overall, saprotrophic, mycorrhizal and pathogenic fungal groups (Fig. 2.3; see Table 2.1 for summary of statistics).

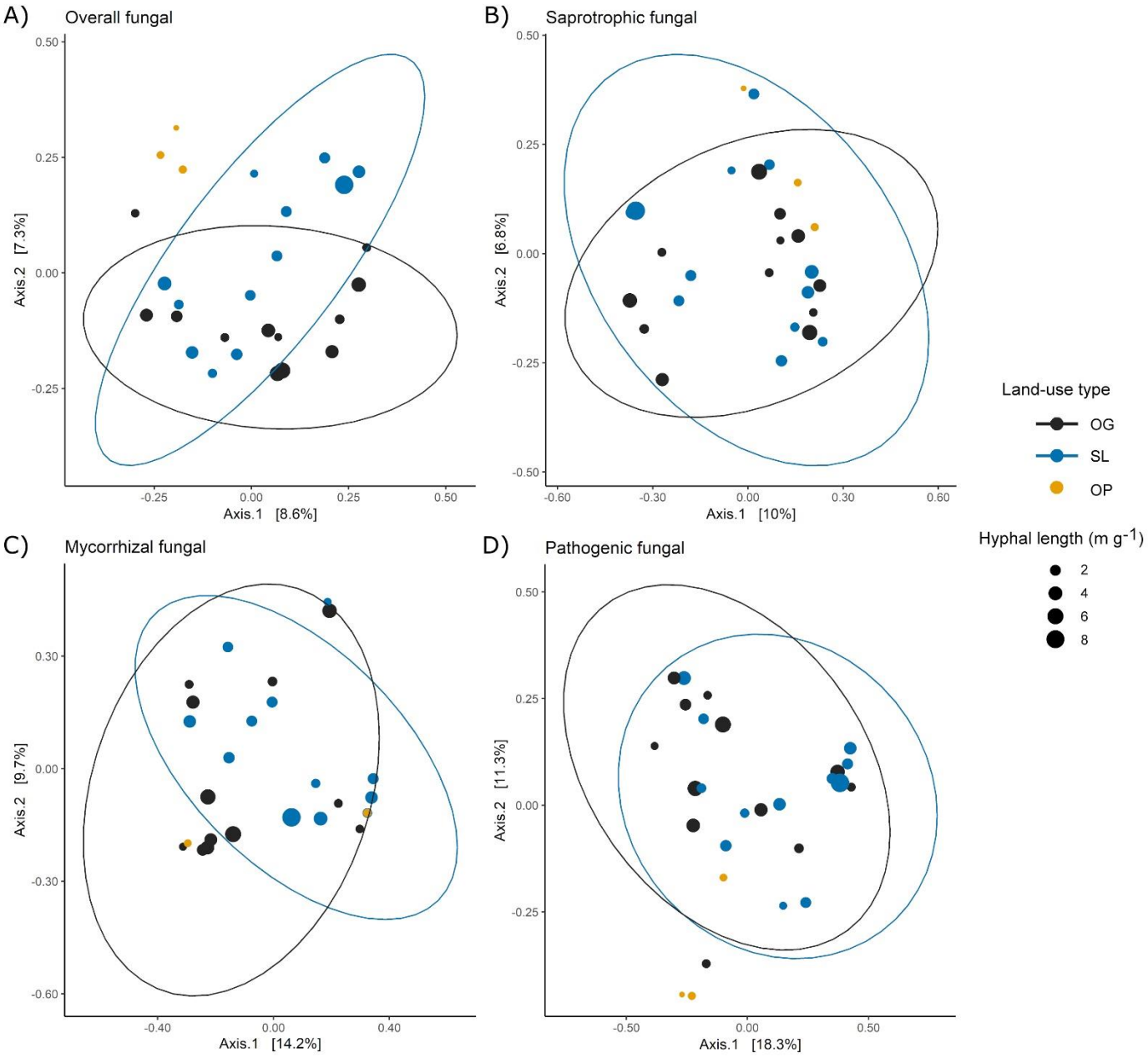

Figure 2.3 *Principle coordinates analysis (PCoA) ordination of A) overall, B) saprotrophic, C) mycorrhizal and D) pathogenic mycelial fungal community Bray-Curtis dissimilarities across old-growth (OG) and selectively logged (SL) forest and oil palm plantation (OP). Points are scaled by hyphal length indicating mycelial production. Ellipses represent t-distribution confidences for OG selectively SL forest. Ellipses are not included for OP samples due to number of samples (n = 3). For mycorrhizal fungal community dissimilarities (C), two OP points are indistinguishable (hyphal length values 0.24 and 0.84 m* g^{-1} *respectively) due to sharing the same PCoA scores for Axes 1 and 2 (coordinates: 0.32, −0.12).*

Table 2.1 PERMANOVA test statistics for differences in fungal guild community dissimilarities between land-use types. Summaries are given for overall models and pairwise comparisons between old-growth (OG) and selectively-logged forest (SL) and oil palm plantation (OP). Significant *p*-values ($p > 0.05$) are highlighted in bold. Pairwise tests were conducted controlling for the False Discovery Rate (FDR).

Fungal guild	Overall model			Pairwise tests								
				OG-SL			OG-OP			SL-OP		
	F	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*
Overall fungal	1.48	0.27	**0.001**	1.08	0.15	0.170	1.84	0.27	**0.043**	1.58	0.24	**0.043**
Saprotrophic	1.23	0.24	**0.023**	1.05	0.15	0.223	1.45	0.23	0.086	1.21	0.19	0.129
Mycorrhizal	1.19	0.23	**0.041**	1.13	0.16	0.171	1.15	0.19	0.171	1.29	0.20	0.171
Pathogenic	1.69	0.30	**0.006**	1.07	0.15	0.305	2.04	0.29	**0.043**	2.10	0.30	**0.043**

Pairwise comparisons identified significant differences between OP and forest land-uses for overall and pathogenic fungal community dissimilarities. No significant differences were found between land-use types for saprotrophic or mycorrhizal community dissimilarity in pairwise comparisons ($p > 0.05$). However, further tests using only OG and SL plots showed no significant effect of land-use type on saprotrophic or mycorrhizal community dissimilarities (PERMANOVA: $p = 0.223$; $p = 0.115$, respectively), indicating the significant effects of land-use type across the full disturbance gradient was driven by OP. Community dissimilarity dispersions were homogenous between all land-use types for all fungal groups (betadisper: $p > 0.05$). No significant differences in community dissimilarities were found between OG and SL for any fungal group ($p > 0.05$), despite significant differences in soil, environmental and vegetation properties between forest land-uses (see below). However, relative abundance of AM fungi was significantly higher in SL relative to OG, and ErM fungal relative abundance was higher in SL relative to all other land-use types (Fig. 2.4; see

Table 2.2 for means of all mycelial fungal community attributes by land-use type; test statistics for significant differences are reported in Table 2.3).

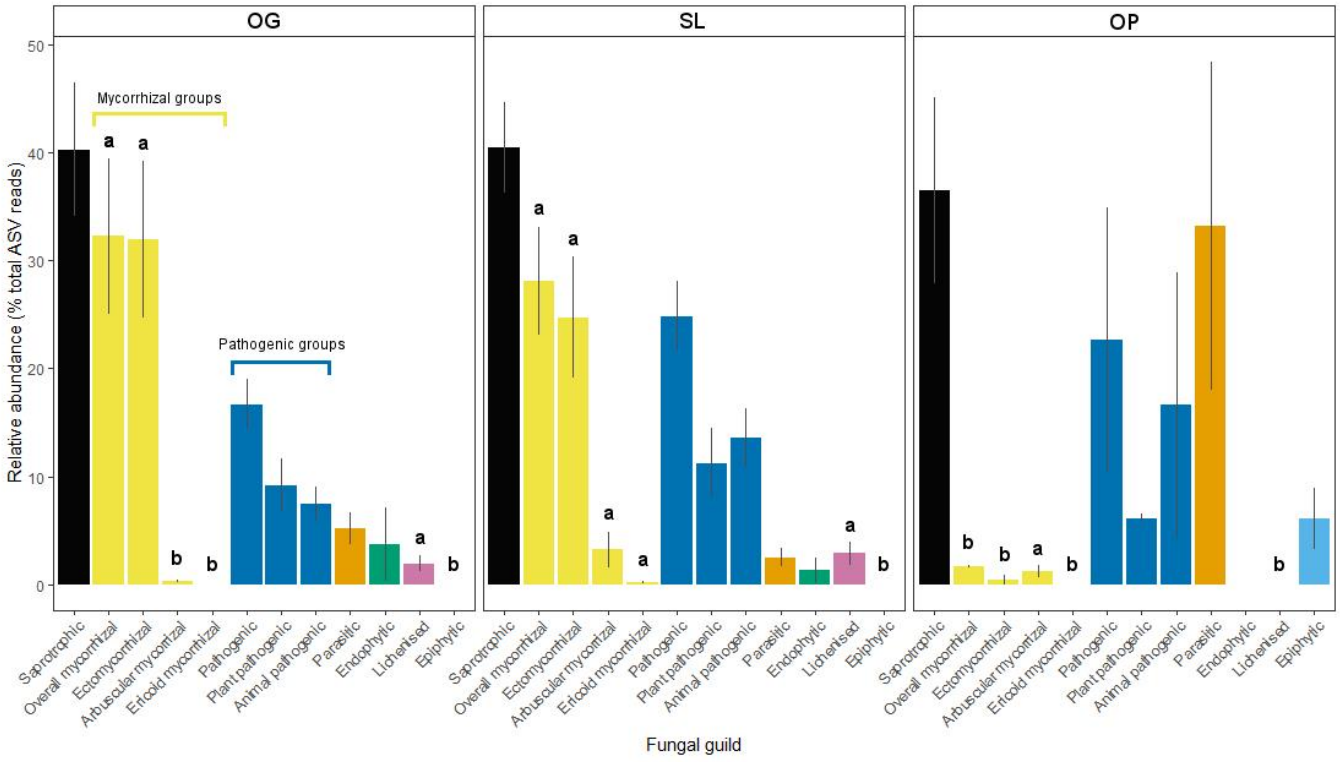

Figure 2.4 *Relative abundances of fungal guilds for old-growth (OG) and selectively logged (SL) forest and oil palm plantation (OP). Error bars represent standard errors. Lower case letters indicate statistically different or similar groups across all three land-use types identified by post-hoc tests after linear mixed modelling or Kruskal-Wallis analysis ($p < 0.05$). Mycorrhizal and pathogenic guilds have been further divided into subtypes as indicated.*

Table 2.2 Mean (± 1 SD) mycelial production (hyphal length) and fungal guild community attributes (Amplicon Sequence Variant (ASV) richness, Shannon alpha diversity and relative abundances) by land-use type for old-growth (OG) and selectively-logged forest (SL), and oil palm plantation (OP). Superscript letters indicate statistically different groups at the $p < 0.05$ level identified in post-hoc tests after linear mixed model analysis.

Parameter	Fungal guild	Land-use type		
		OG	SL	OP
Hyphal length (m g^{-1} of dry sand)	-	2.83 ± 1.79 [a]	2.70 ± 2.02 [a]	0.60 ± 0.32 [b]
Richness	Overall fungal	0.41 ± 0.18	0.42 ± 0.14	0.30 ± 0.17
(No. observed ASVs per 10 reads)	Saprotrophic	2.04 ± 1.17	2.03 ± 0.81	1.90 ± 0.82
	Mycorrhizal	1.01 ± 0.63 [a]	0.97 ± 0.28 [a]	0.31 ± 0.20 [b]
	Pathogenic	1.67 ± 0.62	1.43 ± 0.67	1.14 ± 0.48
Shannon alpha diversity index	Overall fungal	3.78 ± 1.04	4.03 ± 0.34	3.70 ± 0.58
	Saprotrophic	2.58 ± 1.03	2.76 ± 0.59	2.90 ± 0.36
	Mycorrhizal	1.29 ± 0.56	1.38 ± 0.39	0.57 ± 0.52
	Pathogenic	1.74 ± 0.51	1.57 ± 0.65	1.55 ± 0.55
Relative abundance	Saprotrophic	40.27 ± 21.35	40.42 ± 14.42	36.47 ± 14.97
(% total reads)	Mycorrhizal	32.25 ± 24.89 [a]	28.10 ± 17.42 [a]	1.64 ± 0.23 [b]
	Ectomycorrhizal	31.94 ± 25.00 [a]	24.73 ± 19.48 [a]	0.43 ± 0.75 [b]
	Arbuscular mycorrhizal	0.32 ± 0.52 [b]	3.20 ± 5.79 [a]	1.21 ± 0.96 [ab]
	Ericoid mycorrhizal	0.00 ± 0.00 [b]	0.17 ± 0.37 [a]	0.00 ± 0.00 [b]
	Pathogenic	16.64 ± 8.07	24.83 ± 11.16	22.65 ± 21.11
	Plant pathogenic	9.18 ± 8.55	11.22 ± 11.13	6.06 ± 0.78
	Animal pathogenic	7.46 ± 5.50	13.61 ± 9.41	16.59 ± 21.38
	Parasitic	5.20 ± 5.00	2.48 ± 3.01	33.16 ± 26.34
	Endophytic	3.71 ± 11.77	1.27 ± 4.19	0.00 ± 0.00
	Lichenised	1.93 ± 2.54 [a]	2.89 ± 3.78 [a]	0.00 ± 0.00 [b]
	Epiphytic	0.00 ± 0.00 [b]	0.00 ± 0.00 [b]	6.07 ± 4.93 [a]

Table 2.3 Linear mixed model (LMM) test statistics for significant differences in fungal guild relative abundances between land-use types. Summaries are given for overall models and post-hoc comparisons between old-growth (OG) and selectively-logged forest (SL) and oil palm plantation (OP). Significant *p*-values ($p > 0.05$) are highlighted in bold. *p*-values for pairwise tests were adjusted using the Tukey method.

Fungal guild	Overall model			Pairwise tests					
				OG - SL		OG - OP		SL - OP	
	F	R^2	*p*	*t*-ratio	*p*	*t*-ratio	*p*	*t*-ratio	*p*
Total mycorrhizal	14.52	0.53	< **0.0001**	0.42	0.907	5.23	< **0.001**	4.96	< **0.001**
Ectomycorrhizal	14.93	0.53	< **0.0001**	1.12	0.512	5.43	< **0.0001**	4.72	< **0.001**
Arbuscular mycorrhizal	4.86	0.27	**0.017**	-3.06	**0.014**	-1.52	0.301	0.42	0.908
Ericoid mycorrhizal	4.86	0.27	**0.017**	-2.96	**0.018**	0.00	1.000	1.87	0.169
Lichenised	5.34	0.32	**0.027**	0.18	0.983	3.04	**0.027**	2.89	**0.035**

Total pathogenic fungal relative abundance was marginally significantly higher in SL compared to OG when tested without OP samples. The vast majority of mycorrhizal reads were attributed to EcM fungi in forest plots (89.6 %: 98.31 % in OG; 80.90 % in SL), but were mostly AM fungi in OP (69.4 % AM; 30.6 % EcM). Total mycorrhizal and EcM fungal relative abundances were significantly lower in OP compared to forest plots (Fig 2.4). Mean parasitic fungal relative abundance was an order of magnitude higher in OP relative to OG and SL, although no significant differences between land-use types was found due to the considerable variation in OP samples (post-hoc tests: $p > 0.05$). For alpha diversity metrics, only mycorrhizal fungal ASV richness was significantly affected by land-use type ($F = 5.80$, $R^2 = 0.33$, $p = 0.025$; Fig. 2.5 A), with lower values in OP compared to forest plots (OG – OP: $p = 0.028$; SL – OP: $p = 0.018$).

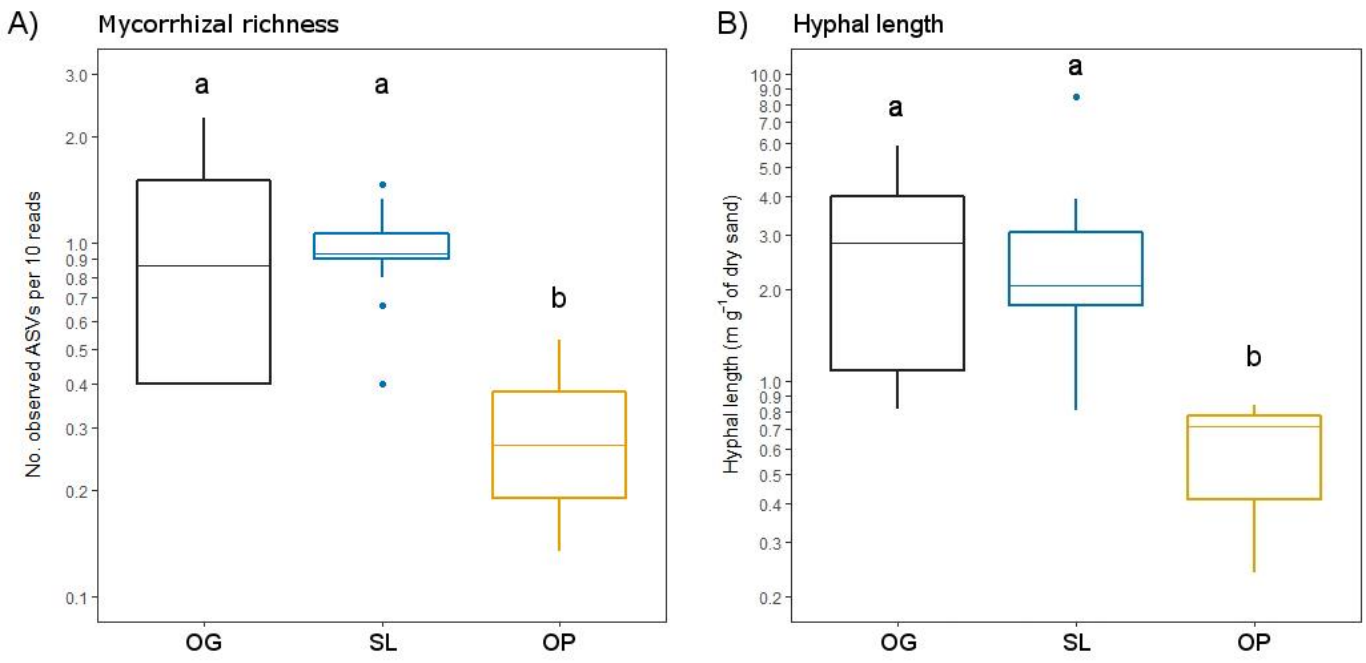

Figure 2.5 *A) Mycorrhizal Amplicon Sequence Variant (ASV) richness and B) mycelial productivity (hyphal length) in old-growth and selectively logged forest and oil palm plantation. Lower case letters indicate statistically different or similar groups across all three land-use types identified by post-hoc tests ($p < 0.05$). Values are shown on a log scale to represent differences corresponding to statistical tests.*

Alpha diversity indices (ASV richness, Shannon index) did not differ between OG and SL for any fungal group (post-hoc tests: $p > 0.05$). Indicator analysis identified certain fungal taxa of the families *Aspergillaceae*, *Sporocadaceae* and *Nectriaceae* to be most indicative of OG forest, while those of *Ophiocordycipitaceae* were characteristic of SL forest and *Nectriaceae*, *Aspergillaceae* and *Ophiocordycipitaceae* characteristic of OP.

Hyphal length values ranged from 0.24 to 8.50 m g^{-1} of dry sand across the disturbance gradient, and were significantly affected by land-use type ($F = 6.50$, $R^2 = 0.33$, $p = 0.006$; Table 2.2; Fig. 2.5 B). Hyphal length values were significantly lower in OP relative to forest land-use types (OP – OG: $p = 0.007$; OP – SL: $p = 0.008$) but did not significantly differ between OG and SL ($p = 0.999$).

Relative to OG, significantly higher values were associated with SL for soil bulk density, altitude and proportion of pioneer species, and lower values for LAI and

canopy, woody and total NPP (means by land-use type summarised in Table 2.4; test statistics for significant differences are reported in Table 2.5).

Table 2.4 Means (± 1 SD) of soil, environmental and vegetation characteristics by land-use type for old-growth (OG) and selectively-logged forest (SL), and oil palm plantation (OP). Superscript letters indicate statistically different groups at the $p < 0.05$ level identified in linear mixed model or Kruskal-Wallis analysis and post-hoc tests. Dashes indicate metrics that were not assessed for characterisation of OP.

Group	Parameter	Land-use type		
		OG	SL	OP
Soil	pH	5.08 ± 0.88	4.15 ± 0.85	5.05 ± 0.76
	Total C (%)	3.88 ± 0.87	5.72 ± 2.86	3.24 ± 1.09
	Total N (%)	0.29 ± 0.08	0.38 ± 0.13	0.27 ± 0.06
	Total P (μg g^{-1})	310.89 ± 115.69 ^{b}	226.52 ± 60.50 ^{b}	1220.36 ± 719.72 ^{a}
	Inorganic P (μg g^{-1})	19.04 ± 8.14 ^{b}	24.26 ± 15.72 ^{b}	374.04 ± 315.77 ^{a}
	C:N ratio	13.71 ± 2.90	14.62 ± 2.34	11.52 ± 1.59
	Sand (%)	23.91 ± 4.21	22.34 ± 7.60	32.00 ± 3.46
	Silt (%)	20.53 ± 3.81 ^{ab}	17.34 ± 6.56 ^{b}	34.34 ± 6.92 ^{a}
	Clay (%)	55.56 ± 5.67 ^{ab}	60.33 ± 9.60 ^{a}	33.66 ± 7.09 ^{b}
	O-layer depth (cm)	3.07 ± 0.34 ^{ab}	4.47 ± 1.29 ^{a}	1.96 ± 1.04 ^{b}
	Soil bulk density (g cm^{3})	0.54 ± 0.11 ^{b}	0.80 ± 0.13 ^{a}	0.99 ± 0.18 ^{a}
	Soil moisture (%)	26.24 ± 4.42	25.05 ± 3.53	24.98 ± 1.36
Environmental	Soil temperature (˚C)	24.57 ± 0.37 ^{ab}	24.21 ± 0.35 ^{b}	25.15 ± 0.06 ^{a}
	Altitude (m)	262.42 ± 34.71 ^{b}	431.58 ± 86.85 ^{a}	326.33 ± 3.51 ^{ab}
	Slope (˚)	19.82 ± 7.59	24.90 ± 8.97	17.60 ± 1.39
Vegetation	Stem density (no. stems DBH ≥ 10 cm per subplot)	18.67 ± 4.92 ^{a}	20.25 ± 8.07 ^{a}	7.00 ± 1.00 ^{b}
	Basal area (m^2 ha^{-1})	26.94 ± 11.23 ^{b}	18.20 ± 8.24 ^{b}	79.10 ± 10.45 ^{a}
	Dipterocarp basal area (m^2 ha^{-1})	1.19 ± 0.72 ^{a}	0.46 ± 0.32 ^{ab}	0.00 ± 0.00 ^{b}
	LAI	4.31 ± 0.22 ^{a}	3.33 ± 0.56 ^{b}	3.10 ± 0.10 ^{b}
	Mean diameter (cm)	23.18 ± 3.41 ^{b}	20.15 ± 2.63 ^{b}	75.50 ± 0.69 ^{a}
	Max diameter (cm)	60.44 ± 21.34 ^{ab}	42.48 ± 11.86 ^{b}	86.93 ± 4.67 ^{a}
	Proportion of pioneer species (% total basal area)	0.02 ± 0.08 ^{b}	0.31 ± 0.29 ^{a}	-
	Canopy NPP (Mg C ha-1 year-1)	6.19 ± 1.78 ^{a}	3.79 ± 0.73 ^{b}	-
	Woody NPP (Mg C ha-1 year-1)	4.40 ± 2.16 ^{b}	12.92 ± 6.65 ^{a}	-
	Root NPP (Mg C ha-1 year-1)	1.14 ± 0.46 ^{ab}	2.44 ± 1.77 ^{a}	0.73 ± 0.22 ^{b}
	Total NPP (Mg C ha-1 year-1)	11.31 ± 2.45 ^{b}	19.15 ± 7.12 ^{a}	-

Table 2.5 Linear mixed model (LMM) or Kruskal-Wallis* test statistics for significant differences in soil, environmental and vegetation characteristics between land-use types. Summaries are given for overall models and post-hoc comparisons between old-growth (OG) and selectively-logged forest (SL) and oil palm plantation (OP). Significant *p*-values ($p > 0.05$) are highlighted in bold. *p*-values for pairwise tests were adjusted using the Tukey method for LMMs and Bonferroni method for Dunn tests*. Post-hoc tests were only conducted for variables that were measured across all three land-use types.

Group	Parameter	Overall model			Pairwise tests					
					PF - LF		PF - OP		LF - OP	
		F / $\chi 2$*	R^2	p	t-ratio / z-test*	p	t-ratio / z-test*	p	t-ratio / z-test*	p
Soil	Total P	16.73	0.61	**0.002**	1.15	0.514	-4.56	**0.004**	-5.59	**0.001**
	Inorganic P	23.88	0.67	**0.000**	-0.63	0.809	-6.55	**0.000**	-6.04	**0.000**
	Silt	5.12	0.34	**0.033**	1.12	0.530	-2.22	0.115	-3.19	**0.024**
	Clay*	6.41	-	**0.041**	0.64	1.000	-1.88	0.182	2.47	**0.041**
	O-layer depth*	6.96	-	**0.031**	1.39	0.497	-1.35	0.532	2.63	**0.025**
	Soil bulk density	11.43	0.58	**0.004**	-3.17	**0.041**	-4.58	**0.003**	-1.92	0.186
Environmental	Soil temperature	6.75	0.41	**0.015**	1.66	0.278	-2.28	0.101	-3.67	**0.009**
	Altitude*	8.91		**0.012**	2.98	**0.009**	1.38	0.501	1.38	0.501
Vegetation	Stem density	8.33	0.39	**0.002**	-0.08	0.996	3.85	**0.002**	3.90	**0.002**
	Basal area	10.46	0.47	**0.003**	1.55	0.322	-3.40	**0.010**	-4.57	**0.001**
	Dipterocarp basal area*	5.89	-	0.053	-1.04	0.900	-2.42	**0.046**	1.46	0.429
	LAI	13.76	0.59	**0.001**	4.57	**0.006**	4.06	**0.002**	0.74	0.741
	Mean diameter	105.12	0.90	**0.000**	1.86	0.214	-12.52	**<.0001**	-13.97	**<.0001**
	Max diameter	5.46	0.35	**0.024**	1.79	0.235	-1.84	0.195	-3.26	**0.016**
	Proportion of pioneer species*	4.29	-	**0.038**	-	-	-	-	-	-
	Canopy NPP	11.73	0.48	**0.014**	-	-	-	-	-	-
	Woody NPP	20.51	0.49	**0.004**	-	-	-	-	-	-
	Root NPP	4.83	0.36	**0.034**	-2.21	0.134	1.11	0.525	2.89	**0.033**
	Total NPP	9.51	0.41	**0.022**	-	-	-	-	-	-

Root NPP, soil clay content and organic layer depth in OP were significantly lower relative to SL, while soil silt content was significantly higher. OP soil bulk density was significantly higher relative to OG. Total and inorganic soil P were an order of magnitude higher in OP relative to both OG and SL. While stem density was

significantly lower in OP relative to forest land-uses, basal area and mean stem diameter were significantly higher. Maximum stem diameter was also higher in OP relative to SL, however, all belong to the same species of oil palm. Plot-level tree community dissimilarity significantly differed between OG and SL (PERMANOVA: $F = 1.43$, $R^2 = 0.19$, $p = 0.028$; betadisper: $p > 0.05$).

2.4.2 Relationships between forest mycelial fungal community attributes, soil, environmental and vegetation characteristics and mycelial production

Overall, saprotrophic, mycorrhizal and pathogenic fungal community dissimilarities were significantly related to soil and vegetation characteristics, although overall variance explained was low for each group (see Table 2.6 for summary of statistics).

Table 2.6 Best soil, environmental and vegetation characteristics as predictors of fungal group dissimilarities in forests plots, identified by forward selection (adjusted R^2 and $p > 0.05$) in distance-based redundancy analysis (db-RDA). Variation in fungal community dissimilarities (adjusted R^2) is partitioned by soil/environmental and vegetation components. Significance of individual predictors and components were tested using partial db-RDA.

Group	**Predictor**	***F***	***p***	**Soil/env properties**			**Vegetation properties**			**Soil/env + vegetation properties**	**Overall model**
				F	***p***	R^2_{adj}	***F***	***p***	R^2_{adj}	R^2_{adj}	R^2_{adj}
Overall fungal	pH	1.68	0.009	1.68	0.009	0.03	1.61	0.021	0.03	0.00	0.05
	LAI	1.61	0.021								
Saprotrophic	Inorganic P	1.55	0.012	1.55	0.012	0.02	-	-	0.00	0.00	0.02
Mycorrhizal	pH	1.85	0.002	1.85	0.002	0.04	1.61	0.020	0.03	0.00	0.06
	Dipterocarp basal area	1.61	0.020								
Pathogenic	pH	1.96	0.006	2.04	0.002	0.08	1.93	0.000	0.07	0.00	0.16
	Tree comm. axis 2	1.97	0.012								
	Basal area	1.85	0.002								
	Inorganic P	1.85	0.002								

The best predictors selected for overall fungal community dissimilarity were soil pH and LAI. Of these, soil pH was negatively related to relative abundance of animal pathogenic fungi (F = 8.63, R^2 = 0.27, p = 0.008), while LAI was negatively related to relative abundance of AM fungi (F = 8.04, R^2 = 0.28, p = 0.015). The only predictor selected for saprotrophic community dissimilarity was soil inorganic P, while the best predictors for mycorrhizal fungal community dissimilarity were pH and dipterocarp basal area. Soil pH, tree community PCoA axis 2, tree basal area and soil inorganic P were all identified as predictors of pathogenic fungal community dissimilarity. Plot-level tree community dissimilarity was significantly related to plot-level community dissimilarity of mycorrhizal fungi (r = 0.55, p = 0.015; Fig. 2.6), but no other fungal group (p > 0.05).

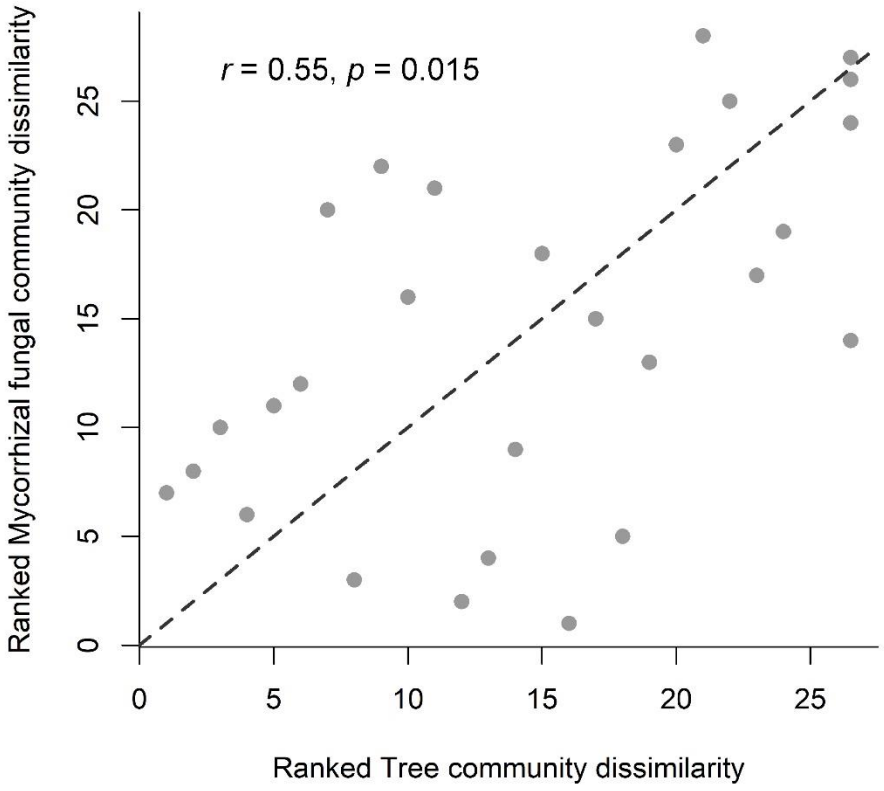

Figure 2.6 *Relationship between ranked tree and mycorrhizal community dissimilarities. Statistics were provided by Mantel test with Spearman's rank correlation. The r-value represents the Mantel coefficient, and significance level was calculated using 9,999 permutations.*

Dipterocarp and mycorrhizal fungal community dissimilarities were not significantly related at the plot-level ($p > 0.05$).

Hyphal length was not significantly associated to any mycelial fungal community attributes (H3), although a negative relationship with EcM fungal relative abundance was marginally significant ($F = 3.57$, $R^2 = 0.13$, $p = 0.072$). There was no significant link between hyphal length and any of the vegetation properties measured (H2), including tree productivity metrics, but was significantly positively related to soil inorganic P ($F = 5.25$, $R^2 = 0.19$, $p = 0.032$; Fig. 2.7).

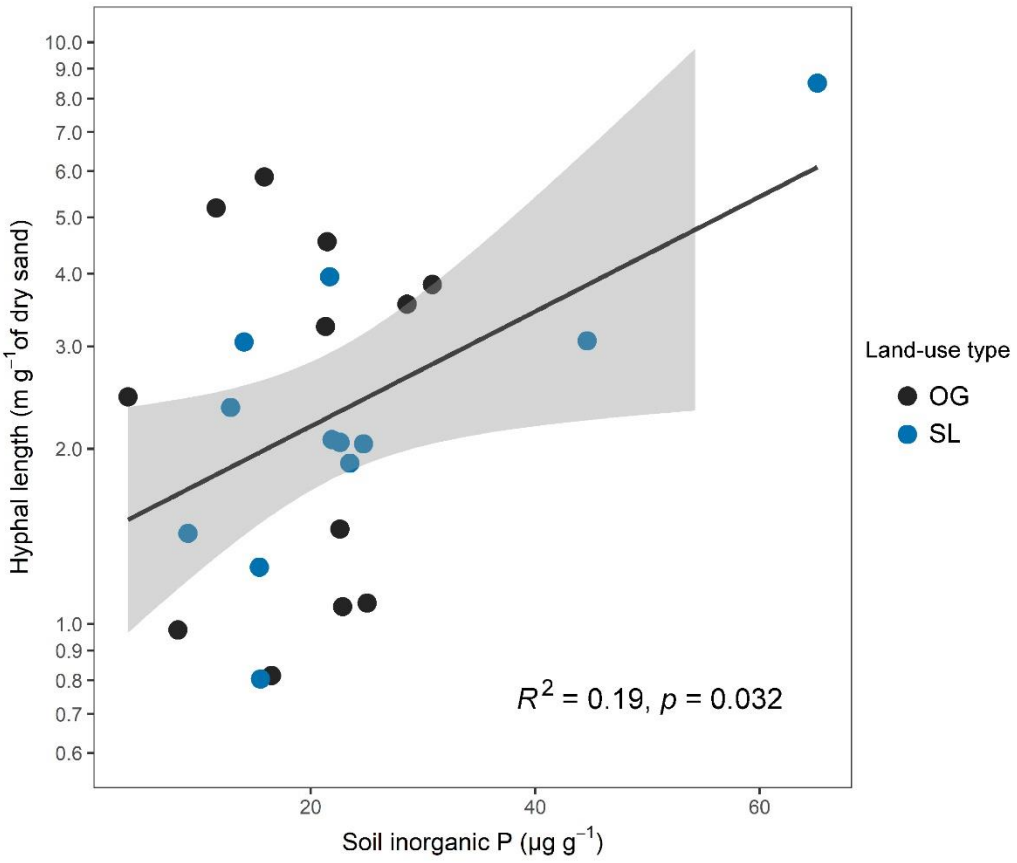

Figure 2.7 *Relationship between mycelial production (hyphal length) and soil inorganic P concentrations across old-growth (OG) and selectively logged (SL) forest. Hyphal length values are shown on a log scale corresponding to statistical tests. This relationship was found to be non-significant when the data point with high values in both parameters (top-right) was excluded from analysis ($F = 0.83$, $R^2 = 0.04$, $p = 0.371$).*

However, the association between hyphal length and soil inorganic P was primarily driven by one sampling point in SL forest with high values in both parameters (Fig. 2.7), and was found to be non-significant when this data point was excluded from analysis ($F = 0.83$, $R^2 = 0.04$, $p = 0.371$).

2.5 Discussion

No significant shifts were found in community structure of any mycelial fungal group between OG and SL forest (Fig. 2.3), despite clear differences in soil and vegetation properties (higher soil bulk density, proportion of pioneer trees, woody and total NPP, and lower LAI and canopy NPP in logged forest) and plot-level tree community composition, broadly in line with previous findings from these study sites (Elias et al., 2019; Both et al., 2019; Riutta et al., 2018). This finding contrasts our hypothesis (H1) and recent surveys which found the compositions of bulk soil fungal communities in tropical Southeast Asian dipterocarp forest to be highly sensitive to logging (McGuire et al., 2015; Kerfahi et al., 2014). Our results suggest that actively foraging fungi may be more resilient to disturbance than the wider fungal community in bulk soil. However, direct comparability with other studies may be affected by methodological differences in sampling related to community capture rates (i.e. micro-environmental conditions inside in-growth bags potentially selecting for certain fungal species (Ekblad et al., 2013; Wallander et al., 2001). It should also be highlighted that the in-growth bag method recovers only active hyphae, therefore avoiding confounding effects of relic DNA on soil microbial community patterns that can be a concern in studies across environmental gradients (Lennon et al., 2018). The total number of ASVs detected was lower than found in other recent ITS amplicon sequencing studies of bulk soil fungal communities in the region, which may exceed 25,000 (Elias, unpublished data), which

we similarly attribute to these reasons. Differences were identified in other mycelial fungal attributes between OG and SL forest, including a significant increase in the relative abundances of AM and ErM fungi in SL forest. The vast majority of forest mycorrhizal reads comprised EcM fungi (Fig 2.4). The canopy of lowland rainforests of Borneo is typically dominated by species belonging to the Dipterocarpaceae, which are an EcM-associating family (Brearley, 2012; Taylor and Alexander, 2005). Although our finding may relate to presence of host tree species, high EcM relative to AM fungal relative abundance may also result from amplification bias associated with ITS primers (Hart et al., 2015). Although mean dipterocarp basal area (Table 2.4) and relative abundance of EcM fungi (Table 2.2; Fig. 2.4) were lower in SL forest, no significant differences were detected in either metric due to the high variability in both. Nevertheless, the relative increase in abundances of AM and ErM fungi in SL forest (the only other mycorrhizal types identified; Fig. 2.4) is considered to indicate increasing evenness in mycorrhizal types and diminished dominance of EcM reflecting differences in vegetation indicated by the increased proportion of non-dipterocarp pioneer species in SL forest, which typically form arbuscular mycorrhizas (McGuire et al., 2008). This shift may have implications for nutrient and C cycling, as recent correlative studies have suggested EcM- rather than AM-dominated communities may promote soil C storage on a global scale (Averill et al., 2014) through their ability to access N and P (Liu et al., 2018) from organic sources, potentially competing with free-living soil decomposers requiring N for the breakdown of organic matter (Averill et al., 2014). An increase in relative abundances of AM fungi may, therefore, have implications for the release of C from the soil as N becomes more available for soil saprotrophs. Alterations in soil C-cycling processes in SL dipterocarp forest have been observed, although as litter decomposition has been found to be slowed in logged forest

due to subtle changes in forest microclimatic conditions (Both et al., 2017), the overall consequences for biogeochemical cycling and ecosystem functions are unclear. Alpha diversity itself (ASV richness and Shannon index) did not statistically differ between OG and SL forest for any fungal group.

Overall fungal community structure within in-growth bags was significantly different between OP plantation and OG and SL forests, and the impact of OP as a driver of differences over land-use types for saprotrophic, mycorrhizal and pathogenic mycelial fungal communities were also observed (Fig. 2.3), which corroborates the dramatic effects of forest conversion on bulk soil fungal communities (McGuire et al., 2015). Mycorrhizal alpha diversity was also strongly affected, with much lower values in oil palm relative to forest plots. As no differences were found between OG and SL forest, overall mycelial fungal communities appear to follow a similar pattern to soil bacterial communities, which have been shown to be generally unaffected by logging but distinctly different in oil palm plantation (Lee-Cruz et al., 2013; Tripathi et al., 2016).

In contrast to expectations (H1), mycelial production did not significantly differ between OG and SL forest, but was significantly lower in OP relative to both forest land-use types (Fig. 2.5 B). Hyphal length was also not found to correspond to the differences observed in mycelial community attributes, soil properties and vegetation community between SL and OG, which may reflect the resilience of some soil functions to selective logging (e.g. enzyme activity; McGuire et al., 2015). The variation within both OG and SL forest was considerable and of a comparable magnitude (Table 2.2; Fig. 2.5 B), suggesting that variation in soil, environmental and vegetation characteristics not directly associated with logging are responsible for the variation in

hyphal length in these forests. The resilience of both mycelial production and relative abundance of mycelial EcM fungi to selective logging implies the extramatrical EcM mycelium may be largely retained in SL forest, when individuals of EcM-associating species remain present. Mycorrhizal mycelial networks are crucial for tree seedling establishment (Nara, 2006), and may facilitate interplant exchange of resources with trees sharing the same mycorrhizal partnerships (Gorzelak et al., 2015). Our findings indicate implications for the potential restoration of these degraded forests, as EcM mycelial networks vital for supporting dipterocarp recruitment and survival may remain even after individuals of this family have been removed. Although basal area was significantly highest in OP, significantly lower mean root NPP was found in OP relative to SL. There was also a complete removal of dipterocarp species through forest conversion to agricultural plantation. Furthermore, although canopy NPP was not measured in the OP site, significantly lower soil organic layer depth (Table 2.4) may indicate reduced litter inputs – especially as dead palm fronds are typically removed and collected in localised areas as standard in OP. This suggests a combination of a lack of EcM fungi, due to replacement of by AM-associating oil palm species (Phosri et al., 2010), diminished belowground allocation of C by trees and reduced organic matter inputs may be down-regulating mycelial production rates in this land-use type. This is despite a ten-fold increase in the availability of limiting nutrients (inorganic P; Table 2.4) in OP due to the use of fertiliser. As the OP plantation was established after the selective-logging of these forests, lower hyphal length values, mycorrhizal abundance and richness appears to result from magnitude of EcM host removal rather than time since disturbance. The significant reduction in the soil (mycorrhizal) mycelium through the extreme disturbance of agricultural forest conversion represents a substantial barrier to the restoration of these systems.

Across OG and SL forest, mycelial fungal community attributes significantly varied with vegetation and soil properties (H2), but did not correspond with mycelial production (H3). Soil microbial community assemblage, particularly fungi, have been shown to correlate with aboveground plant taxonomic and phylogenetic structure in addition to local soil properties (Barberán et al., 2015). Soil pH was a significant predictor of community composition for all fungal groups, particularly important for mycorrhizal and pathogenic fungi, a pattern observed across large scales in temperate ecosystems (Dupont et al., 2016). Mycorrhizal community structure was surprisingly not affected by relative proportion of soil sand or clay content (although silt content was weakly related), previously found to be a strong predictor of EcM communities in Bornean lowland dipterocarp rainforest (Essene et al., 2017); a possible result of sand used inside in-growth bags masking the influence of soil texture. Tree and mycorrhizal community structure were significantly correlated at the plot-level (Fig. 2.6), likely driven by the significant relationship between mycorrhizal fungal community dissimilarity and total dipterocarp basal area (Table 2.6). Previous studies in Bornean lowland dipterocarp rainforest have shown EcM communities to be related to dipterocarp species assemblage in addition to strong effects of soil properties, suggesting dipterocarp species distributions across different soil types to be mediated by assemblage of their mycorrhizal partners (Essene et al., 2017). However, no significant correlation was found between mycorrhizal fungal and dipterocarp community dissimilarities, indicating overall abundance rather than composition of dipterocarps is more important in structuring actively foraging mycorrhizal fungal communities in the present study.

Mycelial productivity was significantly positively related to soil inorganic P (Fig. 2.7). Although mycelial biomass has previously been shown to be greater in more

P-deficient forests (Potila et al., 2009), the proliferation of mycorrhizal hyphae into nutrient 'hotspots' is a mechanism observed both in laboratory experiments and natural systems (Ekblad et al., 2013), whilst the role of inorganic P in controlling rates of mycelial production has been demonstrated in forests using hyphal in-growth bags augmented with mineral P, and field manipulations using fertiliser applications (Hagerberg et al., 2003; Ekblad et al., 2013; Potila et al., 2009; Camenzind et al., 2016). The positive relationship found in the present study may therefore represent greater mycelial production in localised areas with higher inorganic P concentrations in an otherwise P-limited ecosystem. This suggests that variation in mycelial production in tropical forest may be primarily driven by local inorganic P availability, largely independent of vegetation characteristics, productivity and associated mycelial community attributes. However, the significant relationship between mycelial production and soil inorganic P was found to be mainly dependent on one sampling point in SL with high values in both parameters (Fig. 2.7), which limits the strength of interpretation. It is recommended that future studies consider higher spatial resolution soil sampling and incorporate larger mineral P gradients to confirm this mechanism.

The in-growth bag method has been found to adequately represent mycorrhizal mycelial productivity, as reflected by $\delta^{13}C$ (Wallander et al., 2001) and molecular (Kjøller, 2006) analyses of bags in EcM-dominated systems. However, our results indicate that this may not be the case in tropical forest, with the largest proportion of overall reads belonging to ASVs identified as saprotrophs. As such, hyphae measured cannot be directly attributable to one fungal group or mycorrhizal type in this study. To clarify productivity and turnover rates specifically relating to mycorrhizal fungal types, future studies may incorporate molecular or biomarker analyses, or include additional measures to reduce saprotrophic mycelial production (Wallander et al., 2013). A high

level of variability was found in mycelial fungal community dissimilarities across forest plots. Our analysis focused on the topsoil, as this is where the vast majority of nutrient turnover occurs. Here, fine-scale environmental heterogeneity can drive greater spatio-temporal fungal community variation compared to underlying mineral soil where communities may differ (Bahram et al., 2015). It is recommended that future studies consider the effects of forest degradation on mycelial fungal communities and productivity at different soil depths, which may identify different patterns along the soil profile. It is acknowledged that care must be taken in the interpretation of differences found between forest land-uses and OP due to differences in sampling in the OP site (i.e. spatial scale and number of replicates). However, as lower replication would be expected to increase statistical error in OP, significant differences found in this land-use type are expected to be consistent with broad-scale patterns.

In conclusion, selective logging did not significantly shift mycelial fungal community structure or productivity from OG forest, suggesting mycelial fungal communities and function may be relatively resilient to forest degradation compared to fungi in bulk soil. Results indicate the extramatrical EcM mycelium to be largely retained in selectively logged forest, with positive implications for potential restoration of dipterocarp forest by providing existing mycorrhizal networks for tree seedling establishment. However, SL forest was associated with higher relative abundances of AM and ErM fungi relative to OG, which may have consequences for soil C cycling and storage in lowland rainforests in Borneo. Mycelial production was not related to vegetation characteristics or NPP, but to higher soil inorganic P concentrations associated with topography; suggesting that (belowground) productivity is driven by availability of limiting nutrients in tropical forest. In contrast, land conversion to oil palm plantation was shown to have a significant effect on overall, saprotrophic,

mycorrhizal, and pathogenic mycelial fungal community structures, reducing mycorrhizal relative abundance and diversity. Mycelial production was significantly lower in oil palm relative to forest, despite soil inorganic P concentrations being an order of magnitude greater under this land-use type. The impact of forest conversion on fungal community attributes and mycelial productivity may have wide repercussions for nutrient dynamics, plant-soil interactions and restoration potential over large scales as oil palm plantation has rapidly become a major land-use across Southeast Asia.

3 Impacts of logging gaps on soil microbial community attributes and nutrient cycling

3.1 Abstract

The rainforests of Borneo are a globally important biodiversity hotspot and carbon (C) sink, and are under increasing pressure by rapid land-use change. Conversion to industrial plantation has reduced forest cover on Borneo by >30 % in recent decades, while the majority of remaining forest is degraded through selective logging. Here timber extraction results in canopy gaps, which can alter microclimate, vegetation and soil properties, and significantly affect biogeochemical cycles underpinned by soil microbial communities. Understanding of soil microbial responses to environmental heterogeneity caused by selective logging gaps (SLG) in Southeast Asian tropical rainforest remains limited. To address this, a survey of soil microbial communities, soil physicochemical properties, nutrient supply rates and microclimate was conducted across logged forest in closed canopy forest (CCF) and SLG with varying disturbance intensities. Bacterial and fungal communities were characterised using 16S and ITS amplicon sequencing. Results showed that soil pH, bulk density and maximum soil moisture were significantly higher in SLG. Nitrate (NO_3^-) supply rates and inorganic phosphorus (P) pools were lower in SLG, indicating reduced nutrient cycling. Bacterial and fungal community structures were significantly affected by SLG, with lower relative abundances of total mycorrhizal and EcM fungi, and higher relative abundance of AM fungi compared to CCF. In SLG, disturbance intensity was strongly positively related to ammonium (NH_4^+) supply rates, and negatively to total mycorrhizal and EcM relative abundances. Findings suggest nitrogen (N) mineralisation may be enhanced by reduced competition for organic N sources between EcM fungi and saprotrophs with changes in mycorrhizal types affecting ecosystem C and nutrient cycling. Overall

findings demonstrate impacts of SLG on key soil microbial groups that regulate crucial nutrient and C cycles, with the potential to alter biogeochemical functioning at the landscape scale. Evaluations of impacts of forest degradation and forest restoration potential should incorporate SLG effects on belowground communities and function.

3.2 Introduction

The tropical forests of Borneo are a global biodiversity hotspot (Myers et al., 2000), storing vast amounts of carbon (C) through a complex network of plant-soil interactions (Qie et al., 2017). These forests are under pressure from rapid degradation due to commercial timber extraction and widespread conversion to plantation agriculture (Gaveau et al., 2014; Gaveau et al., 2016; Bryan et al., 2013; Ferraz et al., 2018), with fragmentation and degradation threatening its capacity as a carbon sink (Qie et al., 2017; Asner et al., 2018). More than 30 % of the original forest cover on Borneo has been lost since these land-use practices began in the early 1970's. Very little of the forest remains undisturbed, with approximately 70 % affected by selective logging for commercially valuable species of the Dipterocarpaceae (Gaveau et al., 2014; Gaveau et al., 2016). The removal of large individual trees and clearance for landings and skid trails opens gaps in the forest canopy (selective logging gaps; SLG). As a result, the vast majority of remaining forest is a human-modified, heterogeneous mosaic comprising a mixture of selectively logged (SL) closed-canopy forest (CCF) and SLG at various stages of regeneration (Ellis et al., 2016; Bossel and Krieger, 1991).

Naturally occurring canopy gaps play an essential role in forest regeneration and maintenance of structural complexity, biodiversity and heterogeneity of soil and environmental conditions that influence nutrient availability and biogeochemical cycling (Muscolo et al., 2014). The artificial creation of canopy gaps mimicking natural disturbances (i.e. treefall) for forest regeneration is now practiced in silviculture for sustainable forest management and conservation across multiple biomes (Zhu et al., 2014; Muscolo et al., 2017). However, intensive gap creation by SL in tropical forest can have negative consequences, including increasing susceptibility to fire (Matricardi et al., 2013; Cochrane, 2001) and long-lasting impacts on vegetation population

dynamics and diversity that can persist for over half a century post-disturbance (Yamada et al., 2013; Xu et al., 2015).

Canopy gaps can drastically alter microclimatic conditions, as increased solar radiation reaching the forest understorey affects air and soil temperatures (Marthews et al., 2008), while soil moisture regimes are also affected by increased rainfall reaching the ground and reduced plant transpiration (Scharenbroch and Bockheim, 2007; Zhu et al., 2003; Zirlewagen and Von Wilpert, 2001). In tropical forests, canopy gaps are generally associated with wetter soil conditions (Denslow et al., 1998; Saner et al., 2009; Ostertag, 1998), although this remains contested and soil moisture and temperature dynamics may be dependent on disturbance intensity (gap size) determining relative effects of root water extraction and soil surface evaporation (Marthews et al., 2008). Changes in microclimate along with altered plant productivity and inputs, including reduced litterfall (Saner et al., 2009; Lin et al., 2015), have knock-on effects for local soil characteristics and biogeochemical cycling (Scharenbroch and Bockheim, 2008a). Gaps may function as nutrient-cycling 'hotspots' (Schliemann and Bockheim, 2011), with studies observing greater organic matter decomposition (Lin et al., 2015), net mineralisation and nitrification rates (Ritter, 2005; Denslow et al., 1998), altering soil nutrient bioavailability through increasing labile inorganic phosphorus (P) fractions and total nitrogen (N) pools (Hu et al., 2016; Scharenbroch and Bockheim, 2008b). However, disturbance intensity and gap age may determine the extent and direction of these processes (Ritter, 2005; Denslow et al., 1998; Muscolo et al., 2007a). Increased rainfall reaching the topsoil has also been found to cause erosion and leaching, reducing overall soil fertility in gaps (Arunachalam and Arunachalam, 2000). Soil compaction in landings and skid trails through use of heavy machinery for timber extraction is another major disturbance associated with selective logging (Hartmann et

al., 2013; Grigal, 2000; Marshall, 2000; Alexander, 2012; Malmer and Grip, 1990). Along with removal of organic matter, these disturbances can have significant consequences for soil microbial communities and function (Hartmann et al., 2012).

Forest biogeochemical cycling is driven by complex plant-soil interactions and reciprocal feedbacks between aboveground vegetation and belowground soil microbial communities (Cortois et al., 2016; van Der Putten et al., 2013; Bever et al., 2010; van der Heijden et al., 2008; Wardle et al., 2004). Microbial communities in turn are sensitive to alterations in soil physiochemical properties associated with land-use change (Tripathi et al., 2012; Jesus et al., 2009). Despite this, most studies have focussed on aboveground community dynamics and processes in gaps (see Muscolo et al., 2014), and few have evaluated belowground patterns in soil microbial diversity that underpins ecosystem functioning (Yang et al., 2017b; Li et al., 2019). The impacts of canopy gaps on soil microbial communities are complex and not necessarily unidirectional. Attributes such as total, bacterial and fungal microbial biomass have been found to be lower in gaps relative to closed canopy forest due to reduced litter inputs and root densities (Arunachalam and Arunachalam, 2000; Schliemann and Bockheim, 2014). Other studies detected no differences (Luizão et al., 1998), or observed greater microbial biomass in small gaps (Muscolo et al., 2007a; Yang et al., 2017b) that may decrease again with increasing gap size (Muscolo et al., 2007a; b; Muscolo et al., 2010; Yang et al., 2017b). Biomass of certain microbial groups may also be differentially affected, e.g. bacteria favoured over fungi with increasing disturbance intensity (Arunachalam and Arunachalam, 2000), and microbial community structure, diversity and activity can be shifted, varying according to gap size along with soil conditions (Yang et al., 2017a; Yang et al., 2017b; Xuan et al., 2018; Li et al., 2019).

A small number of recent studies have evaluated the effects of selective logging in tropical forest in Southeast Asia on soil microbial community structure, diversity (Tripathi et al., 2016; Lee-Cruz et al., 2013; Kerfahi et al., 2014; Elias et al., 2019; McGuire et al., 2015) and function (Chapter 1). Fungal community attributes, particularly ectomycorrhizal (EcM) fungal relative abundance and diversity, have been shown to be highly sensitive to logging disturbance (Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015). Bacteria and protists appear to be more resilient (Tripathi et al., 2016; Lee-Cruz et al., 2013) through a strong association with soil properties often independent of land-use type (Tripathi et al., 2012). However, studies conducted so far have largely assessed impacts via comparison of selectively logged forest with old-growth forest and/or agricultural plantation relying on broad land-use classifications. SLGs have the potential to greatly alter soil microbial communities and function underpinning vital biogeochemical cycles, although impacts in Southeast Asian rainforest remain unclear. This represents a significant knowledge gap, requiring finer-scale studies to improve understanding and predictions of effects of environmental heterogeneity associated with logging disturbance. There is an urgent need to improve current understanding as the vast majority of forest on Borneo is now heavily modified as a result of SL. The aim of this study was to evaluate the impacts of SLGs on soil microbial community attributes and nutrient cycling in Bornean lowland dipterocarp rainforest, with the following specific hypotheses:

H1. Soil physicochemical properties and nutrient cycling rates will differ between CCF and SLG, corresponding to differences in environmental and vegetation characteristics.

H2. Soil bacterial community attributes (community composition and alpha diversity) will not differ between CCF and SLG when controlling for effects associated with site.

H3. Soil fungal community attributes (community composition, functional composition and alpha diversity) will differ between CCF and SLG.

H4. Within SLG, soil fungal community attributes, soil properties and nutrient cycling rates will be related to disturbance intensity.

3.3 Methods

3.3.1 Study site

This study was conducted in selectively logged lowland dipterocarp rainforest in the state of Sabah, northern Malaysian Borneo. The climate is characterised as moist tropical (average daily temperature 27 ˚C, annual precipitation 2,600 - 2,700 mm) and without distinct seasonality, although may experience irregular inter-annual dry periods with an average total of ~1.4 months per year.(Walsh and Newbery, 1999; Kumagai and Porporato, 2012). Sampling was carried out in November 2016 within two existing 1 ha research plots within the Kalabakan Forest Reserve (B South 4.732°, 117.619° and B North 4.739°, 117.617°; coded as SAF-01 and SAF-02 respectively in the ForestPlots database), situated within the large-scale forest fragmentation study Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al., 2011). These plots (hereafter referred to as sites) were previously established for long-term evaluation of forest carbon cycling and productivity as part of the Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/; Malhi et al., 2015; Riutta et al., 2018). The two sites chosen for study had similar land-use histories of heavy logging, both having been selectively logged four times: firstly in the mid-1970s (approximately 113 m^3 ha^{-1}

timber removed) followed by three subsequent rounds 1990-2008 (approximately 37-66 m^3 ha^{-1} cumulative timber removed) (Riutta et al., 2018; Fisher et al., 2011).

3.3.2 Sampling design

SLG in the two sites were not discrete, but formed a mostly contiguous matrix with varying degrees of canopy openness. Twelve 6 × 6 m plots were distributed equally across both sites (six plots in each). Within each site, three plots were established in SLG and three in CCF vegetation types in co-located pairs (< 50 m between each SLG and CCF pair). Plot size was chosen relative to the widths of SLGs studied, to avoid close proximity to edge of CCF. Widths of SLGs at narrowest points ranged from approximately 12 - 30 m, estimated from aerial images taken at the time of sampling by drone survey (Cheerson CX-20 Auto-Pathfinder fitted with Apeman Action Camera). Each plot was subdivided into nine 2 × 2 m subplots, and six of these were randomly chosen for sampling of soil physicochemical properties, soil nutrient supply rates, and environmental and vegetation characteristics, with subplot centre marked as the sampling point.

3.3.3 Soil sampling and physicochemical analysis

Three 10 cm depth soil cores were taken around each sampling point using a 3 cm-diameter gouge auger. The depth of the organic soil layer was measured before it was separated from underlying mineral soil and collected. Soil samples were bulked per subplot (n = 6 composite samples per plot), sealed in Ziploc bags and transported to a field laboratory. Each composite sample was hand-homogenised and 10 g subsamples taken for analysis of soil microbial community attributes. These were frozen at -20 ˚C on the day of collection and transported on ice to the UK: 5 g was transported to Centre for Ecology & Hydrology, Wallingford, UK for amplicon sequencing of soil microbial

communities; 5 g was analysed at Lancaster University for total soil microbial biomass C (MBC) and N (MBN). The remaining soil was transported to the Sabah Forest Research Centre, Sepilok for physicochemical analysis. One additional soil sample was taken at three randomly selected sampling points per plot with a volumetric core (3.8 cm diameter, 8 cm depth) to calculate soil bulk density.

pH in water was measured on fresh soils using a pH meter with a combination glass-calomel electrode (a ratio of 1:2.5 soil to deionised water) after shaking overnight at 100 rev m^{-1} on an orbital shaker and standing for 30 min (Landon 1984). The remaining soils were air-dried at 40 °C to constant weight and passed through a 2 mm sieve for homogenisation and removal of roots and stones. Subsamples for Total C and N analysis were dried at 65 °C for 48 hours and milled to a fine powder with a pestle and mortar. Total soil C and N contents were determined by dry combustion at 900 °C using an Elementar Vario Max CN analyser (Elementar Analysensysteme, Hanau, Germany). For soil Total P, samples were digested using sulphuric acid-hydrogen peroxide (Allen, 1989). Inorganic P was extracted using a Bray No. 1 extractant (Bray and Kurtz, 1945). P contents of extracts and digests were determined using the molybdenum-blue method (Anderson and Ingram, 1993), read at 880 nm on a spectrophotometer (HITACHI-UV-VIS, Japan). Soil texture (% Sand, Silt and Clay) was determined using the particle size distribution test (Day, 1965) on one bulked sample per plot (n = 12). Bulk density was calculated from the volume of the core and soil weight after drying at 105 °C for 48 hours and removal of roots and stones (Emmett et al., 2008) to provide one average value per plot (n = 12).

MBC and MBN were determined using a modified chloroform fumigation extraction method (Vance et al., 1987; Brookes et al., 1985). Briefly, microbial biomass

subsamples were passed through a 2 mm sieve to remove roots and stones. For each sampling point, two 2.5 g fresh weight soil were measured into separate 50 ml sample tubes. 12.5 ml 0.5M K_2SO_4 extractant was added to each sample tube (first adjusted to pH-neutral with NaOH) and gently hand shaken. 0.25 ml EtOH-free chloroform was then added to one sample. Sample tubes for fumigated and unfumigated samples were closed and shaken at approx. 300 rev min^{-1} for two hours on an orbital shaker. Sample tubes were centrifuged at 3000 rpm for 10 minutes, and the supernatant was filtered through Whatman no. 42 filter papers. Any remaining chloroform in fumigated extracts was removed by sparging with compressed air for 20 min. Total C and N contents of extracts were measured using a Total Organic Carbon (TOC) analyser (TOC-L, Shimadzu Corporation, Kyoto, Japan). MBC and MBN calculated as the difference between fumigated and unfumigated samples, and expressed in µg g^{-1} dry soil after correction using soil moisture content. Clearly erroneous MBC and MCN values for two gap samples and one forest sample (e.g. negative values) were removed from the final dataset before analysis.

3.3.4 Nutrient supply rates

Soil nutrient availability was measured using resin ion exchange membranes (PRS® Probes, Western AG, Saskatoon, Canada) for anions NO_3, P and S, and cations NH_4, Ca, Mg, K, Fe, Mn, Cu, Zn, B, Pb, Al and Cd. These simulate plant roots through attraction and adsorption of ions in soil, capturing bioavailable nutrient pool dynamics and providing a measure of net soil nutrient supply rates (Qian and Schoenau, 2002). Probes were installed *in situ* in four pairs (one cation and one anion probe) around each sampling point to minimise the effects of localised spatial variability, inserted to a depth of 10 cm. Probes were removed from soil after a period of seven days, cleaned on collection with distilled water and shipped to the manufacturer for chemical analysis.

Probes were bulked per sampling point and eluted with 0.5 M HCL for 1 hour. NO_3 and NH_4 concentrations were measured by colorimetric automated flow injection analysis. Concentrations of all other ions were measured using inductively coupled plasma-optical emission spectroscopy. Nutrient supply rates for each element are given as amounts per area of ion exchange membrane for the duration of burial (i.e. µg 10 cm^{-2} 7 $days^{-1}$).

3.3.5 Environmental and vegetation characteristics

Location and elevation was recorded at the centre of each plot using GPS. Slope measurements were taken at each sampling point using a clinometer. For microclimate measurements, data loggers equipped with soil moisture and temperature probes (Delta-T Devices Ltd., Cambridge, UK) were installed in the centre of each plot to record hourly measurements between November 2016 and March 2018 (490 days) for calculation of soil moisture and soil temperature means, minima and maxima (taken over the entire duration). Due to damage and equipment failure during this period, only soil moisture data from 75 continuous days (November 2016 - January 2017) and soil temperature data for 26 continuous days (November 2016 - December 2016) in B South were used for consistency in statistical analysis (minimum of three data loggers per vegetation type in one site). Photosynthetically active radiation (PAR) was measured at each sampling point upon soil sample collection using a light meter (PP Systems, USA) with the sensor held just above understorey vegetation. For canopy openness, hemispherical photographs were taken at each sampling point using an Opteka 180 ˚ 6.5 mm fish-eye lens (Samyang Optics, Masan, South Korea) focussed to infinity, fitted on a vertically-mounted digital Canon 400D camera (Canon, Tokyo, Japan) with the top of the image oriented North (Hu et al., 2009; Frazer et al., 2001). The canopy gap fraction of images was calculated using the Hemisfer program version 2.2 (Swiss

Federal Institute for Forest, Snow and Landscape research) and expressed as a percentage.

3.3.6 Molecular analysis of soil microbial communities and data pre-processing

DNA was extracted from 0.1 g soil using the *Quick*-DNA™ Soil Microbe Kit and protocol (Zymo Research). 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 (CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC) were used (Kozich et al., 2013). Fungi were targeted by amplifying the ITS2 region using primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). Although the capability of detecting AM fungi using ITS primers is known to be somewhat limited due to bias (Hart et al., 2015), recent studies have shown that patterns in diversity and community composition can be adequately identified within sample types such as soil (Berruti et al., 2017; Lekberg et al., 2018). 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 55 °C (16S) and 52 °C (ITS); annealing times were 30 seconds with extension at 72 °C for 30 seconds; cycle numbers were 25; a final extension of 10 minutes at 72 °C was included. Amplicon sizes were determined using an Agilent 2200 TapeStation system, samples were normalized using SequalPrep Normalization Plate Kit (Thermo Fisher Scientific) and pooled. The pooled library was quantified using a Qubit dsDNA HS kit (Thermo Fisher Scientific) prior to sequencing with an Illumina MiSeq using V3 600 cycle reagents at a concentration of 8 pM with a 5% PhiX Illumina control library. The sequencing run produced in excess of 21 and 18

million reads passing filter (16S and ITS, respectively). Sequences were processed in R using DADA2 to quality filter, merge, de-noise and assign taxonomies (Callahan et al., 2016). 16S forward reads were trimmed to 250 bases. ITS sequence 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. *mergePairs* and *removeBimeraDenovo* functions were used at default settings to merge forward and reverse reads and remove chimeric sequences. The amplicon sequence variants (ASVs) were subject to taxonomic assignment using *assignTaxonomy* and the training database UNITE version 7.2 (UNITE Community, 2017).

Fungal functional guild classifications were assigned to ASVs using the FUNGuild annotation tool (Nguyen et al., 2016). Only ASVs with unambiguous (non-multiple) classifications of "probable" or "highly-probable" confidence rankings were considered for analysis. These were used for calculating relative abundances of fungal guilds and sub-setting saprotrophic, mycorrhizal, EcM, pathogenic and parasitic fungal datasets for analysis of diversity and community dissimilarity. Only ASVs assigned to the kingdom of Bacteria and Fungi were retained for downstream analysis (99.34 % and 99.73 % of total 16S and ITS reads, respectively). Eight samples with abnormally low read counts in all libraries were removed. These all comprised SLG samples, including one entire SLG plot in B North. All singleton ASVs were removed and sample sequencing depth was normalised by rarefying to the minimum read counts of 13,498 (bacteria), 7,124 (overall fungal), 1,983 (saprotrophic fungal), 22 (mycorrhizal fungal), 13 (EcM fungal), 501 (pathogenic fungal) and 19 (parasitic fungal). Alpha diversity indices (ASV richness, Shannon index) and fungal guild relative abundances were

calculated using rarefied datasets. All sequencing data pre-processing was conducted in R version 3.5.1 (R Core Team, 2013) using the *phyloseq* package (Mcmurdie and Holmes, 2013).

3.3.7 Statistical analyses

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2013). ANOVA was used to test differences in soil, environmental and vegetation characteristics and univariate soil microbial community attributes (alpha diversity and fungal guild relative abundances) between CCF and SLG (H1, H2 & H3). Plot-averaged data was used to control for spatial pseudoreplication, and the effect of vegetation type was tested after the site factor to control for potential site effects. To test the relationship between disturbance intensity (canopy openness) and soil characteristics and microbial community attributes (H4), linear mixed effects regression models (LMMs) were constructed in the *lme4* R package (Bates et al., 2015) using data from SLG only. To control for potential within-plot pseudoreplication, plot ID was included as a random intercept term. Normality of model residuals were evaluated using Shapiro-Wilk tests, and variables were log-transformed where necessary to improve model fit and satisfy assumptions of homoscedasticity (ANOVA). Significance was considered at the $p \leq 0.05$ level. For univariate soil microbial community attributes significantly affected by SLG, the soil physiochemical parameters explaining the largest proportion of variance across SL forest were identified through multiple linear regression. Prior to analysis, highly correlated soil variables were identified with correlograms using the *corrplot* R package (Wei and Simko, 2017). Variables correlated with Pearson's $r > 6$ were removed after averaging correlation coefficients by site. The best model was identified through stepwise forward and backward variable selection using AIC as the criterion.

Soil microbial community data were Hellinger-transformed prior to analysis (Legendre and Borcard, 2018) to control for the effect of rare taxa, and merged at the plot level (n = 11) using the merge_samples function in *phyloseq* to control for spatial pseudoreplication. Soil microbial community compositions across CCF and SLG were visualised with PCoA using Bray-Curtis dissimilarities via the *phyloseq*, *vegan* (Oksanen et al., 2019) and *ggplot2* (Wickham, 2016) packages. Differences in soil microbial community compositions between vegetation types (H2 & H3) were tested with PERMANOVA using the adonis *vegan* function and Bray-Curtis community dissimilarities. All permutational tests were run with 10,000 permutations and restricted by site to control for the nested sampling design using the *permute* R package (Simpson et al., 2019). Homogeneity of multivariate dispersion between vegetation types (an assumption of PERMANOVA) for soil microbial community dissimilarities was evaluated using the betadisper *vegan* function. For soil microbial community dissimilarities significantly affected by SLG, the soil physiochemical parameters explaining the largest proportion of variance across SL forest were identified through backwards-selection using PERMANOVA with adonis2, where variables with highest *p*-values in marginal tests were sequentially removed until all predictors were significant. Indicator analysis was conducted to identify specific fungal taxa associated with different vegetation types using the *labsdv* R package (Roberts, 2016; Dufrêne and Legendre, 1997).

3.4 Results

3.4.1 Differences in soil, environmental and vegetation characteristics between CCF and SLG

For all comparisons between CCF and SLG, R^2 values are given after removing variance associated with site, apart from microclimate characteristics, which were only measured

in one site (B South). SLG was associated with significantly higher maximum soil moisture content (R^2 = 0.96, $F_{1,4}$ = 85.61, p < 0.001), PAR (R^2 = 0.68, $F_{1,8}$ = 16.89, p = 0.003), soil pH (R^2 = 0.69, $F_{1,8}$ = 17.73, p = 0.003), soil bulk density (R^2 = 0.48, $F_{1,8}$ = 7.42, p = 0.026), and lower soil Inorganic P content (R^2 = 0.56, $F_{1,8}$ = 10.00, p = 0.013), corresponding with significantly greater canopy openness in SLG (R^2 = 0.93, $F_{1,8}$ = 113.91, p < 0.001) (Fig. 3.1 A-F; see Table 3.1 for summary of all soil, environmental and vegetation characteristics by forest type).

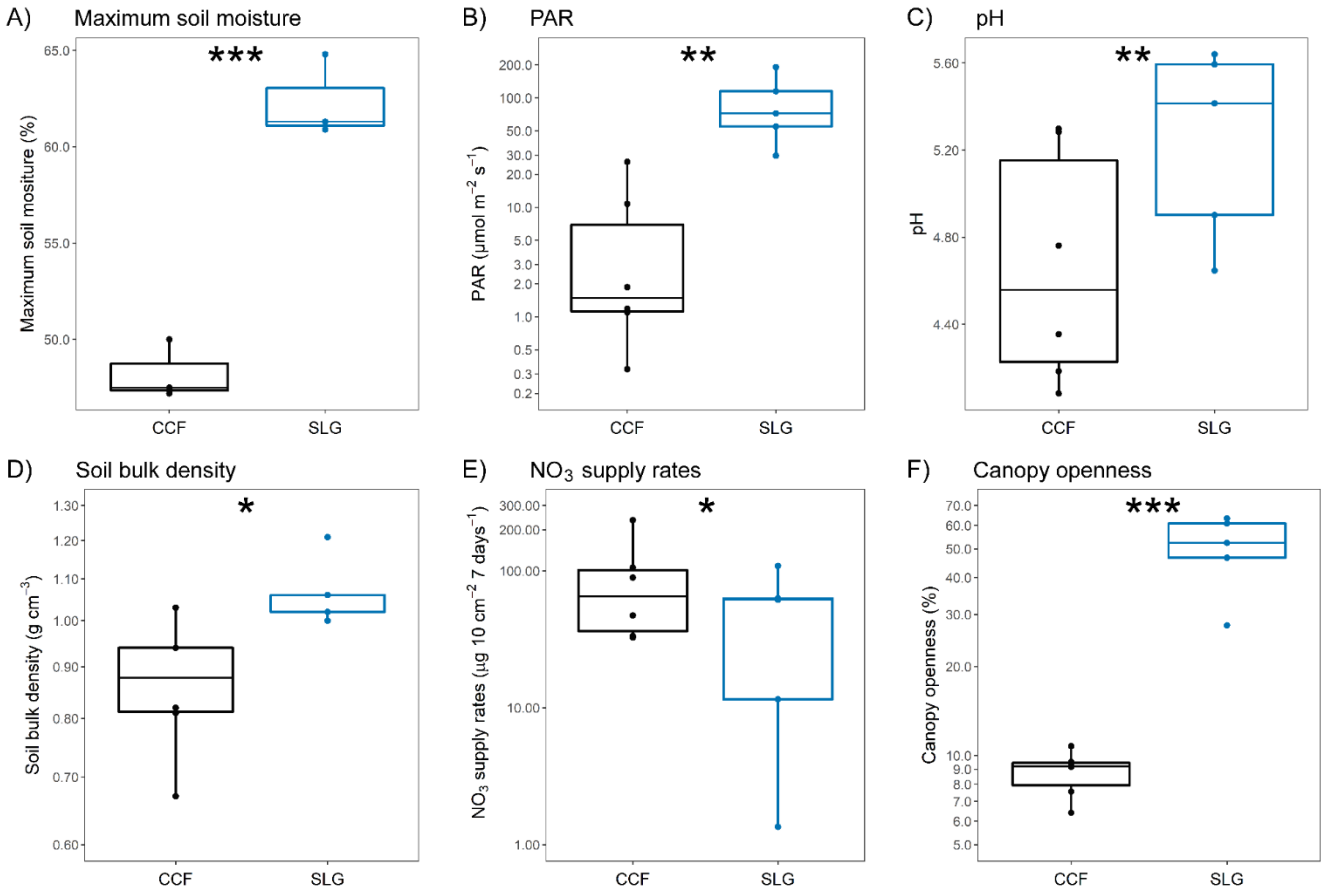

Figure 3.1 *Box and whisker plots of microclimate and soil properties, soil nutrient supply rates and vegetation properties found to significantly differ between closed canopy forest (CCF) and selective logging gaps (SLG) as identified with ANOVA after controlling for site. Asterisks indicate significance level of statistical differences between vegetation types; * p < 0.05, ** p < 0.01, *** p < 0.001.*

Table 3.1 Means (± 1 SD) of all soil, environmental and vegetation properties by vegetation types of closed canopy forest (CCF) and selective logging gaps (SLG). Asterisks indicate statistically different groups at the $p < 0.05$ level identified with ANOVA after controlling for site effects; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Group	Parameter	Vegetation type	
		CCF	SLG
Vegetation	Canopy openness (%)	8.77 ± 1.54 ***	50.18 ± 14.31 ***
	Gap vegetation height (cm)	-	90.13 ± 22.13
Microclimate	PAR (µmol m^{-2} s^{-1})	6.88 ± 10.14 **	92.53 ± 63.28 **
	Mean soil temperature (˚C)	26.41 ± 3.38	27.26 ± 3.65
	Max. soil temperature (˚C)	27.60 ± 3.47	31.80 ± 5.62
	Min. soil temperature (˚C)	25.37 ± 3.15	24.87 ± 3.51
	Mean soil moisture (%)	38.24 ± 5.95	39.77 ± 8.80
	Max. soil moisture (%)	48.23 ± 1.54 ***	62.33 ± 2.15 ***
	Min. soil moisture (%)	33.00 ± 7.40	33.70 ± 5.74
Soil physicochemical	pH	4.66 ± 0.54 **	5.24 ± 0.44 **
	O-layer depth (cm)	4.06 ± 0.78	3.86 ± 2.24
	Sand (%)	61.67 ± 6.41	58.40 ± 8.17
	Silt (%)	13.50 ± 2.43	17.20 ± 4.09
	Clay (%)	24.83 ± 4.96	24.20 ± 5.12
	Bulk density (g cm^{-3})	0.87 ± 0.13 *	1.06 ± 0.09 *
	C (%)	3.85 ± 0.94	3.39 ± 0.59
	N (%)	0.31 ± 0.09	0.28 ± 0.05
	C : N ratio	12.60 ± 1.96	12.14 ± 1.38
	Total P (µg g^{-1})	230.07 ± 83.24	255.35 ± 101.65
	Inorganic P (µg g^{-1})	6.45 ± 1.68 *	4.64 ± 0.64 *
Nutrient supply rates	NO_3 (µg 10 cm^{-2} 7 $days^{-1}$)	90.63 ± 76.96 *	49.29 ± 43.66 *
	NH_4 (µg 10 cm^{-2} 7 $days^{-1}$)	20.20 ± 9.08	13.76 ± 9.87
	Ca (µg 10 cm^{-2} 7 $days^{-1}$)	327.00 ± 270.55	486.28 ± 310.02
	Mg (µg 10 cm^{-2} 7 $days^{-1}$)	129.48 ± 70.28	178.17 ± 92.70
	K (µg 10 cm^{-2} 7 $days^{-1}$)	222.43 ± 67.45	213.40 ± 54.46
	P (µg 10 cm^{-2} 7 $days^{-1}$)	1.22 ± 0.45	1.52 ± 1.14
	Fe (µg 10 cm^{-2} 7 $days^{-1}$)	6.44 ± 2.32	14.57 ± 13.49
	Mn (µg 10 cm^{-2} 7 $days^{-1}$)	9.95 ± 2.85	12.34 ± 15.78
	Zn (µg 10 cm^{-2} 7 $days^{-1}$)	0.73 ± 0.11	0.61 ± 0.23
	S (µg 10 cm^{-2} 7 $days^{-1}$)	21.59 ± 12.07	30.30 ± 8.58
	Al (µg 10 cm^{-2} 7 $days^{-1}$)	10.96 ± 2.94	11.93 ± 3.95
Environmental	Altitude (m)	481.00 ± 111.52	459.40 ± 116.56
	Slope (˚)	17.94 ± 7.27	11.07 ± 5.64

3.4.2 Differences in soil microbial community attributes between CCF and SLG

In total, 10,913 bacterial ASVs (representing 40 phyla; 267 genera) and 13,848 fungal ASVs (12 phyla; 590 genera) were detected across all samples including CCF and SLG (see Fig. 3.2 for summaries of phyla for all soil microbial groups by forest type).

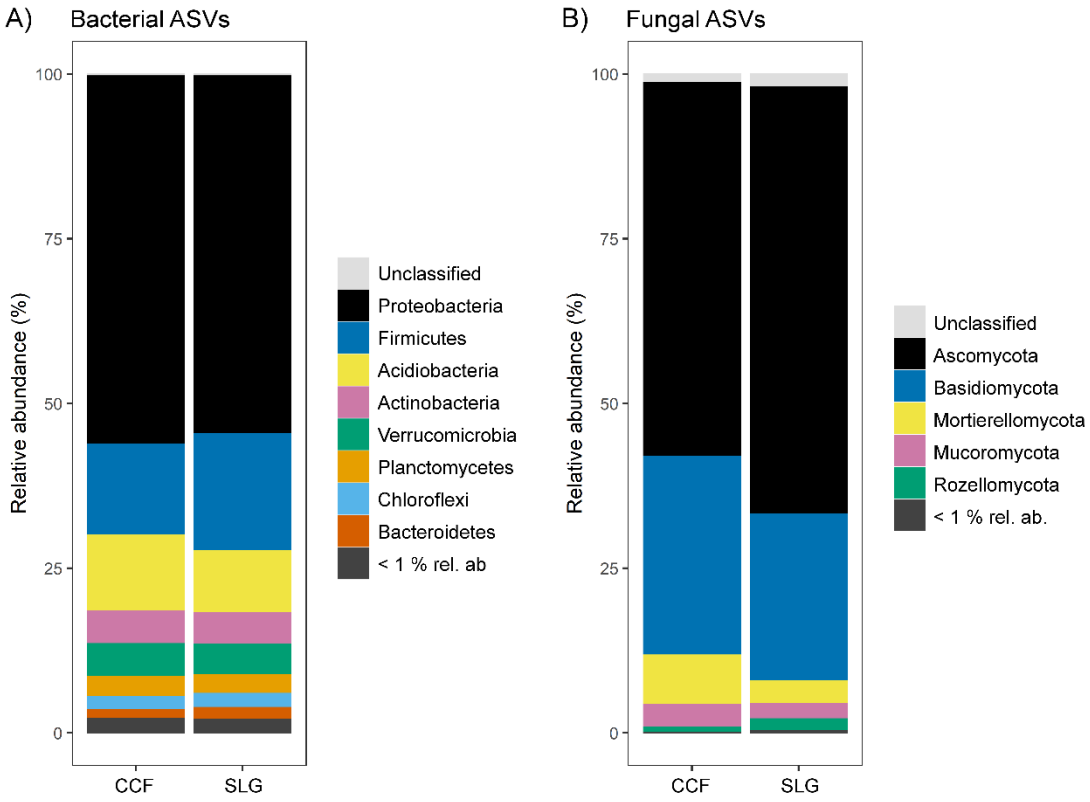

Figure 3.2 *Relative abundance of A) bacterial and B) fungal phyla as a percentage of total Amplicon Sequence Variants (ASVs) in closed-canopy forest (CCF) and selective logging gaps (SLG). Phyla with < 1% relative abundance in both vegetation types are represented as one group.*

Bray-Curtis community dissimilarities significantly differed between CCF and SLG for bacteria (PERMANOVA: R^2 = 0.10, $F_{1,8}$ = 1.01, p = 0.034; Fig. 3.3 A) and overall fungal (R^2 = 0.13, $F_{1,8}$ = 1.34, p = 0.005), saprotrophic fungal (R^2 = 0.14, $F_{1,8}$ = 1.43, p = 0.005) and pathogenic fungal groups (R^2 = 0.15, $F_{1,8}$ = 1.60, p = 0.005) (Fig. 3.3 B-D), while no significant difference was detected for mycorrhizal (p = 0.131), EcM (p = 0.226) or parasitic (p = 0.089) fungal groups. Multivariate dispersion of community

dissimilarities was homogenous between forest types for all soil microbial groups (betadisper: $p > 0.05$).

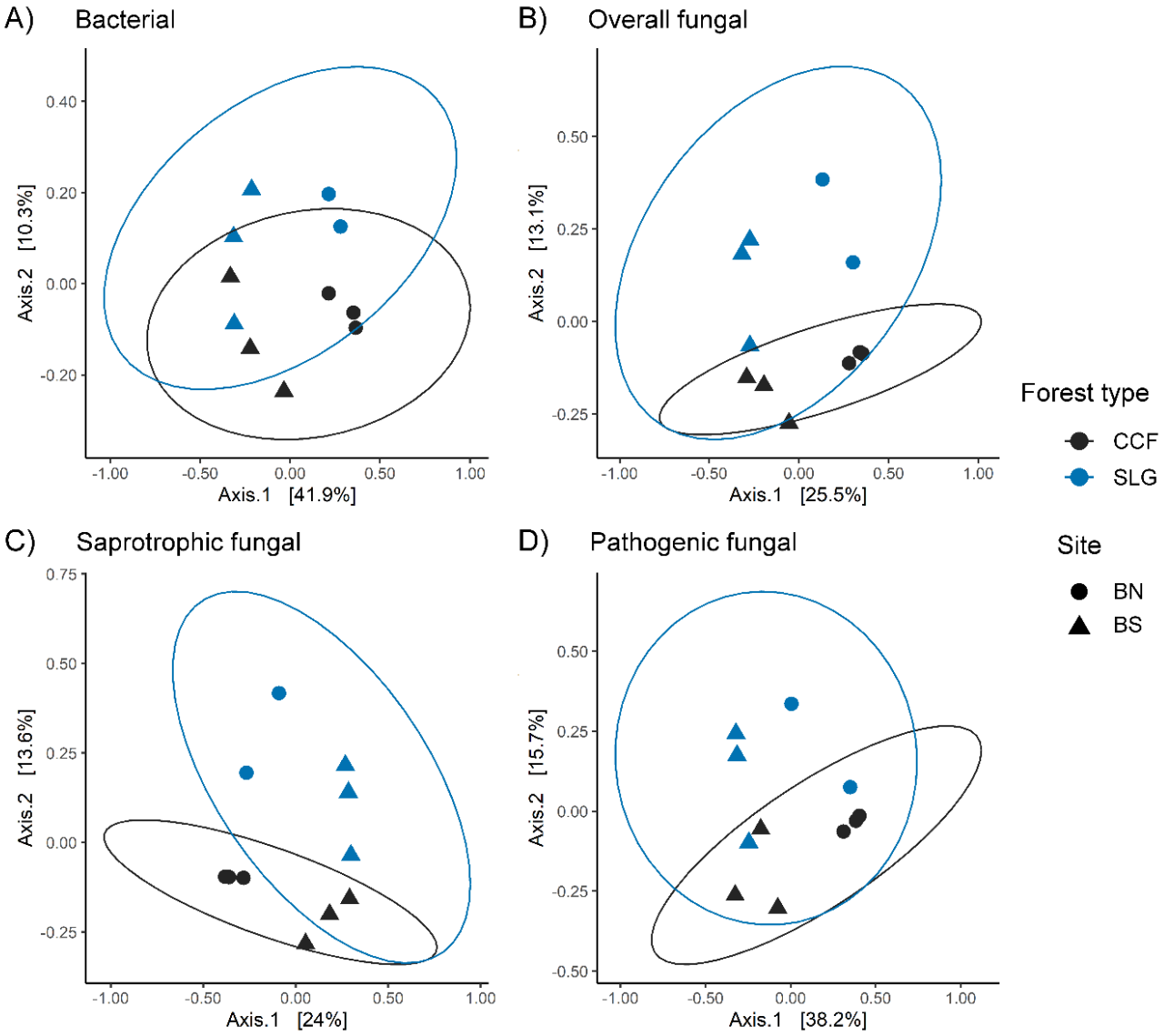

Figure 3.3 *Principle coordinates analysis (PCoA) ordination of Bray-Curtis dissimilarities for soil microbial groups that significantly differed between closed canopy forest (CCF) and selective logging gaps (SLG) identified with PERMANOVA after controlling for site ($p < 0.05$). Shapes indicate samples collected at the two sites B North (BN) and B South (BS). Ellipses represent 95 % confidences with t-distribution.*

No significant differences were detected in MBC, MBN or alpha diversity indices (ASV richness and Shannon diversity index) between CCF and SLG for any soil microbial group ($p > 0.05$; see Table 3.2 for summary of soil microbial attributes by forest type).

Table 3.2 Means (± 1 SD) of all soil microbial community attributes (Total microbial biomass C and N, Amplicon Sequence Variant (ASV) richness and Shannon alpha diversity) and relative abundances of fungal guilds by forest types of closed canopy forest (CCF) and selective logging gaps (SLG). Asterisks indicate statistically different groups at the $p < 0.05$ level identified with ANOVA after controlling for site; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Parameter	Soil microbial group	Forest type	
		CCF	SLG
Total microbial biomass C (µg g^{-1} dry soil)	-	326.11 ± 265.92	166.63 ± 105.56
Total microbial biomass N (µg g^{-1} dry soil)	-	24.09 ± 24.98	21.95 ± 25.86
Richness (no. observed ASVs 10 $reads^{-1}$)	Bacteria	0.42 ± 0.15	0.48 ± 0.19
	Overall fungi	0.70 ± 0.20	0.76 ± 0.13
	Saprotrophic fungi	0.65 ± 0.22	0.67 ± 0.15
	Mycorrhizal fungi	2.82 ± 0.22	2.72 ± 0.53
	EcM fungi	3.29 ± 0.63	2.62 ± 0.88
	Pathogenic fungi	0.51 ± 0.16	0.52 ± 0.08
	Parasitic fungi	13.49 ± 4.10	13.72 ± 2.20
Shannon alpha diversity index	Bacteria	4.98 ± 0.43	4.98 ± 0.53
	Overall fungi	4.34 ± 0.57	4.75 ± 0.30
	Saprotrophic fungi	3.11 ± 0.67	3.33 ± 0.26
	Mycorrhizal fungi	1.41 ± 0.13	1.36 ± 0.25
	EcM fungi	1.15 ± 0.24	0.92 ± 0.36
	Pathogenic fungi	2.00 ± 0.50	2.24 ± 0.30
	Parasitic fungi	0.44 ± 0.29	0.60 ± 0.23
Fungal guild relative abundance (% total fungal ASV reads)	Saprotrophic fungi	63.60 ± 8.24	66.88 ± 5.51
	Mycorrhizal fungi	15.71 ± 9.80 *	4.70 ± 3.00 *
	EcM fungi	14.85 ± 9.43 *	4.11 ± 2.70 *
	AM fungi	0.18 ± 0.12 **	0.45 ± 0.12 **
	Ericoid mycorrhizal fungi	0.68 ± 0.82	0.14 ± 0.24
	Orchid mycorrhizal fungi	0.000 ± 0.000	0.002 ± 0.005
	Pathogenic fungi	15.98 ± 4.35 *	22.98 ± 3.82 *
	Plant pathogenic fungi	10.05 ± 5.27	15.66 ± 3.18
	Animal pathogenic fungi	5.94 ± 2.47	7.32 ± 4.48
	Parasitic fungi	2.83 ± 1.67	3.27 ± 1.32
	Endophytic fungi	0.14 ± 0.06 ***	1.42 ± 1.40 ***
	Lichenised fungi	1.83 ± 0.94 *	0.85 ± 0.49 *

However, relative abundances of mycorrhizal, EcM and lichenised fungi were significantly lower in SLG relative to CCF (Mycorrhizal: R^2 = 0.48, $F_{1,8}$ = 7.28, p = 0.027; EcM: R^2 = 0.49, $F_{1,8}$ = 7.71, p = 0.024; Lichenised: R^2 = 0.58, $F_{1,8}$ = 11.18, p = 0.010; Fig. 3.4), while relative abundances of AM, pathogenic, and endophytic fungi were significantly higher in SLG (AM: R^2 = 0.65, $F_{1,8}$ = 14.64, p = 0.005; Pathogenic: R^2 = 0.46, $F_{1,8}$ = 6.86, p = 0.031; Endophytic: R^2 = 0.77, $F_{1,8}$ = 26.30, p = < 0.001; Fig. 3.4).

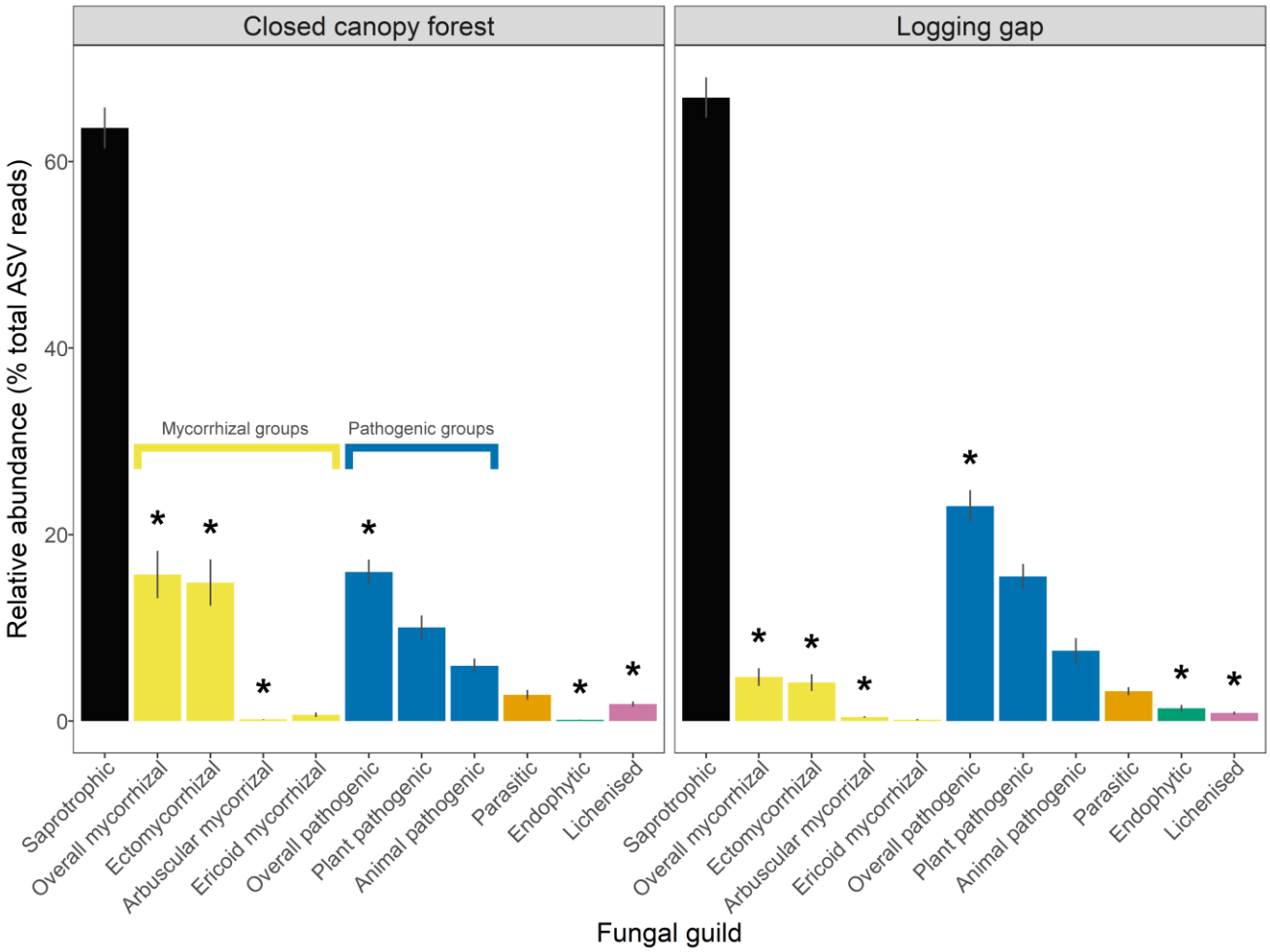

Figure 3.4 *Relative abundances of fungal guilds for closed canopy forest (CCF) and selective logging gaps (SLG). Error bars represent standard errors. Asterisks indicate statistically different groups by vegetation type identified in ANOVA after controlling for site ($p < 0.05$). Mycorrhizal and pathogenic guilds have been further divided into subtypes as indicated.*

Bray-Curtis community dissimilarities for bacteria, overall fungi and pathogenic fungi were best explained by soil pH alone, while for saprotrophic fungi the selected predictors were pH and NO_3 supply rates (see Table 3.3 for summary of all PERMANOVA model statistics).

Table 3.3 PERMANOVA results of soil characteristics best explaining variation in soil microbial Bray-Curtis community dissimilarities, identified through backward-selection using *p*-values in marginal tests controlling for site. Variables are presented in order entered in the model. Partial R^2 represents the relative proportion of explained variance of each predictor.

Soil microbial group	Predictor	*df*	Partial R^2	*F*	*p*	Model R^2
Bacteria	pH	1	0.37	5.23	0.014	0.37
	Error	9				
Overall fungi	pH	1	0.24	2.81	0.002	0.24
	Error	9				
Saprotrophic fungi	pH	1	0.23	2.79	< 0.001	0.34
	NO_3	1	0.11	1.35	0.029	
	Error	8				
Pathogenic fungi	pH	1	0.35	4.76	0.007	0.35
	Error	9				

Soil pH also explained the largest proportion of variance in relative abundances of mycorrhizal (42.7 %), EcM (45.1 %), AM (68.4 %), pathogenic (46.6 %), endophytic (51.8 %) and lichenised fungi (61.1 %) after removing variance associated with site (see Table 3.4 for summary of multiple linear regression results and statistics). Although saprotrophic fungal relative abundance was not significantly affected by vegetation type, multiple regression analysis was also conducted, as most fungal ASV reads were attributed saprotrophic fungi (66.7 % overall: 63.6 % in CCF; 69.4 % in SLG). Total soil phosphorus explained the vast majority of variation in saprotrophic relative abundance (80.2 %) after removing variance associated with site.

Table 3.4 Multiple linear regression results of soil characteristics explaining variation in fungal guild relative abundances. Variables are presented in order entered in the model. The factor 'Site' was entered first in all models to control for site effects. Partial R^2 represents the relative proportion of explained variance of each predictor, calculated from partitioned sums of squares. Corrected partial and model R^2 values represent proportion of explained variance of predictors after removing variance associated with the 'Site' categorical control variable. Continuous predictors were mean-centred and scaled by standard deviation to give standardised coefficients.

Guild	Predictor	*df*	Partial R^2	Corrected partial R^2	*F*	*p*	Standardised coefficients	Corrected model R^2
Mycorrhizal fungi	Site	1	0.04		1.00	0.351		0.68
	pH	1	0.41	0.43	9.29	0.019	-8.57	
	Total P	1	0.24	0.25	5.46	0.052	-9.89	
	Error	7						
EcM fungi	Site	1	0.03		0.68	0.438		0.70
	pH	1	0.44	0.45	10.68	0.014	-8.61	
	Total P	1	0.25	0.25	6.02	0.044	-9.69	
	Error	6						
AM fungi	Site	1	0.02		1.21	0.314		0.88
	pH	1	0.67	0.68	34.31	0.001	0.28	
	Organic layer depth	1	0.13	0.13	6.73	0.041	0.06	
	NO_3	1	0.06	0.06	3.13	0.127	-0.07	
	Error	6						
Pathogenic fungi	Site	1	0.01		0.16	0.701		0.60
	pH	1	0.46	0.47	8.11	0.025	7.52	
	Total P	1	0.13	0.13	2.29	0.174	-4.24	
	Error	7						
Endophytic fungi	Site	1	0.05		0.89	0.378		0.61
	pH	1	0.49	0.52	9.41	0.018	1.29	
	C:N ratio	1	0.09	0.10	1.74	0.229	-0.49	
	Error	7						
Lichenised fungi	Site	1	0.31		42.74	0.003		0.96
	pH	1	0.42	0.61	56.86	0.002	-0.97	
	NO_3	1	0.09	0.13	11.65	0.027	0.35	
	Available P	1	0.08	0.12	11.38	0.028	-0.31	
	Organic layer depth	1	0.04	0.06	6.02	0.070	-0.22	
	NH_4	1	0.02	0.03	3.08	0.154	-0.23	
	Error	4						
Saprotrophic fungi	Site	1	0.00		0.13	0.737		0.94
	Total P	1	0.80	0.80	53.09	0.002	12.17	
	Zn	1	0.08	0.08	5.05	0.088	-1.82	
	C:N ratio	1	0.03	0.03	2.11	0.220	1.50	
	NH_4	1	0.02	0.02	1.04	0.366	3.15	
	NO_3	1	0.01	0.01	0.89	0.399	-2.94	
	Error	2						

3.4.3 Relationships between disturbance intensity and soil characteristics, nutrient cycling rates and microbial community attributes

Within SLG, canopy openness was significantly positively related to supply rates of NH_4 ($F_{1,2}$ = 16.25, p = 0.009; Fig. 3.5 A), Mg ($F_{1,2}$ = 5.14, p = 0.046; Fig. 3.5 B), K ($F_{1,2}$ = 9.62, p = 0.025; Fig. 3.5 C) and Zn ($F_{1,2}$ = 9.51, p = 0.016), and proportion of sand in the soil ($F_{1,2}$ = 48.82, p = 0.020). Of these, supply rates of NH_4 were significantly positively related to supply rates of Zn ($F_{1,2}$ = 20.98, p < 0.001) and proportion of sand ($F_{1,2}$ = 9.47, p = 0.005). For microbial community attributes, canopy openness was significantly negatively related to relative abundance of overall mycorrhizae ($F_{1,2}$ = 5.81, p = 0.024; Fig. 3.5 D) and EcM ($F_{1,2}$ = 4.73, p = 0.039).

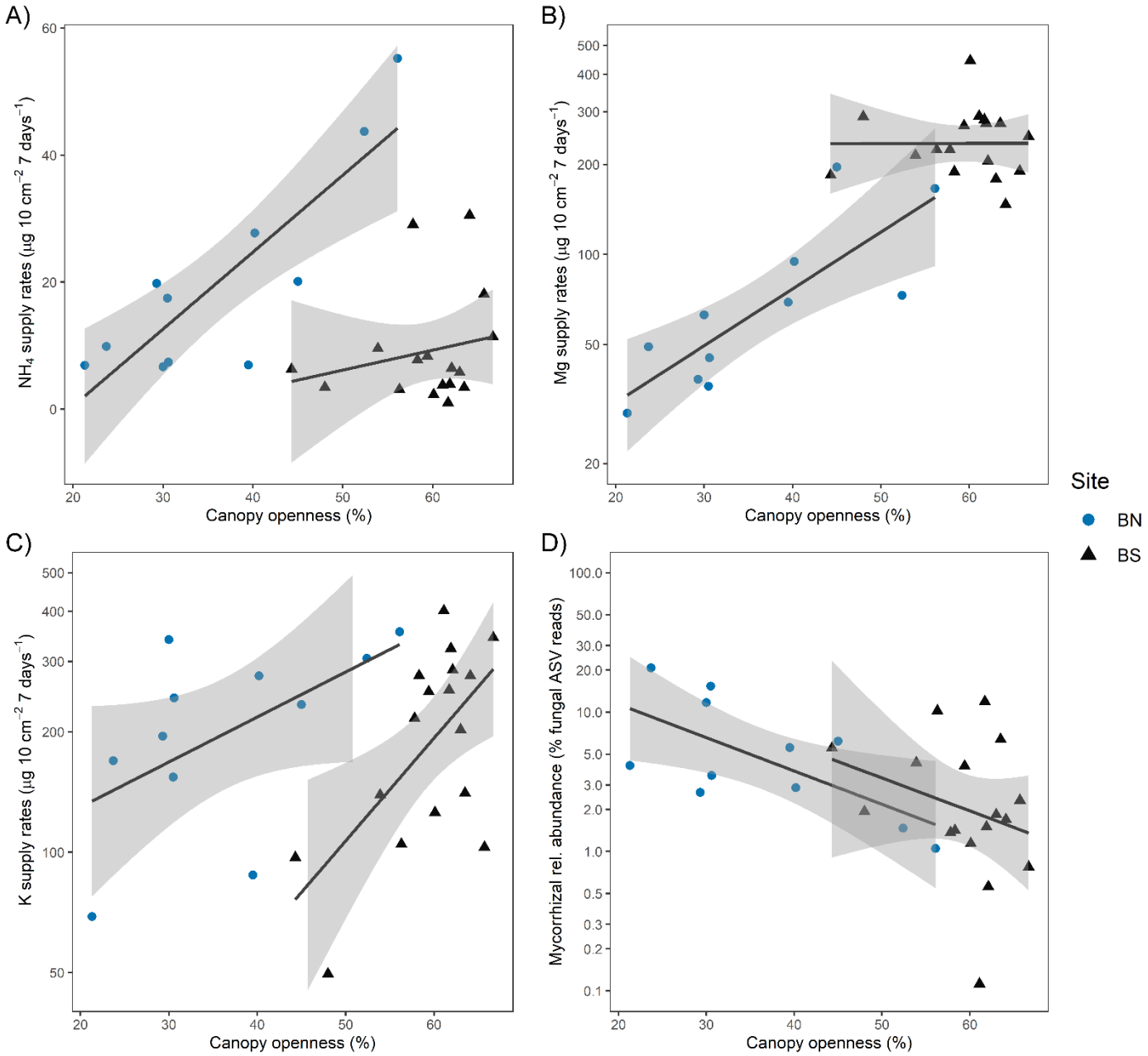

Figure 3.5 *Significant relationships between disturbance intensity (canopy openness) and nutrient cycling rates and mycorrhizal relative abundance within selective logging gaps. Relationships are shown by sites B North (BN) and B South (BS), corresponding to linear mixed model analysis controlling for site effects.*

3.5 Discussion

In support of the initial hypothesis, some soil physicochemical properties significantly differed between CCF and SLG. Of all the microclimatic measures, only soil moisture maxima significantly differed between CCF and SLG, with higher values in SLG (Fig 3.1 A; Table 3.1), likely due to reduced interception by canopy forming trees during rainfall events (Scharenbroch and Bockheim, 2007; Zhu et al., 2003; Zirlewagen and Von Wilpert, 2001). The counteracting effects of increased soil surface evaporation by exposure to solar radiation in SLG (as indicated by significantly higher PAR values; Figure 3.1 B; Table 3.1), understorey transpiration and root water extraction by adjacent trees may explain why no differences were found in mean soil moisture between vegetation types over the period measured (Marthews et al., 2008). Mean soil moisture and maximum soil temperature were higher in SLG relative to CCF, although no significant differences were detected due to increased variability in SLG (Table 3.1); reflecting greater microclimatic heterogeneity (Muscolo et al., 2014). Overall findings suggest microclimatic conditions are broadly similar between CCF and SLG possibly owing to gap size, although SLG experience periodically wetter conditions due to rainfall events in line with other studies in the tropics (Denslow et al., 1998; Saner et al., 2009; Ostertag, 1998).

Soil pH was significantly higher in SLG relative to CCF (Figure 3.1 C; Table 3.1), despite higher soil moisture maxima which may be expected to result in leaching of soil bases with an acidifying effect (Arunachalam and Arunachalam, 2000). This difference can subsequently be attributed to mechanisms associated with vegetation rather than microclimate. Lower pH under CCF is potentially a result of alterations in the quantity and quality of litter inputs. In disturbed tropical forest, the breakdown of litter from more mature stands has been associated with lower soil pH through greater

release of humic acids into the soil (Robinson et al., 2015; Melvin et al., 2011), while the amount of litterfall is higher under a closed canopy relative to gaps (Saner et al., 2009; Lin et al., 2015). Root exudation under CCF may also contribute to rhizosphere acidification, for example carboxylates that are especially produced in P-limited systems (Lambers et al., 2006; Weemstra et al., 2016). Soil bulk density was significantly higher in SLG relative to CCF (Figure 3.1 D; Table 3.1), attributable to soil compaction by heavy machinery used for timber extraction (Hartmann et al., 2013; Grigal, 2000; Marshall, 2000; Alexander, 2012; Malmer and Grip, 1990) and reduced root infiltration (Saner et al., 2009).

Differences in supply rates of certain nutrients were found between CCF and SLG, also in line with the first hypothesis. NO_3 supply rates were significantly lower in SLG (Fig 3.1 D) while NH_4 was not affected (Table 3.1), indicating that N cycling by nitrification may be down-regulated by canopy gap creation. This is contrary to many studies evaluating biogeochemical cycling rates in temperate forest gaps, which have observed increased nutrient availability through soil organic matter turnover, largely resulting from increases in soil temperature enhancing soil microbial activity and decompositional processes (Muscolo et al., 2014; Ritter, 2005; Scharenbroch and Bockheim, 2008b). However, both mineralisation and nitrification processes can depend on disturbance intensity and gap age, with high rates in newly-formed gaps (Ritter, 2005). The present study area has undergone multiple rounds of selective logging since the mid 1970's, with the youngest potential gap age at the time of sampling being 8 years (although the precise age of individual gaps is unknown). Differences in NO_3 supply rates may therefore indicate longer-term impacts of gap creation on nutrient cycling in heavily degraded tropical forest, which may be restricted by decreased litter inputs (Saner et al., 2009; Lin et al., 2015) once fresh substrates have

been broken down. Similarly, soil inorganic P content was significantly lower in SLG, although P supply rates were not found to differ by vegetation type (Table 3.1). This highlights the importance of nutrient pool dynamics in these forests, as static measures (soil inorganic P content) do not take into account variation in P availability over time. However, this could also suggest that while inorganic P pools are reduced in SLG of this age, faster cycling processes in SLG may result in similar supply rates to CCF.

Contrary to expectations (second hypothesis), bacterial community composition did significantly differ between SLG and CCF (Fig 3.3 A). Previous studies finding no differences in bacterial β-diversity between SL and old-growth forest in Borneo have suggested bacterial community assemblage to be broadly resilient to logging disturbance (Lee-Cruz et al., 2013; Tripathi et al., 2016). The findings of the current study outline that this observation may result from heterogeneity within SL forest, and a finer-spatial scale approach is required to understand impacts of SL on bacterial diversity and community structure. Elsewhere in the humid tropics, a small number of studies have found soil bacterial communities to be sensitive to different kinds of forest disturbances. For example, as recently reviewed by Franco et al. (2019), disturbed Amazonian rainforests have been shown to harbour distinct soil bacterial communities relative to primary forest due to fire events (de Carvalho et al., 2016), after anthropogenic deforestation by slash and burn practices (Mendes et al., 2015a; Mendes et al., 2015b; Navarrete et al., 2015) and in secondary regenerating forest on abandoned pasture or agricultural land, with community dissimilarities varying according to land use intensification (de Carvalho et al., 2016). The effects of disturbance on bacterial communty composition appear to be mediated by changes in soil properties, with variation in community dissimilarities particularly linked with soil pH (de Carvalho et al. 2016; Mendes et al., 2015a). Corresponding variation in bacterial community

structure and functional characteristics associated with metabolism suggests taxonomic-functional adaptation of soil bacterial communities after forest clearance (Navarrate et al, 2015). Similarly, in Costa Rican Atlantic (including lowland) forest, bacterial community composition was significantly shifted by a hurricane event opening the forest canopy and increasing woody debris on the forest floor. Here, differences found were attributed to "taxonomic switching" of bacterial functional genera in response to altered canopy material inputs to the soil (Eaton et al., 2020). In the present study, differences found in bacterial community composition along with disturbance-related alterations in vegetation inputs and soil properties are in line with these observations in other comparable tropical systems, rather than appearing resilient to selective logging as previously suggested in studies of Southeast Asian lowland dipterocarp forest (Lee-Cruz et al., 2013; Tripathi et al., 2016).

Overall, saprotrophic and pathogenic fungal community compositions were also significantly affected by SLG (Fig 3.3 B-D). This corroborates the hypothesis that fungal community structure is highly sensitive to forest disturbance in lowland dipterocarp rainforest, as found in recent studies in Southeast Asia (Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015), and reflects limited observations of soil fungal communities in humid tropical forest systems more generally, including rainforests of French Guiana (García de León et al., 2018), Costa Rica (Eaton et al., 2020) and Southwest China (Shi et al., 2019). In particular, Shi et al. (2019) found saprotrophic and pathogenic fungal community attributes shifted along a forest disturbance gradient ranging from individual tree cutting to complete forest clearance, in agreement with the observed effects on these fungal groups in the present study. More specifically, the authors found pathogenic fungal abundance increased with forest disturbance, in line with higher pathogenic fungal relative abundances observed in SLG

relative to CCF. The authors suggested potential mechanisms underlying these differences arising from altered plant-soil interactions: firstly, combined effects of plant community composition and soil pH may drive differences in saprotrophic fungal community attributes by affecting local concentrations of soil P; secondly, disturbance-related increases in understorey vegetation may create more ecological niches for pathogenic fungi by way of increased heterogeneity in root and litter compositions; thirdly, the opening of the forest canopy may allow for increased deposition of airborne fungal spores to the soil, promoting colonisation pathogenic fungi which are often wind-dispersed.

Despite differences observed in community dissimilarities of the above fungal groups, no differences were detected in mycorrhizal or EcM community compositions between vegetation types. Although there may be distinct alterations in vegetation community aboveground, belowground mycorrhizal community structure may be more resilient to disturbance. The extramatrical mycelium produced by EcM fungi, shown to be largely retained after SL (Chapter 1), may extend into gaps from surrounding closed canopy forest. However, care must be taken in interpretation due to the low number of ASV reads used for assessing community composition of mycorrhizal and EcM fungal groups (22 and 13 ASV reads respectively) and the known bias of the ITS region towards amplification of EcM rather than AM fungal taxa (Hart et al., 2015) which may limit sensitivity in detecting differences. Despite similarities in community composition, overall mycorrhizal and EcM fungal relative abundances were significantly lower in SLG, while AM fungi were more abundant (Fig. 3.4; Table 3.2). This pattern reflects the differences found in bulk soil and actively-foraging fungal communities between old-growth and SL forest in the same area (Elias et al., 2019; Chapter 1). This is likely a direct result of gap creation through the removal of

individuals of the Dipterocarpaceae, a family of EcM-associating trees (Brearley, 2012; Taylor and Alexander, 2005). Although dipterocarp species are targeted in selectve logging for their economic value (Appanah and Turnbull, 1998), some individuals may remain even after repeated, heavy logging. This is indicated in recent tree community surveys of the 1 ha plots used in the present study (dipterocarp basal area B North: 0.57 m^2 ha^{-1}; B South: 0.41 m^2 ha^{-1}) (Chapter 1; Both et al., 2019). Increased AM fungal relative abundance in SLG subsequently reflects a shift to non-dipterocarp, AM-associating vegetation, the dominant mycorrhizal type across tropical ecosysems (McGuire et al., 2008). These results also highlight that dipterocarp trees left during SL may remain an important component of CCF vegetation, influencing relative abundances of mycorrhizal types. As discussed in Chapter 1, shifts from EcM- to AM-dominated communities may have important implications for biogeochemical cycling. EcM fungi have been associated wth soil C accumulation by competing with saprotophs for nutrients (N and P) required for the breakdown of organic matter (Averill et al., 2014; Liu et al., 2018). A reduced EcM dominance therefore has potential consequences for C release from tropical forest soils. However, this effect may be negated by overall reduced organic matter inputs (i.e. litterfall) associated with lower *in situ* soil respiration rates in SLG relative to CCF as found in Southeast Asia (Saner et al., 2009). In the same study, SLG-associated differences in soil temperature and fine root biomass also significantly contributed to soil respiration rates. Future studies incoporating controlled laboratory experiments are therefore recommend to unpick the relative effects of soil microbial communities, microclimate and substrate inputs on C and nutrient cycling and fluxes in SL forest. No differences were found in alpha diversity indices between CCF and SLG for any soil microbial group (Table 3.2) despite alterations in soil characteristics, and a significant relationship previously identified between dipterocarp

basal area and EcM richness across selectively logged and old-growth forest in the region (Elias et al., 2019).

Variation in all soil microbial attributes affected by SLG was predominantly explained soil pH even after controlling for site effects (Tables 3.3 & 3.4), indicating that differences between CCF and SLG are primarily driven by the influence of vegetation type on soil pH. Linkages between pH and soil microbial community assemblages and diversity are well established in temperate (Lauber et al., 2008; Lauber et al., 2009; Rousk et al., 2010; Dupont et al., 2016) and tropical ecosystems (Jesus et al., 2009; de Carvalho et al., 2016; Mendes et al., 2015a). Soil pH has in particular been identified as the primary driver structuring bacterial communities and diversity in tropical forest in Southeast Asia (Tripathi et al., 2012). However, although increased soil pH levels associated with certain land use practices in the tropics (e.g. agricultural crop and pastureland) have been shown to increase bacterial diversity as a result of these mechanisms (Tripathi et al., 2012), bacterial diversity was not found to be significantly higher in SLF relative to CCF despite elevated pH levels towards neutral.

Within SLG, canopy openness was significantly negatively related to overall mycorrhizal and EcM relative abundances, while positively associated with supply rates of certain key soil nutrients (NH_4, Mg, K, Zn) (Fig. 3.5) and soil sand content. Disturbance intensity therefore plays an important role in soil nutrient cycling processes in these systems, in support of the final study hypothesis. However, increasing NH_4 supply rates with canopy openness may contradict assumptions about disturbance intensity and N-cycling (Muscolo et al., 2007a). A positive relationship between gap size and N mineralisation has been observed in temperate (Ritter, 2005) and tropical (Denslow et al., 1998) systems, but only in newly-created gaps (< 17 months and 12

months old, respectively) where increased nutrient cycling rates have been attributed to decomposition of fresh litter inputs resulting from disturbance. The time since SL in the current study and lack of difference in NH_4 supply rates between CCF and SLG (Table 3.1) suggests a different mechanism underlying N mineralisation. Mycorrhizae, particularly EcM, are now known to be able to mobilise soil N from organic sources and not be reliant on previous breakdown by other soil saprotrophs (Lindahl and Tunlid, 2015). A reduction in mycorrhizal relative abundance may subsequently increase the availability of organic N to be mineralised by other soil microorganisms (Averill et al., 2014). *In situ* manipulations of root and mycorrhizal relative abundances, e.g. with fungal hyphal and fine root exclusion cores (Johnson et al., 2001; Langley et al., 2006), coupled with monitoring of N-fraction dynamics is suggested to identify drivers of N-cycling rates in SLG. Further study of the influence of disturbance intensity on microclimatic conditions is also recommended, as inferences were limited in the present study due to equipment failure.

In conclusion, this study found significant shifts in both fungal and bacterial community attributes, soil physicochemical properties and nutrient cycling rates between CCF and SLG, emphasising the importance of fine-scale studies to evaluate the impacts of selective logging in highly heterogeneous degraded tropical forest. A strong reduction in relative abundances of mycorrhizal and EcM fungi and a significant increase in AM fungi in SLG may have consequences for soil carbon fluxes, although controlled experiments are required to unpick underlying mechanisms. The importance of EcM-associating dipterocarp trees remaining within CCF after selective logging is highlighted. Differences in all soil microbial community attributes were primarily related to soil pH, which was also related to vegetation type. Lower NO_3 supply rates and inorganic P pools indicate reduced nutrient cycling in SLG of this age due to

reduced litterfall. Within SLG, disturbance intensity was significantly positively related to certain key soil nutrients, including a strong association with NH_4 supply rates, while negatively related to mycorrhizal and EcM relative abundance. Findings indicate mineralisation rates in SLG may be enhanced by reduced competition for organic soil N sources between EcM fungi and other soil saprotrophs. Field manipulations of mycorrhizal hyphae and fine roots may help to identify key drivers of mineralisation rates.

Alterations in soil microbial community attributes and nutrient cycling through creation of SLG has major implications for biogeochemical and ecosystem functions at the regional scale, as selectively logged forest now represents the major natural forest type on Borneo. Evaluations and predictions of the impacts of SL should incorporate SLG effects on belowground communities and processes, which may influence restoration potential and recovery of biodiversity and vital ecosystem services in degraded tropical forest.

4 Resistance and resilience of soil microbial functioning to logging and drought in tropical rainforest

4.1 Abstract

Soil is a global reservoir of carbon (C), where the accumulation and release of C to the atmosphere is governed by soil microbes. Land-use and climate change has the potential to shift microbial community structure and functional diversity, impacting on crucial biogeochemical processes including C cycling. Degradation of tropical forest threatens the capacity of these highly biodiverse ecosystems to store C by altering complex plant-soil interactions. Forest disturbance is accelerating in Southeast Asia, most extremely on the island of Borneo through widespread selective logging (SL). Recent studies have highlighted SL-induced alterations in soil microbial communities, with bacterial and fungal community compositions in selective logging gaps (SLG) significantly differing from those in closed canopy forest (CCF). This has major implications for soil-atmosphere C exchanges and the sensitivity of soil functions to environmental perturbations associated with predicted increased frequency of climate change extremes. However, resistance and resilience of soil microbial functions to these disturbances remains unclear. A controlled laboratory incubation experiment was conducted to determine SLG and CCF effects on baseline soil respiration (R_S), and R_S responses to drought and rewetting. Results show that baseline R_S was lower in SLG relative to CCF soils, highlighting important impacts of SL disturbance on microbial heterotrophic R_S previously unidentified in field survey due to confounding vegetation and microclimatic factors. Resistance of soil function to reduced moisture did not differ between CCF and SLG. Some evidence was found for greater resilience of SLG soil functioning to drought, although SLG R_S responses were highly variable. R_S in droughted-rewetted soils were significantly higher than controls at the final recovery

stage, indicating prolonged alterations in soil functioning that may relate to changes in soil microbial ecophysiological traits. Findings indicate functioning of degraded tropical forest soil may not be resilient to drought events which are predicted to increase in intensity and frequency across tropical regions, with major implications for soil C feedbacks to the atmosphere under future climate change scenarios.

4.2 Introduction

Soils represents the largest terrestrial carbon (C) pool on the planet, storing more C than the sum of all plants and the atmosphere (Singh et al., 2011). As such they offer a vital sink for anthropogenic CO_2 emissions associated with climate change (Stockmann et al., 2013). Soil microbes are key regulators of crucial soil C cycling processes by way of complex and reciprocal plant-soil interactions (van der Heijden et al., 2008; Wardle et al., 2004), governing relative accumulation of soil C or feedbacks of carbon dioxide (CO_2) to the atmosphere through soil respiration (R_S) (Malik et al., 2018). Anthropogenic pressures threaten to upset the balance of soil C storage or release globally (Sanderman et al., 2017). Alterations in soil abiotic and biotic conditions through human land-use change can drastically shift soil microbial community structure, with potential significant and irreversible impacts on the vital ecosystem functions they regulate (Bonner et al., 2019; Fichtner et al., 2014; Rodrigues et al., 2013; Fraterrigo et al., 2006; Hartmann et al., 2012; Hartmann et al., 2013), further exacerbated by effects of climate change (Auffret et al., 2016). However, significant questions remain about the resistance and resilience of soil microbial communities and subsequent functions to environmental disturbance (Allison and Martiny, 2008; Shade et al., 2012; Griffiths and Philippot, 2013). Extremely high levels of diversity in soil microbial communities may offer functional redundancy and plasticity, with resultant communities performing broadly the same soil processes (Nannipieri et al., 2017; Grządziel, 2017). As such, understanding of the direction and magnitude of R_S responses to interactive effects of land-use and climate change is widely lacking, despite the crucial need for accurate predictions of future impacts (Nazaries et al., 2015).

Tropical forests and their soils are globally important reservoirs of biodiversity and C (Paz et al., 2016), but they are threatened by extensive deforestation and

degradation through rapid land-use change (Zarin, 2012; Saatchi et al., 2011; Chaplin-Kramer et al., 2015; Guillaume et al., 2015) particularly in Southeast Asia (Laurance, 2007a). On Borneo, over 40% of the forest cover has been lost over the last 40 years due to conversion to monoculture oil palm plantation (Carlson et al., 2012; Gaveau et al., 2014). There is now increased pressure on the remaining forest to provide vital ecosystem services (Qie et al., 2017; Asner et al., 2018; Ferraz et al., 2018), with the majority (> 70 %) of remaining forest being heavily degraded by selective logging (SL) (Gaveau et al., 2014). Certain soil microbial groups have shown a sensitivity to SL disturbance in these forests (Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015). This has significant implications as soil microbial processes account for a major portion (up to 80%) of CO_2 emissions from forest ecosystems (Yuste et al., 2004), and even small alterations can have a large effect (Lu et al., 2014). However, the impacts of SL on belowground C cycling and R_S are currently unclear. Moreover, there is a lack of knowledge of the resistance and resilience of soil microbial communities in SL forest to environmental perturbations associated with climate change. Specifically, there is uncertainty regarding soil microbial sensitivity to drought events - the intensity and frequency of are predicted to increase across tropical regions including Southeast Asia (Coelho and Goddard, 2009; Rifai et al., 2019).

Selective logging characteristically includes the opening of canopy gaps as a result of the removal of large individual trees and the creation of skid trails and logging roads (Asner et al., 2004). A previous field survey identified alterations in soil bacterial and fungal community compositions as a result of the creation of selective-logging gaps (SLGs) in logged-over Bornean rainforest (Chapter 2), relating to shifts in soil physicochemical properties (i.e. increased soil bulk density, indicating compaction, and reduced soil acidity). Although changes in certain key soil microbial functional groups

may have implications for nutrient and C-cycling, the impacts of SLG creation on these crucial functions is unknown. Limited studies in Malaysian forest suggest overall R_S rates are lower within SLGs (Saner et al., 2009; Saner et al., 2012; Adachi et al., 2006). However, these field studies have been unable to unpick the relative contributions of soil microbial communities and vegetation to overall CO_2 efflux, as well as microclimatic conditions which may govern rates of soil CO_2 efflux.

Soil microbial activity and R_S are fundamentally linked to soil moisture availability. Low soil moisture conditions associated with drought are subsequently associated with reduced soil CO_2 efflux rates, although the magnitude of change relates to the particular physiological traits and adaptive capacity of soil microbes (de Nijs et al., 2019). Following drought, short-term pulses of elevated R_S are often observed directly after rewetting of soils, through enhanced microbial mineralisation of soil organic C and N known as the 'Birch Effect' (Birch, 1958; Zhou et al., 2016). This results from the re-activation of dormant soil microbes, and stimulated burst in microbial growth and turnover due to the increased availability of more easily broken down (labile) C substrates, largely through accumulation of dead microbial material (necromass) and plant inputs during antecedent low soil moisture conditions (Blazewicz et al., 2014; Karlowsky et al., 2018). These R_S pulses can occur between minutes and several days post-rewetting (Song et al., 2017; Huxman et al., 2004), with the magnitude of elevated CO_2 production rates related to the intensity of drought (Canarini et al., 2017). An understanding of the magnitude and duration of these responses is crucial for understanding soil C losses and storage (de Nijs et al., 2019; Canarini et al., 2017; Cleveland et al., 2010).

Evidence suggests that exposure to drought and rewetting can shape soil microbial community composition, potentially selecting for communities that are more resistant to low moisture conditions (Griffiths et al., 2000) and that recover more rapidly post-disturbance (Evans and Wallenstein, 2012). Even short-term drought events can significantly alter soil microbial communities, with changes persisting long after return to pre-drought conditions. This can have long-term effects for soil microbial functioning long after drought events (Meisner et al., 2018). In intact tropical forest, throughfall manipulation studies have identified shifts in soil microbial ecophysiological characteristics with long-term drying, towards functional traits associated with the breakdown of complex C molecules through extracellular enzyme production (Bouskill et al., 2016b). The R_S of these soils was shown to be more resilient to further drying and rewetting than control soils in controlled microcosm experiments, a potential hysteretic response as soil microbial communities acclimate to drought conditions as an adaptation to previous exposure. However, very few studies have investigated resistance and resilience of soil functions to the interactive effects of forest ecosystem disturbance and climate perturbations (Chaer et al., 2009; Griffiths and Philippot, 2013).

Alterations in soil physical properties through SL disturbance may also have knock-on effects for R_S by affecting soil drying rates and dynamics in response to drought. Initial evaporation of soil moisture occurs at the soil surface, with drying rates governed by meteorological conditions (atmospheric demand). With progressive drying, the evaporative boundary moves down the soil profile to below the depleted soil surface layer, where drying rates are determined primarily by soil properties (Yamanaka et al., 1998; Aydin et al., 2005). Soil compaction through timber harvesting practices can negatively impact upon soil porosity and pore connectivity, subsequently reducing hydraulic conductivity (Hartmann et al., 2013) and increasing soil water (matric)

potential (i.e. the force by which moisture is held in the soil matrix) (Box and Taylor, 1962). This can ultimately reduce soil evaporation rates (Aydin et al., 2005). As such, soil compaction associated with creation of SLGs may buffer effects of soil drying under drought conditions, with implications for microbial activity and soil functions.

Owing to the complex interactions between soil physicochemical properties, soil microbial communities and microclimatic conditions determining overall soil functions, understanding the impacts of tropical forest ecosystem disturbance remains a significant challenge. Few studies have investigated resistance and resilience of soil functions to the interactive effects of forest degradation and drought perturbations, despite the rapidly growing area of disturbed tropical forest worldwide and predicted future climate scenarios. The overarching aim of this study was to assess the resistance and resilience of soil functioning in CCF and SLG to drought and rewetting through controlled laboratory manipulations, with a specific focus on R_S (CO_2 efflux rates) as a functional measure. This study was structured around the following specific hypotheses:

H1. Baseline R_S will be lower in SLG relative to CCF due to effect of soil compaction through SL disturbance, found through previous survey (Chapter 2).

H2. SLG soils will demonstrate greater resistance to drought relative to CCF soils. As there were no previously detected differences in soil moisture minima between CCF and SLG under study (Chapter 2), this is predicted as a result of buffering of soil drying in SLG under drought conditions due to compaction of SLG soils (increasing soil water matric potential and reducing hydraulic conductivity), rather than a hysteretic response of soil microbial communities (i.e. acclimation to drought conditions through previous exposure to low soil moisture conditions).

H3. The magnitude of elevated R_S following rewetting will increase with drought intensity in both CCF and SLG soils.

H4. SLG soils will demonstrate greater resilience to drought after rewetting relative to CCF soils. R_S of CCF soils is predicted to recover slower than SLG after rewetting, as shifts in soil microbial ecophysiological traits increases breakdown of more complex C compounds (e.g. cellulose and lignin) potentially in greater supply under CCF due to tree inputs, increasing C cycling in CCF soils.

4.3 Methods

4.3.1 Study site

Soil was collected from SL lowland dipterocarp rainforest in the Malaysian State of Sabah in Northern Borneo. Samples were taken from twelve established 6 × 6 m study plots located within SLG and adjacent CCF across two sites previously characterised for soil bacterial and fungal microbial communities, soil physicochemical properties, microclimate and vegetation characteristics (Chapter 2).

4.3.2 Soil sampling

Within each 6 x 6 m plot, three points were randomly selected for sampling. Around each selected sampling point, three soil cores were taken for experimental incubation (totalling 36 cores) using plastic piping (8 cm deep, 4 cm inside diameter). The ends were sealed on collection with rubber lids. Soil cores were maintained intact for this study to preserve soil structural properties, more closely representing field conditions. In each plot, three additional cores were collected in the same way for determining soil water holding capacity (WHC), field soil moisture content and field % WHC. On collection, soil cores were transported to a laboratory and stored in a cool box with

frozen gel packs. Cores were then shipped to Lancaster University, UK, where they were kept refrigerated at 4 °C prior to MC and WHC analysis and experimental incubation.

4.3.3 Calculation of soil (%) WHC

Soil WHC was determined after Öhlinger (1995). The fresh weights of the 36 cores taken for determining soil WHC were recorded before immersion in deionised water for 24 hours to reach maximum saturation. The lower opening of the cores were covered with plastic mesh and filter paper secured with electrical tape prior to immersion, to prevent loss of material. Core saturated weight was recorded after leaving cores to freely drain overnight (approx. 21 hours) to remove excess water, covered with cling film to prevent evaporation from the upper core opening. Core dry weight was recorded after drying cores in an oven at 105˚ C for approx. 48 hours. Soil was then removed from plastic piping, mesh and filter paper which was weighed separately. The mass of water in saturated cores was calculated by subtracting dry core weight from saturated core weight. The mass of dry soil in each core was calculated by subtracting the weight of plastic piping, mesh and filter paper from the dry core weight. Maximum soil WHC (g water g $soil^{-1}$) was determined by dividing the mass of dry soil by the mass of water in saturated cores. Field soil moisture content was determined by subtracting dry core weight from fresh core weight and dividing by mass of dry soil. Field % WHC (%) was determined by dividing field soil moisture content by maximum WHC, and multiplying by 100.

4.3.4 Experimental incubations and gas sampling

The fresh weights of all cores used for the incubation experiment were recorded on removing rubber lids. The lower opening of incubation cores was covered with plastic

mesh and filter paper to prevent loss of material, before mounting on a plastic draining plate. Intact cores were placed upright in 1L Mason jars for experimental incubation (Fig. 4.1).

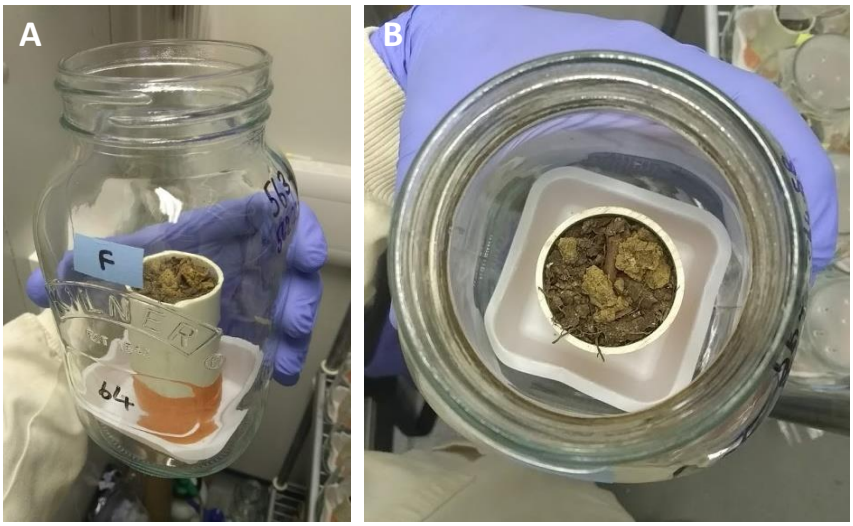

Figure 4.1 *Side (A) and top (B) view of 8 x 4 cm intact soil core installed in mason jar for experimental incubation.*

For each field sampling point (three per plot), each of the three cores collected was randomly assigned to one of three experimental moisture treatments: 1) control (average field % WHC); 2) mild drought; 3) severe drought. Cores were separated into three experimental blocks (A, B and C) according to their respective plot sampling point (i.e. one true replicate per block), and arranged by moisture treatment in alternating CCF and SLG pairs (Fig. 4.2).

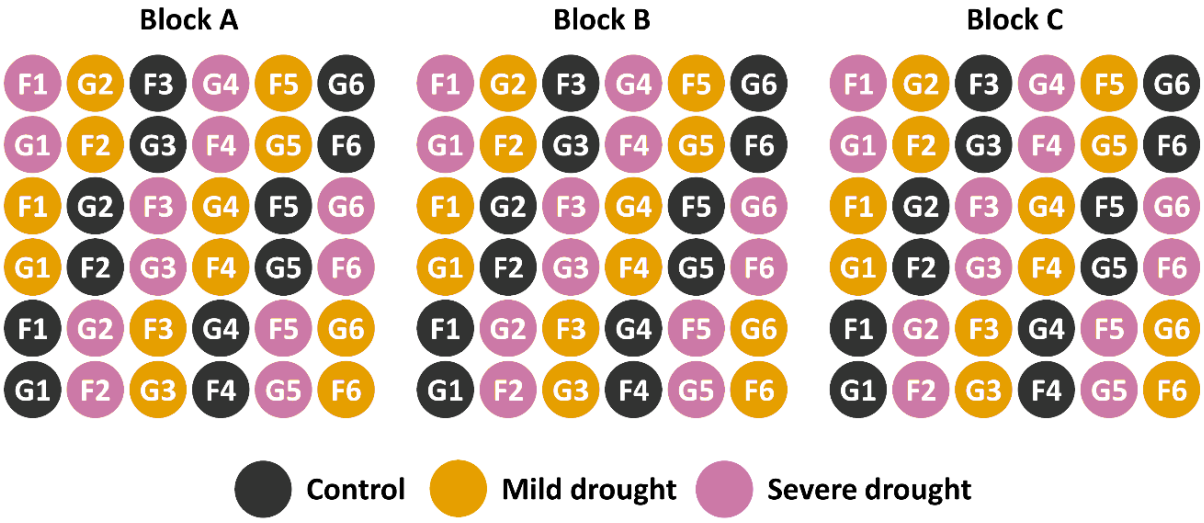

Figure 4.2 *Schematic of experimental incubation setup. Cores were arranged in blocks of paired closed-canopy forest (F) and selective logging gap (G) cores by plot (1-6) and moisture treatment (control, mild drought and severe drought).*

Cores were installed in a controlled temperature room maintained at 24 ˚C for the duration of the study. This was the average soil temperature across all CCF and SLG plots measured *in situ* during the previous soil survey (Chapter 2). Jars were placed on one shelf at the same height to maximise uniformity in temperature across all cores (Fig. 4.3), with the nested block design providing additional control of small variations in local microclimate conditions within the room. When not under drought conditions, jars were covered with a moisture-resistant flexible film (Parafilm; Bemis, USA) punctured with air holes, to reduce soil evaporation rates while allowing gas exchange to avoid anaerobic conditions.

Figure 4.3 *Soil cores mounted in mason jars installed at equal height in a controlled temperature (CT) room.*

For soil % WHC adjustment, synthetic rain was prepared using autoclaved deionised water with additions of sodium chloride (NaCl: 0.29 g l^{-1}), calcium chloride dihydrate ($CaCl_2.2H_20$: 0.09 g l^{-1}), calcium sulphate dihydrate ($CaSO_4.2H2O$: 0.07 g l^{-1}), magnesium sulphate heptahydrate ($MgSO_4.7H_2O$: 0.13 g l^{-1}) and sulphuric acid (98 % H_2SO_4: 0.23 g l^{-1}) based on available chemical composition data of rain collected at Danum Valley Field Station, Danum Valley Conservation Area, Sabah, Borneo (4.95°, 117.79°), in the same region as the present study plots (data were obtained from the World Data Centre for Precipitation Chemistry; http://wdcpc.org; Vet et al., 2014). Synthetic rain was used rather than pure deionised water to minimise leaching of nutrients from soils during the incubation, and more closely represent field conditions. 60 % maximum soil WHC was chosen to represent average field moisture conditions, using the approximate % WHC of all cores measured for WHC (CCF and SLG). The weights of soil cores at 60 % WHC was determined by estimating the mass of dry soil in each core, using core fresh weight (subtracting average plastic pipe weight) and

average soil moisture content for each plot, then multiplying by average maximum WHC for each plot.

All cores were adjusted to and maintained at 60 (± 3) % soil WHC (monitored every three days minimum) for an equilibration period of one week prior to the measurement of baseline CO_2 efflux and experimental drought treatments. This was to allow microbial communities to revive after refrigeration, and stabilisation of soil CO_2 efflux. The start of the equilibration period (and of all subsequent experiment time points) was staggered by one day between blocks, to allow time for % WHC monitoring and adjustment, and gas sampling throughout the duration of the incubation experiment. After equilibration, only control treatment cores were maintained at 60 % WHC. The paraffin film was removed from jars of mild and severe drought treatment cores, and % WHC was monitored daily. When drought treatment cores reached approximately half the control % WHC when averaged across all CCF and SLG cores (i.e. 30 % WHC; after seven days of drying), mild drought treatment cores were readjusted back to 60 % WHC and re-covered with paraffin film. Severe drought treatment cores were left to dry for approximately double the drying period of mild treatment cores (a total of 15 days) before readjusting back to 60 % WHC and re-covering with paraffin film. After rewetting, both mild and severe drought treatment cores were maintained at 60 % WHC for a recovery period of 11 days.

CO_2 efflux rates were measured at four experimental time points: 1) before drought (BD), i.e. after stabilisation period for baseline CO_2 efflux; 2) after drought (AD), for mild and extreme drought treatments and respective controls; 3) initial recovery (IR), three days after rewetting of mild and extreme drought treatment cores; 4) final recovery (FR), eleven days after rewetting of mild and extreme drought

treatment cores. CO_2 sampling was conducted using a Picarro gas analyser (Picarro Instruments, USA). Jars were sealed using a custom lid fitted with inlet and outlet pipes in a closed system with the Picarro analyser, using silicon grease to ensure an airtight seal. Increase in CO_2 concentration was allowed to stabilise for approximately one minute, based on real-time visualisation using the analyser display. CO_2 concentrations were then recorded in ppm at one second intervals for six minutes. CO_2 concentration data for each measurement were trimmed to the last 350 points to retain a period of linear increase over time, and rate of change in ppm was calculated using linear regression. CO_2 efflux rates were then calculated in µg CO_2-C cm^{-2} $hour^{-1}$ using the following formula:

$$CO_2\ efflux\ rate\ = \frac{3{,}600 * m * V * C_M * P}{A * R * T}$$

where m is the rate of change on CO2 concentration (ppm s^{-1}), V is the volume of chamber used during measurement corrected for soil core volume (m^3), C_M is the molecular mass of C (g mol^{-1}), P is absolute gas pressure, A is surface area of core (m2), R is the universal gas constant and T is temperature (Kelvin). As intact cores were used to represent the inherent properties of the entire soil matrix, CO_2 efflux rates were expressed on a per area rather than per g soil basis. This retains integrated soil physicochemical and structural properties influencing soil water and gas dynamics along the soil profile (see for example Briones et al., 2014).

4.3.5 Relative change in CO2 flux rates

Additional indices were calculated for evaluating relative effects of mild and extreme drought treatments on CO_2 efflux rates within and between forest types and experiment time points. Absolute change in CO_2 efflux rates (AC; µg CO_2-C cm^{-2} $hour^{-1}$) was calculated by subtracting CO_2 efflux rates of respective controls from those of mild and

extreme drought treatment cores at each experiment time point. Proportional change in CO_2 efflux rates was calculated as a response ratio (RR %) by dividing CO_2 efflux rates of mild and extreme drought treatment cores by those of respective controls at each time point, subtracting 1 to indicate direction of change, and multiplying by 100.

4.3.6 Statistical analyses

All statistical analyses were conducted in R version 3.6.0 (R Core Team, 2019) and significance in all tests was considered at the $p \leq 0.05$ level. Data were first averaged by moisture treatments within plots to control for spatial pseudoreplication in field sampling and to account for block effects in incubation design (total 36 cores). ANOVA was used to test for differences in CO_2 efflux rates, AC, RR and % WHC between forest types and moisture treatments at each experimental time point, and between experimental time points within forest types and moisture treatments. Data were subset prior to ANOVA tests by experiment time point or forest type as necessary. Differences in all parameters between CCF and SLG at each time point were tested with linear models, fitting vegetation type after the site factor to control for potential site effects in field sampling design. Differences between moisture treatments and time points were tested with linear mixed models (LMMs) in the *lme4* R package (Bates et al., 2015) including plot ID as a random intercept term to control for the nested experimental design. Post-hoc pairwise comparisons between experiment time points and moisture treatments within and between forest types were conducted where necessary with the *emmeans* R package (Lenth et al., 2019) with Bonferroni correction. Significance tests for LMMs were performed using the Satterthwaite degrees of freedom approximation (Luke, 2017). Normality of residuals for all models were evaluated using Shapiro-Wilk tests, and variables were transformed where necessary to improve model fit and satisfy assumptions of homoscedasticity.

4.4 Results

4.4.1 Baseline respiration

Baseline CO_2 efflux was significantly lower in SLG (4.32 ± 2.15 µg cm^{-2}) relative to CCF (7.03 ± 1.87), when tested after the stabilisation period using all samples (Fig. 4.4; R^2_C = 0.30, F = 6.07, p = 0.036). This difference was mainly driven by one SLG plot (G6) with very low values. No significant difference was found when this plot was excluded from analysis (p = 0.065)

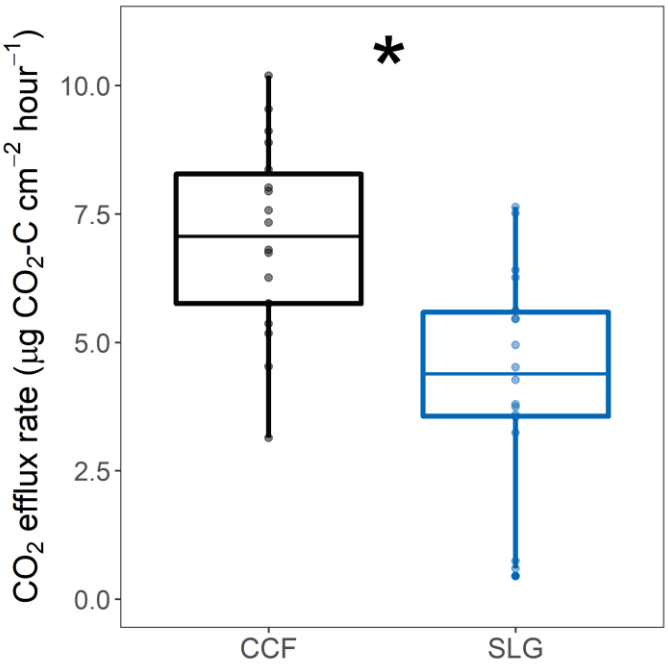

Figure 4.4 *Box and whisker plot of baseline CO_2 efflux rates in closed canopy forest (CFF) and selective logging gaps (SLG) after the 7 day equilibration period before commencing drought treatments. The asterisk indicates a significant difference between forest types at the* $p < 0.05$ *level as identified by ANOVA through linear mixed model (LMM) analysis controlling for site effects and the nested sampling design within plots.*

4.4.2 Effects of drying and rewetting on soil CO_2 efflux rates in CCF and SLG

Drying and rewetting significantly affected soil CO_2 efflux rates within both forest types (Fig. 4.5; see Table 4.1 for summary of all test statistics for effects of moisture treatment at each time point by forest type).

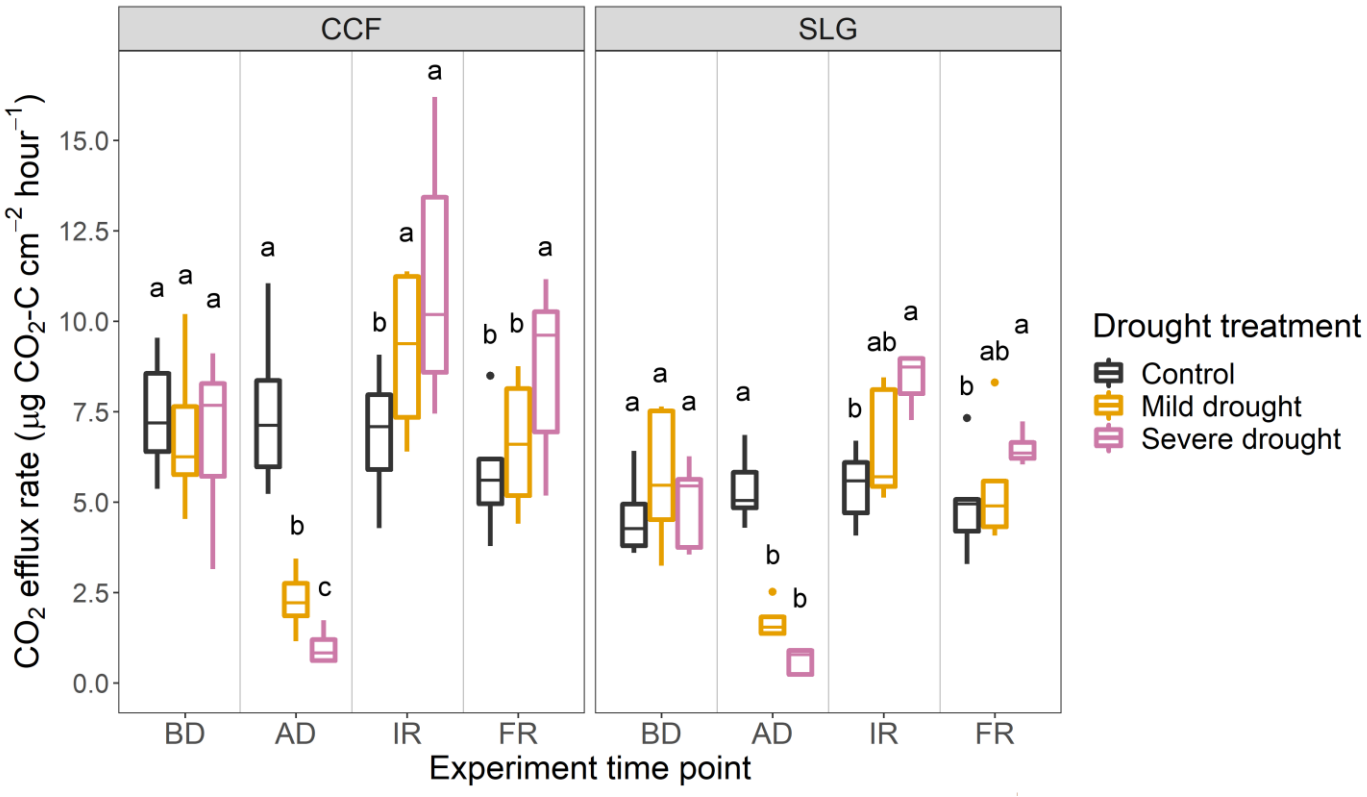

Figure 4.5 *Box and whisker plots of raw soil CO_2 efflux rates for closed canopy forest (CCF) and selective logging gap (SLG) cores for the three moisture treatments at experimental time points: before drought (BD); after drought (AD); initial recovery (IR); final recovery (FR). Lower case letters indicate statistically different or similar means in CO_2 efflux rates between moisture treatments within forest types for each experimental time point at the* $p < 0.05$ *level, identified with ANOVA after controlling for site effects and nested experimental design.*

Table 4.1 ANOVA and post-hoc pairwise test results for the effects of moisture treatment on soil CO_2 efflux rates at each time point by forest types of closed canopy forest (CCF) and selectiv logging gaps (SLG), conducted using linear mixed models (LMMs) controlling for the nested experimental design. *p*-values for pairwise tests were determined using Bonferroni correction.

Time point	Forest type	Overall model		Pairwise tests					
				C-MD		C-SD		MD-SD	
		F	*p*	*t*-ratio	*p*	*t*-ratio	*p*	*t*-ratio	*p*
Before drought	CCF	0.27	0.767	0.66	0.791	0.62	0.814	-0.04	0.999
	SLG	2.83	0.106	-2.29	0.104	-0.59	0.830	1.70	0.251
After drought	CCF	145.95	**0.000**	9.85	**0.000**	17.02	**0.000**	7.17	**0.000**
	SLG	21.68	**0.000**	4.52	**0.003**	6.41	**0.000**	1.89	0.193
Initial recovery	CCF	11.35	**0.003**	-2.93	**0.037**	-4.72	**0.002**	-1.79	0.221
	SLG	11.06	**0.003**	-1.96	0.173	-4.68	**0.002**	-2.72	**0.052**
Final recovery	CCF	8.02	**0.008**	-1.14	0.515	-3.89	**0.008**	-2.76	**0.049**
	SLG	4.17	**0.048**	-0.81	0.705	-2.81	**0.045**	-2.00	0.164

At the after drought time point, mean CO_2 efflux rates of mild and severe drought treatments were significantly lower than respective controls for both CCF and SLG (see Table 4.2 for summaries of mean CO_2 efflux at each experimental time point for each forest type and drought treatment). At the initial recovery time point (three days after rewetting), severe drought treatment CO_2 efflux rates were significantly higher than respective controls for both CCF and SLG. Mild drought treatment CO_2 efflux rates were significantly higher than respective controls for CCF, while those for SLG did not significantly differ. At the final recovery time point (eleven days after rewetting), severe drought treatment CO_2 efflux rates remained significantly higher than respective controls for both CCF and SLG, while mild drought treatment CO_2 efflux rates did not differ from respective controls for either CCF or SLG.

Table 4.2 Means of soil CO_2 efflux rates (± 1 SD) in μg CO_2-C cm^{-2} $hour^{-1}$ for closed-canopy forest (CCF) and selective logging gap (SLG) cores for control (C), mild drought (MD) and severe drought (SD) moisture treatments at the experimental timepoints of before drought (BD), after drought (AD) initial recovery (IR) and final recovery (FR). Superscript letters indicate statistically similar or different mean CO_2 efflux rates between moisture treatments within forest types for each experimental time point at the $p < 0.05$ level identified through ANOVA with post-hoc pairwise tests controlling for the nested experimental design.

Time point	Treatment	Forest type	
		CCF	SLG
BD	C	7.40 ± 1.59	3.96 ± 1.88
	MD	6.82 ± 2.01	4.83 ± 2.68
	ED	6.86 ± 2.26	4.18 ± 2.12
AD	C	7.48 ± 2.15 [a]	4.56 ± 2.17 [a]
	MD	2.28 ± 0.82 [b]	1.44 ± 0.80 [b]
	ED	0.97 ± 0.46 [c]	0.60 ± 0.33 [b]
IR	C	6.88 ± 1.74 [c]	4.61 ± 2.22 [b]
	MD	9.17 ± 2.29 [b]	5.67 ± 2.60 [ab]
	ED	11.09 ± 3.48 [a]	7.14 ± 3.13 [a]
FR	C	5.77 ± 1.60 [b]	4.27 ± 2.16 [b]
	MD	8.68 ± 2.45 [b]	4.67 ± 2.42 [ab]
	ED	6.62 ± 1.83 [a]	5.58 ± 2.27 [a]

4.4.3 Relative effects of drying and rewetting on soil CO_2 efflux between forest types and drought treatments

Neither absolute change in CO_2 efflux rates or RRs differed between CCF and SLG at any experimental time point for either mild or severe drought treatments (Fig 4.6; see Table 4.3 for summary of all test statistics for effects of drought treatment on absolute change in CO_2 efflux and response ratios at each time point by forest type).

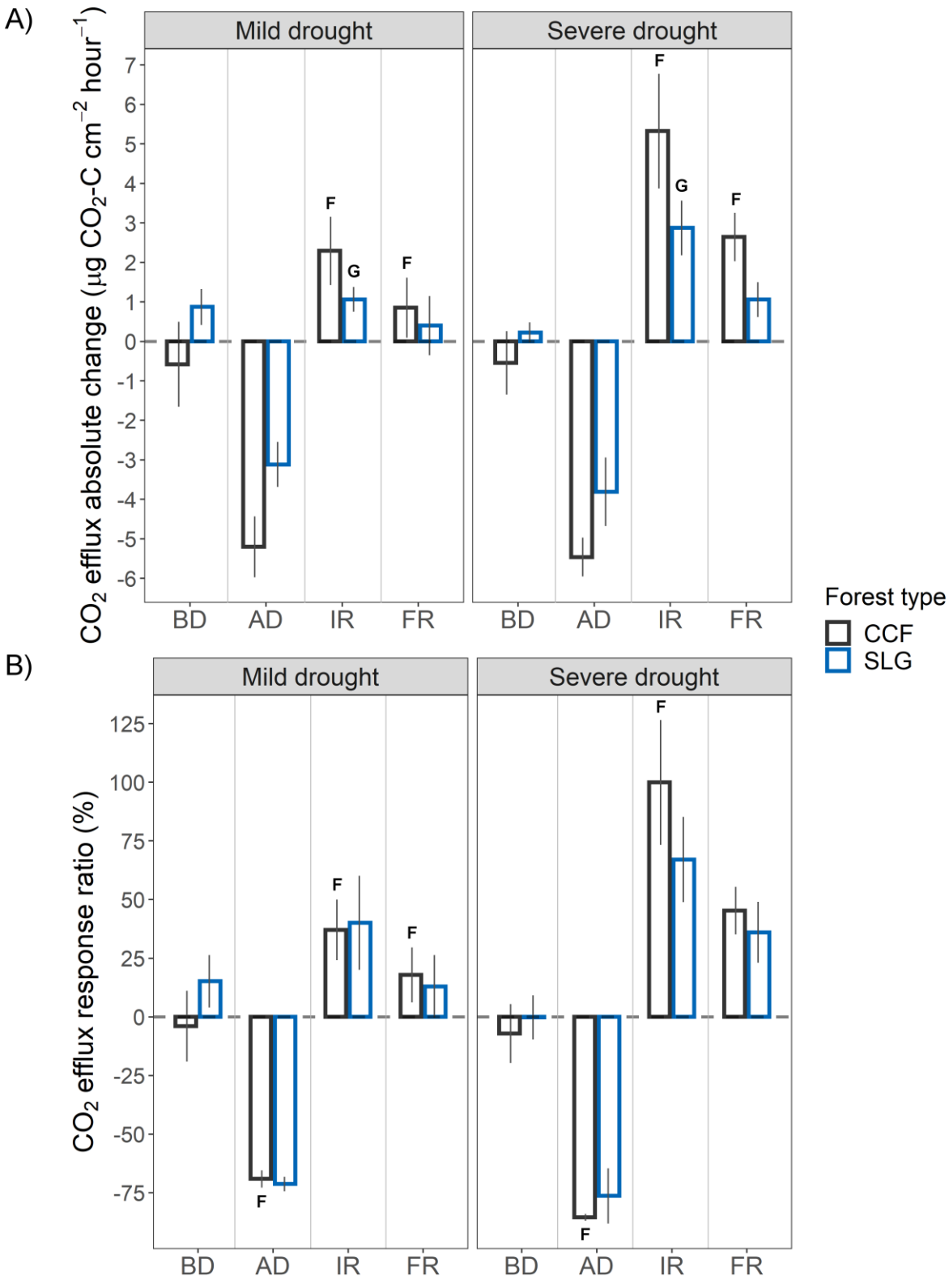

Figure 4.6 Barplots of means (± SE) for A) absolute change and B) proportional change (response ratios) in CO_2 efflux rates relative to controls for closed canopy forest (CCF) and selective logging gap (SLG) soil cores by mild and severe drought treatments at experimental time points: before drought (BD); after drought (AD); initial recovery (IR) and final recovery (FR). Capitalised letters indicate significant differences in absolute change or response ratios between drought types at the same experimental time points within forest types for CCF (F) and SLG (G).

Table 4.3 ANOVA results for differences in absolute change (AC) and proportional change (response ratios; RR) in CO_2 efflux rates between 1) forest types of closed canopy forest (CCF) and selective logging gaps (SLG) and 2) mild and extreme drought types relative to control cores at each time point. Analyses were conducted using linear models for vegetation type controlling for site effects, and linear mixed models (LMMs) for drought types controlling for the nested experimental design.

Parameter	Comparison between	Time point	Within group	*F*	*p*
AC	Forest types	Before drought	Mild drought	1.43	0.262
			Severe drought	1.03	0.336
		After drought	Mild drought	4.27	0.069
			Severe drought	2.52	0.147
		Initial recovery	Mild drought	0.17	0.691
			Severe drought	2.55	0.145
		Final recovery	Mild drought	0.17	0.691
			Severe drought	3.98	0.077
	Drought types	Before drought	CCF	0.00	0.962
			SLG	2.57	0.170
		After drought	CCF	0.24	0.644
			SLG	2.18	0.200
		Initial recovery	CCF	13.05	**0.015**
			SLG	8.72	**0.032**
		Final recovery	CCF	13.66	**0.014**
			SLG	0.73	0.432
RR	Forest types	Before drought	Mild drought	0.95	0.355
			Severe drought	0.24	0.633
		After drought	Mild drought	0.19	0.671
			Severe drought	0.00	0.998
		Initial recovery	Mild drought	0.02	0.904
			Severe drought	1.02	0.338
		Final recovery	Mild drought	0.08	0.787
			Severe drought	0.30	0.595
	Drought types	Before drought	CCF	0.07	0.796
			SLG	3.44	0.123
		After drought	CCF	16.08	**0.003**
			SLG	1.94	0.197
		Initial recovery	CCF	14.29	**0.013**
			SLG	1.02	0.338
		Final recovery	CCF	19.60	**0.007**
			SLG	2.37	0.158

For CCF, absolute change in CO_2 efflux was significantly greater in the extreme relative to mild treatment at the initial recovery and final recovery experiment time points (Fig 4.6 A). For SLG, absolute change in CO_2 efflux was also significantly

greater in the extreme relative to mild treatment at the initial recovery experiment time point, but not final recovery. CCF RRs were of a significantly larger magnitude (positive or negative) in the extreme drought treatment relative to the mild drought treatment at the after drought, initial recovery and final recovery experiment time points (Fig 4.6 B). SLG RRs did not significantly differ between drought treatments at any experiment time points.

4.4.4 Effects of drought treatments on soil % WHC within and between forest types

% WHC of samples significantly differed between treatment time points before drought, after mild drought and after severe drought (Fig 4.7; all pairwise tests: $p < 0.0001$).

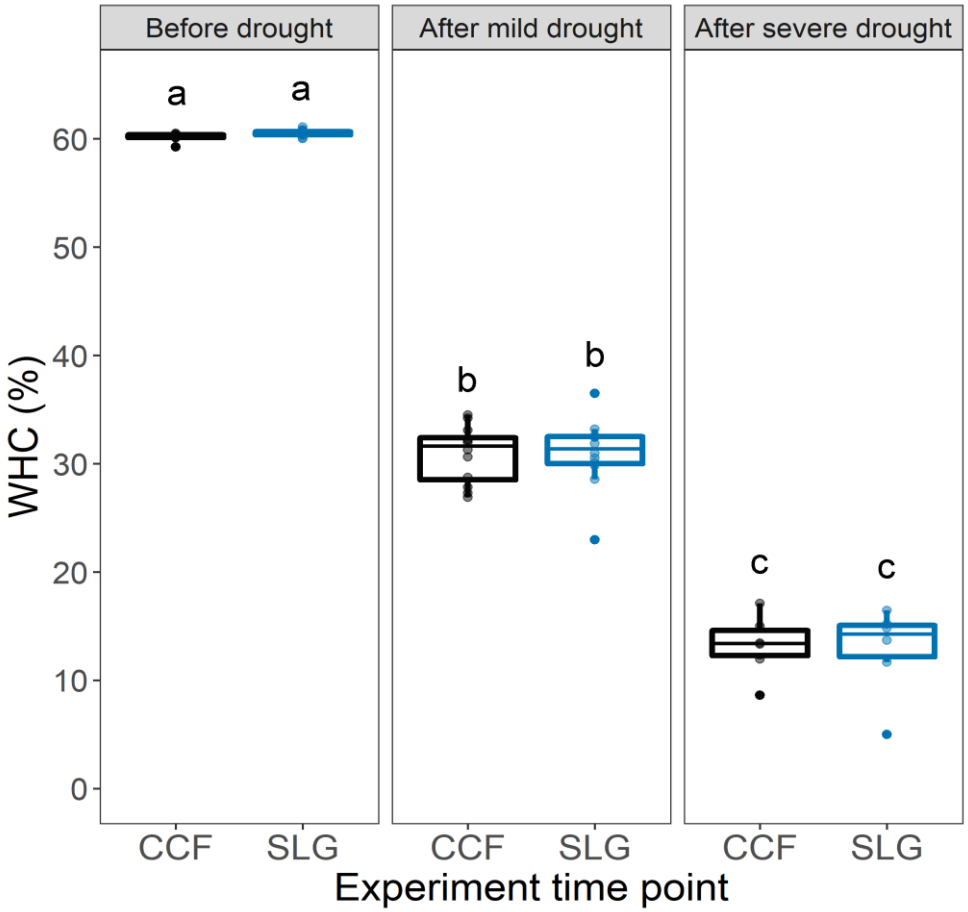

Figure 4.7 *Box and whisker plots of estimated % soil water holding capacity (WHC) in closed canopy forest (CCF) and selective logging gap (SLG) soil cores before drought and after mild and severe drought treatments. Lower case letters indicate statistically different groups between treatment time points within forest types at the* p *< 0.05 level identified with ANOVA and pairwise post-hoc tests.*

No differences were found in % WHC between CCF and SLG at any time point tested for either drought treatment ($p > 0.05$). However, variation around the mean was slightly larger in % WHC of SLG relative to CCF soils (Table 4.4).

Table 4.4 Means of soil % WHC (± 1 SD) for closed-canopy forest (CCF) and selective logging gap (SLG) cores at treatment time points of before drought, after mild drought and after severe drought. Superscript letters indicate statistically similar or different mean % WHC between treatment time points within forest types at the $p < 0.05$ level, as identified through ANOVA with pairwise post-hoc tests controlling for the nested experimental design.

Treatment time point	Forest type	
	CCF	SLG
Before drought	60.19 ± 0.33 [a]	60.52 ± 0.32 [a]
After mild drought	30.89 ± 2.64 [b]	30.99 ± 3.24 [b]
After severe drought	13.24 ± 2.87 [c]	12.80 ± 4.15 [c]

4.5 Discussion

Baseline CO_2 efflux after the equilibration period was found to be significantly lower in SLG relative to CCF (Fig. 4.4), in line with the initial hypothesis that R_S is negatively influenced by SL disturbance. This is consistent with observations in a previous study in SL forest in Sabah, Borneo, where *in situ* field measurements of soil CO_2 efflux was also found to be lower in SLG (Saner et al., 2009). While supporting these observations, findings contrast with other studies in dipterocarp forest of Peninsular Malaysia, where the effect of SL on soil CO_2 efflux was not detected either between CCF and SLG after approximately 50 years of recovery (Adachi et al., 2006), or between old-growth and SL forest (Yashireo et al., 2008). Meanwhile, in other tropical systems, reduced soil CO_2 efflux has been reported in response to clearance of moist deciduous forest in India (Mohanty and Panda, 2011) and plantation forest in Congo (Epron et al., 2006). However, none of these field studies could disentangle the relative effects of vegetation

structure and composition, microclimate, and soil microbial community attributes on altered R_S with forest disturbance. Saner et al. (2009) attributed the suppression of R_S in SLG in Borneo mainly to differences in vegetation (i.e. lower fine-root biomass in SLG), potentially reducing the contribution of autotrophic plant root respiration to overall soil CO_2 production. By removing the influences of vegetation and controlling temperature and soil moisture conditions, the present study highlights the importance of SL-induced changes to soil physicochemical properties and soil microbial communities in shaping microbial heterotrophic respiration responses to forest disturbance which may be an important component of overall R_S. These findings are congruent with those of other tropical soil incubations studies similarly demonstrating reduced R_S in response to forest disturbance under controlled laboratory conditions, for example comparison of CO_2 efflux of soils from natural forest and deforested land in India (Sahini and Behera, 2001). In studies of SL impacts on resistance and resilience of soil microbial functioning in temperate biomes, soil microbial CO_2 production has been linked to severity of soil compaction associated with timber extraction (i.e. through use of heavy machinery) (Hartmann et al., 2013). This was attributed to changes in soil microbial community structure and reduced microbial decomposition under more anaerobic conditions, as well as increased physical protection of soil organic matter and reduced gas diffusivity. Analyses of physicochemical properties in the present study plots found greater soil bulk densities in SLG relative to CCF (Chapter 2), soil compaction may thus be a contributory mechanism down-regulating soil microbial CO_2 production rates and overall R_S in SLG.

Results did not support the initial hypothesis that functioning of SLG soils would be more resistant than CCF soils to drought. Both CCF and SLG soil CO_2 efflux rates were significantly negatively affected by mild and severe drought treatments (Fig.

4.5). For CCF soils, CO_2 efflux was significantly lower after the severe drought relative to the mild drought treatment, while post-drought CO_2 efflux did not differ between drought treatments for SLG. Despite this, no difference was found in either the absolute or relative (%) change in CO_2 efflux rates between CCF and SLG. The prediction that the more compacted soils of SLG would reduce soil evaporation rates through decreased hydraulic conductivity and corresponding increased soil water matric potential (Yamanaka et al., 1998; Aydin et al., 2005; Hartmann et al., 2013; Box and Taylor, 1962) was not corroborated, as there was no difference found in % WHC between CCF and SLG soils after 7 or 15 days of drying (Fig. 4.7).

The observed reduction in R_S of both CCF and SLG soils under drought conditions may represent a combination of mechanisms underpinned by moisture availability, a fundamental factor governing soil microbial community attributes and activity (Manzoni et al., 2012; Moyano et al., 2013; Tecon and Or, 2017; Waksman and Gerretsen, 1931). Firstly, moisture-dependent stable state decompositional processes may be down-regulated by drought (Manzoni et al., 2012), i.e. a slowing of microbial metabolic activity (e.g. mineralisation; Cassman and Munns, 1980; Hueso et al., 2012) and reduction in substrate supply to microbial decomposers through inhibition of soil solute and enzyme mobility (Stark and Firestone, 1995; Schjønning et al., 2003). Subsequent lowering of microbial growth rates in turn reduces overall soil microbial biomass and net microbial activity (Hueso et al., 2012). Secondly, drought can impact on soil microbial community structure itself, as well as functional diversity (Hueso et al., 2012) which may have downstream consequences for C-cycling capabilities (Bouskill et al., 2016b). This occurs as unadapted soil microbes die under low moisture conditions (van Meeteren et al., 2008), while those more tolerant to water stress are selected for (Evans et al., 2011). Different microbial groups may be affected more

strongly, with bacteria generally more sensitive to drought than fungi (Manzoni et al., 2012). The magnitude of these effects therefore depends on the adaptive capacity of the soil microbial communities present to environmental disturbance, which may be influenced by previous exposure to perturbations (de Nijs et al., 2019; Evans et al., 2011; Bouskill et al., 2016b). While there was no evidence of soil structural properties buffering the drying effects of drought in SLG, similar % WHC values and CO_2 efflux rates in CCF and SLG at the time of gas sampling indicate that microbial R_S responds similarly to similar moisture deficits in CCF and SLG, even though soil bacterial and fungal communities have been found to differ in overall composition between these forest types (Chapter 2). This finding supports the notion that neither soil microbial communities of CCF or SLG are more or less acclimated to drought conditions through previous exposure to low moisture conditions, which may present a hysteretic R_S response to drought as has been observed in other controlled tropical forest soil incubation studies, for example higher CO_2 efflux rates from soils under laboratory drought conditions that were previously subjected to short-term throughfall exclusions in Costa Rican forest (Waring and Hawkes, 2014).

In contrast to the reduced soil CO_2 efflux rates observed with drying in the present study, field experiments in tropical forest systems have in some instances shown increased R_S in response to experimental drought treatments, for example in another Costa Rican study (Cleveland et al., 2010). This has also been observed in response to natural drought conditions, as observed in high-frequency measurements of greenhouse gas emissions in Puerto Rican forest during the severe Caribbean drought of 2015, where soil CO_2 efflux increased dramatically by 60 % and 163 % on slopes and in valleys, respectively (O'Connell et al., 2018). Elevated R_S with drought may be attributed to increased soil oxygen (O_2) availability with reduced moisture, or by

increased microbial respiration efficiency due to higher concentrations of dissolved organic carbon (DOC) reaching the soil from the litter layer with reduced throughfall. The latter may also potentially stimulate priming effects, i.e. the breakdown of more recalcitrant soil C pools through addition of concentrated and more labile C substrates (Cleveland et al., 2010). However, in some cases field throughfall exclusions have reduced soil CO_2 efflux, for example during a long-term experiment in Indonesia (van Straaten et al., 2011), or had no impact, for example in tropical forest of Southern China (Deng et al., 2018). According to a recent synthesis of the effects of field drought simulations in tropical forest, the differences between these observations may result from system-specific soil moisture thresholds, where peak R_S occurs somewhere between very wet and very dry soil conditions, and with this point varying by ecosystem (Meir et al., 2015). In the present study, reduced CO_2 efflux rates with a lowering of soil moisture from average field conditions suggests a negative effect of drought on R_S in these systems, although it is important to note the litter layer was removed from soil before incubation and so effects of litter-associated DOC inputs were not included.

The magnitude of CO_2 effluxes after rewetting was higher following the severe relative to the mild drought treatment for both CCF and SLG soils when absolute change in CO_2 efflux was analysed. This supports the third hypothesis that CO_2 efflux pulses are related to drought intensity, as shown in other study systems (Canarini et al., 2017). As the influence of vegetation inputs was removed in this controlled experiment, this likely results from the increased accumulation of microbial necromass during longer periods of low soil moisture conditions, providing a greater labile C source for rapid regrowth and turnover of soil microbes after drought (Blazewicz et al., 2014). There were no differences found in relative magnitude of pulses CO_2 efflux between CCF or SLG (absolute or proportional change) at the initial recovery time point, which may

result from similar microbial biomass pools as found in previous biological analysis (Chapter 2).

The final hypothesis that SLG soils would be more resilient to drought and rewetting compared to CCF was only partially supported. Relative responses in CO_2 efflux after drought and rewetting were found to be similar in CCF and SLG at both the initial and final recovery experiment time points. However, CO_2 efflux rates in CCF soils were significantly higher than respective controls after mild drought treatment 7 days after rewetting, while SLG CO_2 efflux rates did not differ from controls (Fig. 4.5). This suggests that soil communities and function may recover more rapidly in SLG than CCF after less severe drought. Furthermore, the relative effects of drought severity (proportional change) were much more pronounced for CCF soils, as CO_2 efflux rates significantly differed between drought treatments at each timepoint for this forest type, while SLG CO_2 efflux rates did not (Fig. 4.5). The lack of differences detected between drought treatments in SLG may indicate lesser sensitivity of SLG soil function to more extreme drought, particularly as means of absolute change in CO_2 efflux rates and response ratios tended to be smaller relative to CCF (although not significantly) after the severe drought treatment (Fig 4.6). However, absence of clear differences in SLG R_S responses to differing drought intensities or between CCF and SLG after rewetting may also result from higher variation in SLG soils relative to mean values. This suggests that while some SLGs may be more resilient to drought and rewetting, others may be much less so, potentially due to other soil abiotic and biotic properties not characterised by CCF and SLG classifications.

Following the severe drought treatment, both CCF and SLG CO_2 efflux rates remained significantly higher than respective controls at the final recovery time point,

11 days after rewetting. There are two possible mechanisms responsible for this observation. Firstly, continued elevated R_S may indicate that temporary CO_2 efflux pulses associated with a burst in microbial growth and activity on rewetting (Birch, 1958; Zhou et al., 2016; Blazewicz et al., 2014; Karlowsky et al., 2018) may be prolonged in both CCF and SLG soils after intense drought, with recovery times longer than the period studied. Although these pulses may peak in the seconds or minutes after rewetting, it may take several days before soil functions return to pre-drought conditions (Song et al., 2017; Huxman et al., 2004). Secondly, extremely low soil moisture conditions may have permanently altered microbial communities and associated ecophysiological traits, leading to a persistent alteration in soil functioning (Meisner et al., 2018). Although drought was predicted to result in sustained elevation of R_S in CCF soils due to shifts toward microbial breakdown of more complex C compounds associated with canopy cover (Bouskill et al., 2016a; Bouskill et al., 2016b), these findings may indicate alterations in metabolic characteristics and C cycling capabilities of soil microbial communities in both CCF and SLG soils.

A number of study limitations need to be recognised with respect to interpretation of differences (and non-differences) observed in R_S responses to drought and rewetting of CCF and SLG soils. Due to the high number of cores measured and time requirement for gas sampling, CO_2 efflux was only measured at the end point of mild and extreme drought periods and at 7 and 11 days following rewetting. The resolution of gas sampling may therefore limit detectability of differences in CO_2 efflux rates during drought and recovery periods which may be highly dynamic. While CCF soils demonstrated clear R_S responses to drought of differing intensities, impacts on R_S of SLG were less certain due to high variability. Further study incorporating different classes of SLG according to soil biological and physicochemical properties may help to

clarify the range in observed sensitivity of soil function in SLG to environmental perturbations, and improve predictions of responses to land-use and climate change in SL forest. As no further measurements were made after 11 days of recovery, it remains unclear whether elevated R_S following severe drought in CCF and SLG soils at the final recovery stage represents a prolonged but temporary burst in microbial activity, or a persistent or permanent shift in microbial communities and ecophysiological traits related to breakdown of different C fractions. Similarly, the underlying drivers of lower baseline CO_2 efflux rates in SLG relative to CCF are unknown. Analysis of soil microbial functional traits pre- and post-drought perturbations (e.g. extracellular enzyme production) may help to unpick the mechanisms (Bouskill et al., 2016b). Furthermore, substrate addition experiments utilising C compounds of differing structural complexities are also recommended to identify specific differences in soil microbial C cycling capabilities (e.g. Whitaker et al., 2014a; Whitaker et al., 2014b), and subsequent implications of SL and climate induced changes in soil microbial functions. Finally, only a single drying and rewetting cycle was studied, and impacts of repeated drought events which may compound alterations in soil functions (Fierer and Schimel, 2002) remain unresolved.

In conclusion, baseline R_S was found to be lower in SLG relative to CCF soils, corresponding to previously found differences in soil microbial community structure and physicochemical properties between vegetation types. This highlights the important impacts of SL disturbance on soil microbial heterotrophic R_S not previously identified due to extraneous vegetation and microclimatic factors. No evidence was found for differences in resistance of soil functioning to drought between CCF and SLG, which experienced similar soil moisture deficits after mild and severe drought treatments despite differences in soil structural characteristics. Magnitude of CO_2 efflux rates

increased with drought intensity in initial recovery following drought for both forest types. Some evidence was found for greater resilience of SLG soil function to drought and rewetting, although further study including higher resolution of sampling time points and inclusion of different classifications of SLG types may help to identify underlying mechanisms. R_S remained significantly higher than controls at the final recovery stage following the severe drought treatment for both forest types, indicating prolonged alterations in soil functioning that may relate to ecophysiological changes in soil microbial communities as a result of disturbance. While future experiments including repeated drought-rewetting cycles and substrate additions may help to clarify longer term responses of differing vegetation types of SL Southeast Asian tropical forest soils to environmental perturbations, these findings have major implications for increased CO_2 release to the atmosphere in response to climate change events predicted to increase in intensity and frequency across tropical regions.

5 Restoration effects on soil microbes in Bornean lowland dipterocarp rainforest

5.1 Abstract

Rapid loss of forest cover in Borneo due to expansion of monoculture plantation puts increasing pressure on remaining forest to provide globally important ecosystem services, including carbon storage. The majority of remaining forest is heavily degraded through selective logging, impacting on vital biogeochemical cycles underpinned by complex plant-soil microbial interactions. Ecological restoration offers potential for recovery of ecosystem functions in degraded tropical forest, through re-establishing vegetation and soil microbial communities. However, most studies have focussed on aboveground dynamics during rehabilitation, and understanding of patterns in soil microbial community attributes and function remains limited. To address this, a survey of soil microbial communities was conducted across old-growth (OG), unrestored selectively-logged (USL) and restored selectively-logged (RSL) forest in Sabah, Borneo. Results indicate that restoration by enrichment planting can successfully recover levels of bacterial alpha diversity and spatial turnover of bacterial taxa comparable to OG. Fungal diversity appeared to recover more slowly, largely due to saprotrophic fungal richness and Shannon alpha diversity remaining similar to USL. Soil microbial community compositions were generally more similar between USL and RSL, with more distinct communities in OG. An apparent absence of fungal suppressors of plant pathogens and parasites with restoration may have negative implications for reestablishment of planted species. Surprisingly, fewer microbial taxa were shared between OG and RSL compared to other forest types. This indicates potential selection of different soil microbial taxa through current restoration practices, including removal of lianas and understorey vegetation. The observed impact of forest degradation on

bacterial diversity contradicts previous coarser spatial scale studies that found bacterial communities to be broadly resilient to selective logging, emphasising the importance of fine-scale (cm to m) approaches to evaluation of soil microbial biodiversity patterns. Overall findings suggest impediment to rehabilitation of soil microbial community attributes and associated functions, with implications for landscape-scale biogeochemical cycling. Changes in management practices to incorporate rehabilitation of belowground communities may be required for successful biodiversity conservation and recovery of vital ecosystem services including C storage.

5.2 Introduction

Old-growth forests (OG) are rapidly being replaced by human-modified secondary forest worldwide, with highest conversion rates in the tropics (Keenan et al., 2015). The degradation of tropical forest ecosystems by human activity affects their crucial function as global reservoirs of biodiversity and carbon (C) (Myers et al., 2000; Pan et al., 2011; Powers and Jetz, 2019; Baccini et al., 2017; Qie et al., 2017). The forests of Borneo are a hotspot of forest disturbance and loss, driven by commercial timber extraction and conversion to oil palm plantations. A reduction of forest cover by more than 30 % since the early 1970's means increasing pressure on remaining forest to provide vital ecosystem functions, although over 70 % of this remaining forest has been disturbed through selective logging (Gaveau et al., 2014; Gaveau et al., 2016) affecting its capacity as a carbon sink (Asner et al., 2018).

Forest degradation can significantly affect soil physicochemical properties (see Chapter 1), often reducing soil carbon pools (Don et al., 2011; Wei et al., 2014) and altering nutrient availability and overall fertility (Paul et al., 2010; Daljit Singh et al., 2013). This subsequently influences microbial communities (Tripathi et al., 2012; Jesus et al., 2009) and biogeochemical cycles, underpinned by complex plant-soil interactions and reciprocal feedbacks between vegetation and soil microbes (Cortois et al., 2016; van Der Putten et al., 2013; Bever et al., 2010; van der Heijden et al., 2008; Wardle et al., 2004). Although the preservation of primary forest is crucial for biodiversity conservation and the maintenance of ecosystem functions (Gibson et al., 2011), natural and managed restoration of secondary tropical forest has great potential to recover ecosystem services (Chazdon, 2008; Melo et al., 2013; Wright, 2010) including carbon storage (Pan et al., 2011). Rainforest rehabilitation through planting programmes is now a widely used strategy to recover vegetation structure and diversity after disturbance

(Celis and Jose, 2011; Shoo et al., 2016; Bonner et al., 2019). Enrichment planting, involving the reintroduction of tree species lost through human disturbance (usually systematically along regularly placed planting lines), has been adopted across Southeast Asia as a strategy to restore forest floristic composition towards that of OG forest (Perumal et al., 2016). This practice is often accompanied by liana cutting and clearing of understorey vegetation along planting lines, to facilitate establishment of reintroduced seedlings by reducing competition for resources (Face the Future, 2007; 2020). This approach is currently employed in large-scale restoration projects (approaching 30,000 ha) established over recent decades in the Malaysian state of Sabah (Reynolds et al., 2011), where forest degradation has been most extreme (Gaveau et al., 2014). However, success of tropical forest planting programmes has in many cases been limited by lack of context-specific knowledge of the ecology of planted tree species, including plant-soil interactions (e.g. Rodrigues et al., 2009). For enrichment planting, the majority of studies in Malaysia has focussed on the survival, growth and productivity of planted tree species, with little consideration of soil physicochemical and biological properties, or wider ecosystem functions (Perumal et al., 2016). Understanding of the capacity for recovery of tropical forest soil physicochemical properties, microbial community attributes and biogeochemical processes is broadly limited due to few studies having been made (Bonner et al., 2019).

Some studies of restoration planting following forest clearance observed increases in microbial biomass C (MBC) (Deng et al., 2010; Nurulita et al., 2016) and bacterial alpha diversity, with alterations in bacterial community structure that may indicate ecosystem recovery (Deng et al., 2010). The small number of studies undertaken in enrichment planted secondary Malaysian forest also highlight increases in microbial biomass towards OG (Daisuke et al., 2013; Perumal et al., 2016; Daljit

Singh et al., 2013). However, microbial indicators can be system-specific and depend on type, intensity and duration of disturbance (Banning et al., 2011). In general, there is a lack of understanding of the patterns of microbial responses to ecosystem restoration (Banning et al., 2011; Strickland et al., 2017). This outlines a major knowledge gap for understanding the potential for secondary forest recovery, and evaluation of the success of rehabilitation.

While very little is known about impacts of restoration on soil microbial attributes, more is known about effects of disturbance. Selective logging (SL) in SE Asia has been shown to influence soil fungal community composition and diversity, largely through targeted removal of the dominant ectomycorrhizal-associating dipterocarp tree species, having major implications for carbon and nutrient cycling (Chapter 1; Chapter 2; Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015). Soil bacterial communities appear more resilient to disturbance, with two studies conducted in Malaysian Borneo finding no differences in alpha or (community distance-based) beta diversity of bacterial communities between OG and SL forest using 16S amplicon sequencing (Tripathi et al., 2016; Lee-Cruz et al., 2013). However, findings from a higher spatial resolution study in SL (Chapter 2) indicate a finer-scale approach may be necessary to detect impacts of SL on soil microbial structure and diversity. Inference of results from previous landscape-scale surveys may therefore be hindered by coarse sampling resolution (composite samples bulked over 200 m transects), as bacterial communities may vary considerably at the metre- or even centimetre-scale (O' Brien et al., 2016). Furthermore, apparent effects of SL on “true” beta diversity (Lee-Cruz et al., 2013) show a sensitivity of results to definition and calculation of diversity metrics. In some tropical systems, soil microbial alpha and beta diversity have been shown to become uncoupled during disturbance (e.g. through conversion of Amazonian

forest to cattle pasture), through increasing local (alpha) diversity, while spatial turnover of taxa (beta diversity) is reduced. This may result in overall net losses in diversity of soil microbial taxa, and homogenisation of communities across landscapes (Rodrigues et al., 2013). Increases in bacterial alpha diversity have also been observed in agricultural land versus forest in Malaysia (Tripathi et al., 2012). Alterations in soil microbial communities and diversity with ecosystem disturbance may arise from effects on soil physicochemical properties determining both availability of effective resources and creation of different ecological niches (Zhang et al., 2018). Soil microbial biodiversity has the potential to increase with a certain level of disturbance (the intermediate disturbance hypothesis: Zhang et al., 2011; Ferrenberg et al., 2013; Galand et al., 2016; Wilkinson, 1999), while changes in community composition and functional capabilities may directly relate to disturbance intensity (Berga et al., 2012). Reversal of ecosystem disturbance effects through active restoration may therefore recover soil microbial attributes along with availability of effective resources and ecological niches. However, effects of SL disturbance and restoration on bacterial diversity patterns in these ecosystems is unresolved, limited by both sampling resolution and lack of unification in analytical approaches to comparisons of diversity at different scales. This represents a vital knowledge gap for evaluating consequences of disturbance, and crucially potential mitigation through ecosystem rehabilitation.

One particular relationship used to study spatial biodiversity patterns is the decrease in similarity of community compositions with increasing geographic distance, known as distance-decay (Nekola and White, 1999; Morlon et al., 2008). Although such biogeographical approaches have been widely used for macro-organisms, advances in molecular techniques have allowed for studies focussing on microbial communities (Green et al., 2004; Martiny et al., 2006). A central element of the theory underlying

the distance-decay relationship attributes decreases in community dissimilarity to spatial changes in environmental conditions (Soininen et al., 2007). SL has been shown to create highly heterogenous forest environments in terms of vegetation structure, plant composition, environmental and soil conditions related to microbial community compositions (see Chapter 2). As the distance-decay relationship can be derived using distances ranging from centimetres to kilometres simultaneously (e.g. Barreto et al., 2014), this approach offers a method to directly compare rates of spatial turnover in microbial taxa (beta diversity) as a result of environmental heterogeneity between OG, SL and restored forest across scales not previously studied.

To address these knowledge gaps, we evaluated differences in soil microbial community attributes, soil physicochemical properties, and environmental and vegetation characteristics between OG, logged-unrestored (USL) and logged-restored (RSL) forest in Bornean lowland dipterocarp rainforest across different spatial scales. We conducted this study with the following specific hypotheses:

H1. Bacterial community attributes will be affected by forest type, with bacterial alpha diversity greater in USL due to ecosystem disturbance effects on effective resources and functional niches (intermediate disturbance hypothesis). This will correspond to lower spatial turnover of taxa, as observed in similar study systems. Bacterial diversity patterns will be more similar between OG and RSL due to active restoration recovering available resources and ecological niches.

H2. Fungal community attributes will be affected by forest type, with differences in community composition, alpha diversity and spatial turnover of taxa driven by USL. Fungal community attributes in OG and RSL will be more similar, corresponding to greater shared fungal taxa between OG and RSL than

OG and USL. This is expected due to more similar vegetation composition, including mycorrhizal-associating tree species, and litter inputs influencing saprotrophic fungal composition.

H3. Overall microbial biomass indicators will increase with restoration towards OG, as previously observed in other studies of enrichment planted SL forest in Malaysia.

H4. Differences in soil microbial attributes between forest types will correspond to differences in soil physicochemical properties and environmental and vegetation characteristics, as observed in previous studies of SL disturbance in these systems.

5.3 Methods

5.3.1 Study sites

This study was conducted in the state of Sabah, northern Malaysian Borneo. The climate is characterised as moist tropical (average daily temperature 27 ˚C, annual precipitation 2,600 - 2,700 mm) and without distinct seasonality, although may undergo irregular inter-annual dry periods averaging a total of ~1.4 months of the year (Walsh and Newbery, 1999; Kumagai and Porporato, 2012). Sampling was conducted in March 2018 at a total of nine sites across adjacent OG, USL and RSL lowland dipterocarp rainforest (3 sites in each). USL and RSL forest were situated within the Innoprise Face Foundation Rainforest Rehabilitation Project (INFAPRO) area (4.99°, 117.86°). This large-scale restoration initiative, in partnership with the Yayasan Sabah Foundation, aims to restore 25,000 ha within the Ulu-Segama forest management unit (Face the Future, 2007). USL and RSL forests were both selectively-logged once in 1989. The RSL forest has undergone rehabilitation by enrichment planting since 2000, with

mixtures of dipterocarp and various fruit tree species planted at 3 m intervals along transects 10 m apart. Planting lines are maintained regularly by liana cutting and removal of understorey vegetation (Face the Future, 2007). OG forest was located in the adjacent Danum Valley Conservation Area (4.95°, 117.79°), a 438 km^2 rainforest reserve that has undergone little or no anthropogenic disturbance legally protected from commercial timer operations since 1976 (Marsh and Greer, 1992).

5.3.2 Sampling design for soil, environmental and vegetation characteristics

Three sampling sites were established in each forest type of OG, USL and RSL. Sites were situated a minimum of 500 m apart (measured using a GPS), with similar distances of 600 – 1,500 m between sites of different forest types. This allowed for direct comparison of soil microbial attributes, soil physicochemical, environmental and vegetation characteristics. At each of the nine sites, a geospatial transect design was used for soil sampling and measurement of environmental and vegetation characteristics. Three connected transects were established, radiating out from one centre point and positioned at 120 ˚ to one another. The first transect was oriented towards due North. Sampling points for soil physicochemical properties and environmental metrics were located at the centre point, and then at increasing distances of 10 cm, 30 cm, 90 cm, 2.7 m, 8.4 m and 24.3 m along each transect relative to the centre. Distances were calculated using a factor of three, chosen to allow assessment of spatial heterogeneity in soil microbial communities over scales of different orders of magnitude.

At each sampling point, one soil core was collected a using a 3 cm-diameter gouge auger to a depth of approximately 10 cm for analysis of soil microbial community attributes and physicochemical analysis. The depth of the organic soil layer was

measured before it was separated from underlying mineral soil, sealed in a Ziploc bag and transported to a laboratory. Here samples were hand-homogenised and approximately 10 g subsamples taken for analysis of soil microbial community attributes. These were frozen at -20 ˚C on the day of collection and transported on ice to the UK for analysis of soil microbial communities: 5 g was transported to Centre for Ecology & Hydrology, Wallingford for amplicon sequencing and 5 g to Lancaster University for Phospho-Lipid Fatty Acid (PLFA) analysis. The remaining soil was transported to the Sabah Forest Research Centre, Sepilok for physicochemical analysis. Nineteen soil samples were collected per site, with a total of 171 overall across all forest types.

Environmental metrics were measured during sampling at each of the sampling points. Soil temperature (approximate depth 0-10 cm) and air temperature at the soil surface (5-15 cm) were measured with using a thermistor (Salter, UK). Photosynthetically active radiation (PAR) was measured using a light meter (PP Systems, USA) with the sensor held just above the soil surface.

For vegetation characteristics, all stems with diameter at breast height (DBH) > 5 cm were recorded and circumferences measured within a 2.5 m buffer of all transects, for calculation of stem density and basal area. This DBH was chosen to capture finer-scale variation in tree abundance. Stem density and basal area were calculated at the site-level (n = 9).

5.3.3 Soil physicochemical analysis

pH in water was measured on fresh soils using a pH meter with a combination glass-calomel electrode (a ratio of 1:2.5 soil to deionised water) after shaking overnight at 100 rev m^{-1} on an orbital shaker and standing for 30 min (Landon, 1984). The remaining

soils were air-dried at 40 °C to constant weight and passed through a 2 mm sieve for homogenisation and removal of roots and stones. Subsamples for Total C and N analysis were dried at 65 °C for 48 hours and milled to a fine powder with a pestle and mortar. Total soil C and N contents were determined by dry combustion at 900°C using an Elementar Vario Max CN analyser (Elementar Analysensysteme, Hanau, Germany). For soil Total P, samples were digested using sulphuric acid-hydrogen peroxide (Allen, 1989). Inorganic P was extracted using a Bray No. 1 extractant (Bray and Kurtz, 1945). P contents of extracts and digests were determined using the molybdenum-blue method (Anderson and Ingram, 1993), read at 880 nm on a spectrophotometer (HITACHI-UV-VIS, Japan).

5.3.4 Soil Phospholipid Fatty Acid (PLFA) analysis

A subset of soil samples were analysed for PLFAs to provide indicators of total microbial biomass and relative abundances of bacteria and fungi across forest types. Due to the intensive extraction requirements, 36 of the 171 samples were analysed (four samples per site). These corresponded in each site to the transect centre point, and 30 cm, 2.7 m and 24.3 m sampling points along the first transect. Soil samples were freeze dried, coarse roots and stones were removed prior to analysis. PLFAs were extracted from 1.8 g freeze dried soil using a modified version of the Bligh and Dyer extraction method (White et al., 1979). Extracts were analysed using an Agilent 6890 Gas Chromatograph with Flame Ionisation Detector (GC-FID; Agilent Technologies, Unites States) using an RTx-1 capillary column (60 m × 0.32 mm ID, 0.25 µm film thickness). PLFA peaks were identified using retention times calibrated against known standards. As indicators of Gram-positive bacterial biomass, the branched-chained fatty acids C15:0i, C15:0a, C16:0i, 7Me-C17:0, C17:0i and C17:0a were used (Lechevalier and Lechevalier, 1988; O'Leary and Wilkinson, 1988; Haack et al., 1994; Zelles, 1999;

Rinnan and Bååth, 2009; Whitaker et al., 2014a). For Gram-negative bacteria, the monounsaturated fatty acids C16:1ω7c, C16:1ω5, C18:1ω7c and cycloproprane fatty acids cyC17:0 and cyC19:0 were used (Zelles, 1999; Whitaker et al., 2014a; Rinnan and Bååth, 2009). For fungi, the fatty acids C18:2ω6,9 and C18:1ω9 were used (Bååth and Anderson, 2003; de Deyn et al., 2011). Total bacterial biomass was calculated as the sum of Gram-positive and Gram-negative PLFAs and the fatty acid C15:0 (de Deyn et al., 2011). Fungal to bacterial ratio (F : B) was calculated as the proportion of total bacterial relative to total fungal PLFAs. Total microbial PLFAs were determined as the sum of all identified PLFAs, including those above and the additional fatty acids C14:0, C16:1, C16:0, C17:1ω8, C17:0br, C18:0br, C18:1ω5, C18:0 and C19:1. PLFA contents were expressed as μg g^{-1} dry soil. Due to errors during extraction, four samples were lost (two OG and two USL samples, all from different sites). These were omitted from subsequent analysis, resulting in a total of 32 PLFA samples.

5.3.5 Molecular analysis of soil microbial communities and data pre-processing

DNA was extracted from 0.2 g soil using the PowerSoil® DNA Isolation Kit and protocol (MoBio Laboratories). 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). Bacteria were targeted using V3-V4 16S rRNA amplicon primers CCTACGGGAGGCAGCAG and GCTATTGGAGCTGGAATTAC. For fungi, the ITS2 region was amplified using primers GTGARTCATCGAATCTTTG and TCCTCCGCTTATTGATATGC (Ihrmark et al., 2012). Although the capability of detecting AM fungi using ITS primers is debated (Hart et al., 2015), recent studies have shown that patterns in diversity and community composition can be adequately identified within sample types such as soil (Berruti et al., 2017; Lekberg et al., 2018).

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 55 °C (bacteria) 52 °C (fungi); annealing times were 30 seconds with extension at 72 °C for 30 seconds; cycle numbers were 25 for bacteria and fungi; a final extension of 10 minutes at 72 °C was included. Amplicon sizes were determined using an Agilent 2200 TapeStation system, samples were normalised using SequalPrep Normalization Plate Kit (Thermo Fisher Scientific) and pooled. The pooled library was quantified using a Qubit dsDNA HS kit (Thermo Fisher Scientific) prior to sequencing with an Illumina MiSeq using V3 600 cycle reagents at a concentration of 8 pM with a 5% PhiX Illumina control library. The sequencing run produced in excess of 21 and 18 million reads passing filter for 16S and ITS amplicons, respectively. Sequences were processed in R using DADA2 to quality filter, merge, de-noise and assign taxonomies (Callahan et al., 2016). Forward sequence reads were used for 16S (trimmed to 250 bases), while forward and reverse were used for ITS (trimmed to 225 and 160 bases, 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. *mergePairs* and *removeBimeraDenovo* functions were used at default settings to merge ITS forward and reverse reads and remove chimeric sequences. The amplicon sequence variants (ASVs) were subject to taxonomic assignment using *assignTaxonomy* and the training database UNITE version 7.2 (UNITE Community, 2017).

Fungal functional guild classifications were assigned to ASVs using the FUNGuild annotation tool (Nguyen et al., 2016). Only ASVs with unambiguous (non-multiple) classifications of “probable” or “highly-probable” confidence rankings were

considered for analysis. These were used for calculating relative abundances of fungal guilds and sub-setting saprotrophic, mycorrhizal, ectomycorrhizal and pathogenic fungal datasets for assessment of diversity and community dissimilarity.

Sequencing data were pre-processed (steps described below) and alpha diversity indices (ASV richness, Shannon index) and fungal guild relative abundances calculated in R version 3.6.0 (R Core Team, 2019) using the *phyloseq* package (Mcmurdie and Holmes, 2013). Three samples with abnormally low read counts in the bacterial dataset were identified by histogram and removed prior to analysis (two in different USL sites, one in RSL). Only ASVs assigned to the kingdoms of Bacteria or Fungi were retained for downstream analysis, and all singleton ASVs were removed. Sub-setting by fungal guilds was conducted on the full unrarefied dataset to maximise the number of ASV reads available for analysis of functional groups. Sample sequencing depth was normalised for each group by rarefying to the minimum read counts per sample for bacterial (3,778 reads), and overall fungal (3,868), saprotrophic (472), mycorrhizal (20), ectomycorrhizal (6) and pathogenic (69) fungal groups.

5.3.6 Statistical analyses

All statistical analyses were conducted in R version 3.6.0 (R Core Team, 2019), and significance of all tests was considered at the $p \leq 0.05$ level. To test the differences in univariate soil microbial community attributes (alpha diversity metrics and fungal guild relative abundances) and soil, environmental and vegetation characteristics between forest types, linear mixed effects regression models (LMMs) were constructed in the *lme4* R package (Bates et al., 2015). Post-hoc pairwise comparisons were conducted with the *emmeans* R package (Lenth et al., 2019) with Bonferroni correction to identify statistically different variable means between OG, USL and RSL forest types. To

control for potential within-site pseudoreplication, site ID was included as a random intercept term. Normality of model residuals were evaluated using Shapiro-Wilk tests and QQ-plots, and variables were log-, square root- or exp- transformed where necessary to improve model fit.

Soil microbial community data were Hellinger-transformed prior to analysis (Legendre and Borcard, 2018) to control for the effect of rare taxa, and merged at the site level (n = 9) using the merge_samples function in *phyloseq* to control for spatial pseudoreplication. Soil microbial community compositions across forest types were visualised with PCoA using Bray-Curtis dissimilarities via the *phyloseq*, *vegan* (Oksanen et al., 2019) and *ggplot2* (Wickham, 2016) packages. Differences in soil microbial community compositions between forest types were tested with PERMANOVA using the adonis *vegan* function and Bray-Curtis community dissimilarities. All permutational tests were run with 9,999 permutations. Homogeneity of multivariate dispersion between vegetation types (an assumption of PERMANOVA) for soil microbial community dissimilarities was evaluated using the betadisper *vegan* function. Pairwise comparisons of soil microbial community dissimilarities between forest types could not be carried out due to the low number of true replicates, restricting the number of possible permutations for calculating significance level. UPGMA (unweighted pair-group method with mathematic average) hierarchical cluster analysis was performed and dendrograms constructed using the hclust R function (R Core Team, 2019) to identify groups of more (dis)similar sites and evaluate community dissimilarities between forest types.

Numbers of shared and distinct soil microbial ASVs between forest types were visualised with Venn diagrams using the group.venn function in the *RAM* R package (Chen et al., 2018). Indicator analysis was conducted to identify specific soil microbial

taxa uniquely associated with individual forest types, as well as pairs of forest types (i.e. only significantly occurring in two of the three forest types) using the mulitpatt function in the *indicspecies* R package (de Caceres and Legendre, 2009). This provided Indicator Values as an index of association between forest type and soil microbial ASVs, and *p*-values denoting significant indicator taxa generated using the same permutational design described above.

To evaluate differences in the rate of spatial turnover of taxa in soil microbial communities (distance decay of (dis)similarity) between forest types, pairwise Bray-Curtis community dissimilarities for soil microbial groups and corresponding geographic distances were calculated between the 19 sampling points in each site. This provided a total of 171 pairs per site, with geographic distances ranging from 10 cm to 42.09 m. Linear regression was used to obtain the coefficient (slope) of the distance decay relationship (*Y*), between log-transformed Bray-Curtis dissimilarities and log-transformed geographic distances for each site and soil microbial group (Barreto et al., 2014; Nekola and White, 1999). ANOVA with Tukey HSD post-hoc tests were used to test differences in *Y*-values between forest types for each soil microbial group ($n = 9$).

5.4 Results

In total, 37,057 bacterial ASVs (representing 43 phyla; 737 genera) and 21,298 fungal ASVs (12 phyla; 611 genera) were detected across all OG, USL and RSL samples (see Fig 5.1 A & B for number of bacterial and fungal ASVs partitioned by those unique to and shared between forest types).

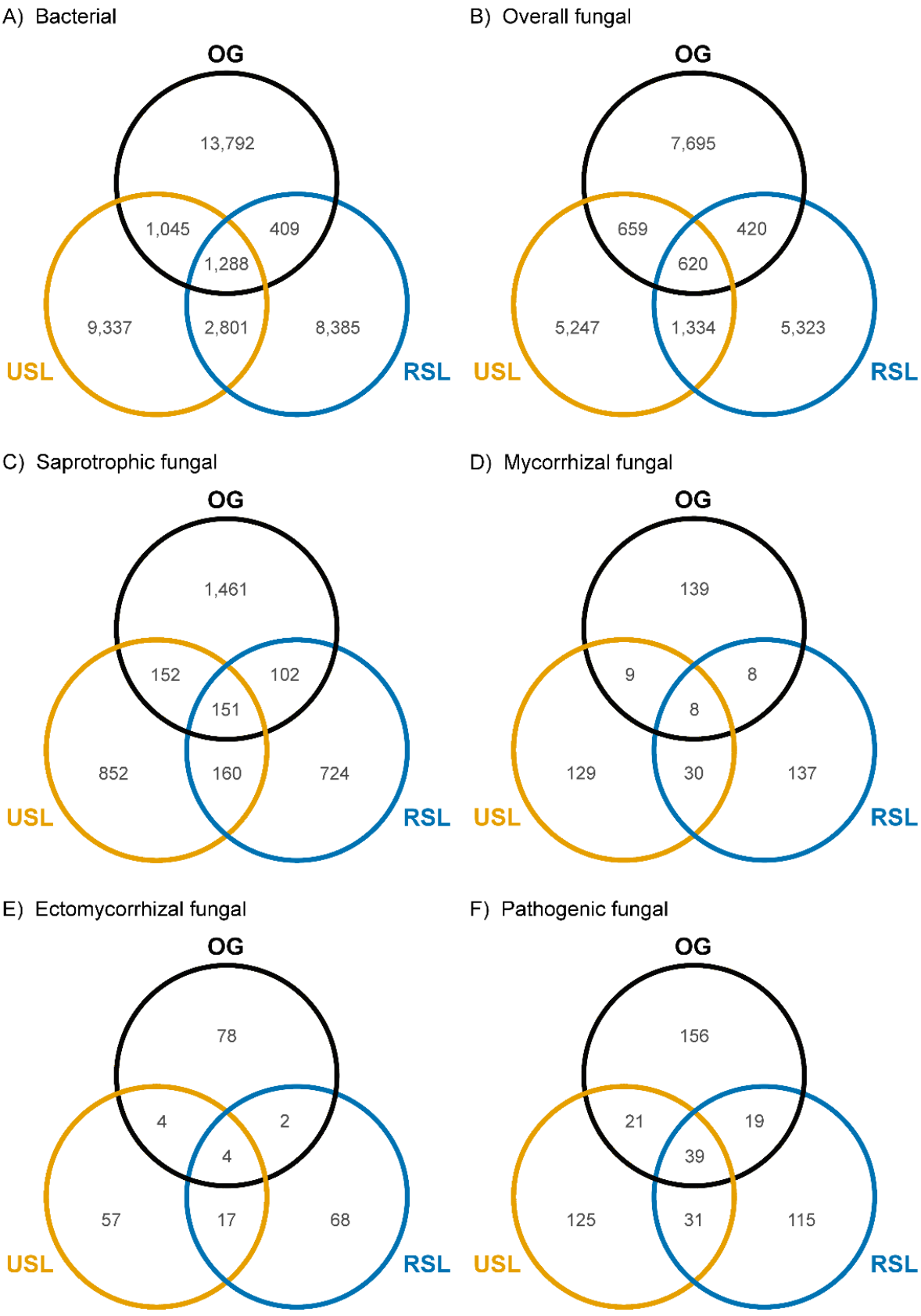

Figure 5.1 *Venn diagrams of numbers of Amplicon Sequence Variants (ASVs) unique to and shared between different forest types for all soil microbial groups studied*

5.4.1 Differences in soil microbial alpha and beta diversity

Mean bacterial Shannon alpha diversity was significantly higher in USL relative to OG, while RSL was statistically similar to USL and OG (Fig. 5.2 A; see Table 5.1 for means of all soil microbial community attributes; see Table 5.2 for summary of test statistics for differences in alpha diversity metrics between forest types for all soil microbial groups).

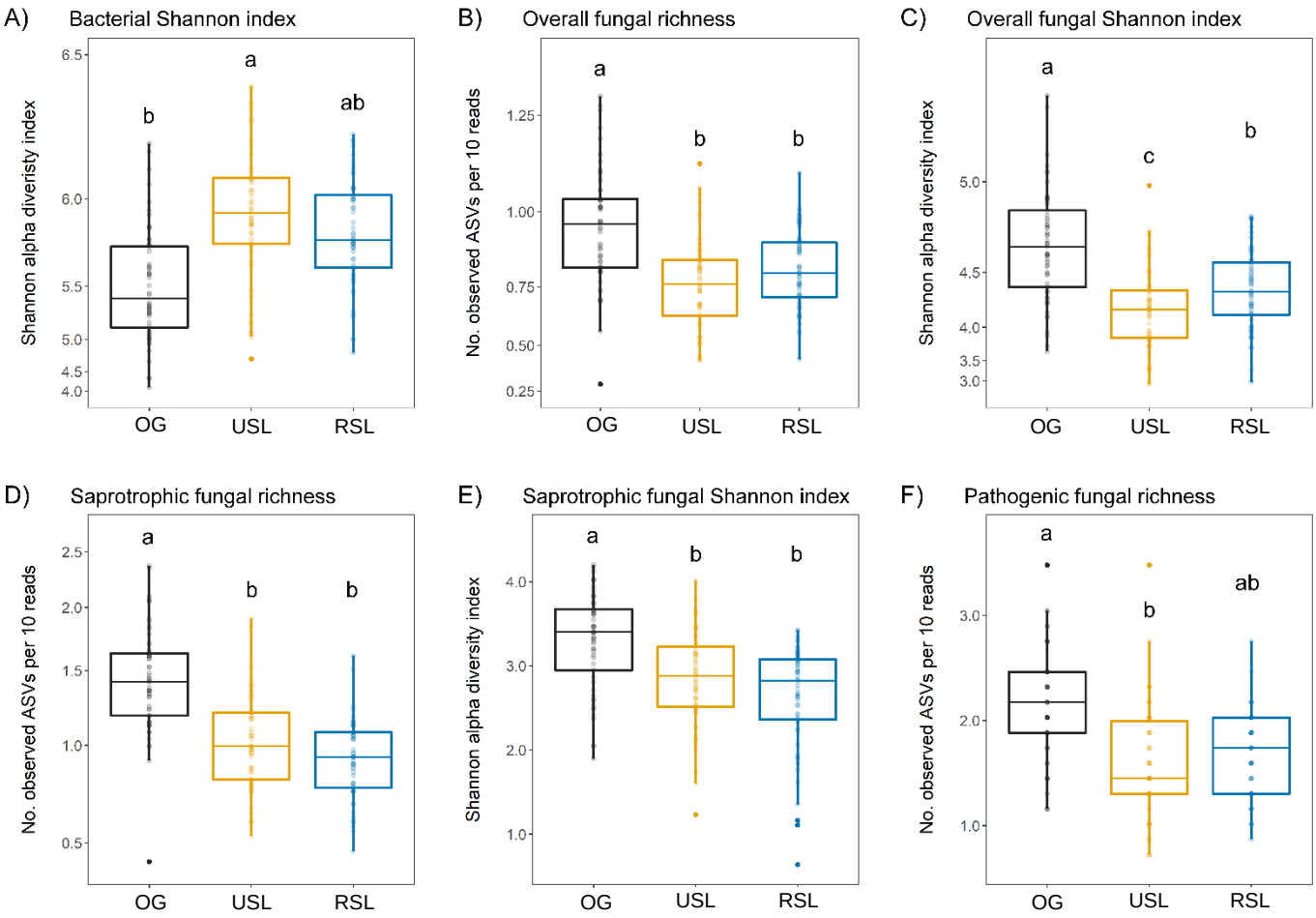

Figure 5.2 *Box and whisker plots of soil microbial alpha diversity metrics (richness and Shannon index) derived from Amplicon Sequence Variants (ASVs) significantly differing between old-growth (OG), restored selectively logged (RSL) and unrestored selectively logged (USL) forest. Lower case letters indicate statistically different or similar groups at the* $p < 0.05$ *level identified in post-hoc tests after linear mixed model or Kruskal-Wallis analysis.*

Table 5.1 Means (± 1 SD) of all soil microbial community attributes by forest type for old-growth (OG), logged-unrestored (USL) and logged-restored (RSL) forest. Superscript letters indicate statistically different or similar groups at the $p < 0.05$ level identified in post-hoc tests after linear mixed model or Kruskal-Wallis analysis.

Parameter	Soil microbial group	Forest type		
		OG	USL	RSL
Total PLFAs (μg g^{-1} dry soil)	Total microbial	51.27 ± 21.85	52.85 ± 17.58	59.13 ± 14.91
	Bacterial	26.56 ± 11.88	27.05 ± 8.90	30.19 ± 7.55
	Fungal	2.50 ± 0.64	3.42 ± 1.25	3.51 ± 1.11
Fungal : bacterial ratio	-	0.11 ± 0.04	0.13 ± 0.04	0.12 ± 0.02
Richness	Bacteria	1.72 ± 0.42	1.80 ± 0.59	1.69 ± 0.49
(no. observed ASVs 10 $reads^{-1}$)	Overall fungi	0.94 ± 0.18 ^{a}	0.75 ± 0.17 ^{b}	0.80 ± 0.14 ^{b}
	Saprotrophic fungi	1.46 ± 0.37 ^{a}	1.04 ± 0.29 ^{b}	0.93 ± 0.23 ^{b}
	Mycorrhizal fungi	2.39 ± 1.29	2.63 ± 1.29	3.14 ± 1.36
	Ectomycorrhizal fungi	4.59 ± 1.97	4.12 ± 1.73	5.20 ± 2.02
	Pathogenic fungi	2.17 ± 0.54 ^{a}	1.54 ± 0.58 ^{b}	1.67 ± 0.42 ^{ab}
Shannon alpha diversity index	Bacteria	5.41 ± 0.45 ^{b}	5.88 ± 0.38 ^{a}	5.79 ± 0.32 ^{ab}
	Overall fungi	4.62 ± 0.36 ^{a}	4.10 ± 0.45 ^{c}	4.31 ± 0.37 ^{b}
	Saprotrophic fungi	3.30 ± 0.57 ^{a}	2.84 ± 0.56 ^{b}	2.63 ± 0.63 ^{b}
	Mycorrhizal fungi	1.13 ± 0.54	1.24 ± 0.57	1.39 ± 0.58
	Ectomycorrhizal fungi	0.82 ± 0.49	0.72 ± 0.44	0.94 ± 0.47
	Pathogenic fungi	2.16 ± 0.37	1.63 ± 0.61	1.91 ± 0.41
Fungal guild relative abundance	Saprotrophic fungi	44.73 ± 16.13	54.05 ± 24.82	42.72 ± 21.30
(% total fungal ASV reads)	Mycorrhizal fungi	30.96 ± 18.21	31.70 ± 25.59	47.24 ± 24.97
	EcM fungi	30.21 ± 18.39	29.95 ± 26.62	45.98 ± 25.58
	AM fungi	0.66 ± 1.28	1.63 ± 2.41	1.11 ± 1.12
	Ericoid mycorrhizal fungi	0.09 ± 0.41	0.10 ± 0.19	0.14 ± 0.31
	Orchid mycorrhizal fungi	0.00 ± 0.01	0.01 ± 0.10	0.00 ± 0.02
	Pathogenic fungi	17.22 ± 8.17 ^{a}	11.51 ± 6.89 ^{a}	7.27 ± 4.18 ^{b}
	Plant pathogenic fungi	10.93 ± 6.06 ^{a}	4.56 ± 5.06 ^{b}	4.21 ± 3.42 ^{b}
	Animal pathogenic fungi	6.29 ± 4.71 ^{ab}	6.95 ± 4.84 ^{a}	3.06 ± 2.55 ^{b}
	Parasitic fungi	5.68 ± 3.59	2.37 ± 2.87	2.59 ± 3.62
	Endophytic fungi	0.22 ± 0.50	0.47 ± 1.13	0.14 ± 0.59
	Lichenised fungi	1.45 ± 1.23 ^{a}	0.17 ± 0.28 ^{ab}	0.05 ± 0.10 ^{b}
	Epiphytic fungi	0.14 ± 0.81	0.05 ± 0.23	0.04 ± 0.15

Table 5.2 Linear mixed model (LMM) or Kruskal-Wallis* test statistics for significant differences in soil microbial alpha diversity metrics (richness and Shannon index) between forest types. Summaries are given for overall models and post-hoc comparisons between old-growth (OG), logged-unrestored (USL) and logged-restored (RSL) forest. *p*-values for pairwise tests for LMM and Kruskal-Wallis analyses were adjusted using the Tukey and Bonferroni methods, respectively. Significant *p*-values ($p > 0.05$) are highlighted in bold.

Soil microbial group	**Diversity metric**	**Overall model**			**Pairwise tests**					
					OG - USL		**OG - RSL**		**USL - RSL**	
		R^2	F/χ^2*	*p*	*t*-ratio/Z*	*p*	*t*-ratio/Z*	*p*	*t*-ratio/Z*	*p*
Bacteria	Shannon index	0.21	9.68	**0.014**	-4.27	**0.013**	-3.05	0.053	1.23	0.480
Overall fungi	Richness	0.21	22.03	< **0.001**	6.37	< **0.001**	4.79	< **0.001**	-1.59	0.255
	Shannon index	0.26	29.87	< **0.001**	7.56	< **0.001**	5.16	< **0.001**	-2.41	**0.045**
Saprotrophic fungi	Richness	0.36	31.10	**0.001**	5.91	**0.003**	7.48	**0.001**	1.57	0.329
	Shannon index	0.20	21.84	< **0.001**	-4.55	< **0.001**	-6.43	< **0.001**	-1.87	0.150
Pathogenic fungi	Richness	0.21	7.58	**0.023**	3.69	**0.024**	2.93	0.060	-0.76	0.739

Conversely, overall fungal richness and Shannon alpha diversity were significantly higher in OG relative to USL and RSL (Fig. 5.2 B & C), with overall fungal Shannon alpha diversity higher in RSL relative to USL. Saprotrophic fungal richness and Shannon alpha diversity were significantly higher in OG compared to USL and RSL (Fig. 5.2 D & E). Pathogenic fungal richness was higher in OG compared to USL, with RSL similar to both forest types (Fig. 5.2 F).

Spatial turnover of microbial taxa (regression coefficient of community dissimilarity distance-decay relationship) only differed between forest types for bacteria ($R^2 = 0.89$, $F = 23.75$, $p = 0.001$; Fig. 5.3). Significantly lower *Y*- values (indicating slower spatial turnover of taxa) were found in USL compared to OG and RSL (post-hoc tests: USL-OG: $p = 0.001$; USL-RSL: $p = 0.006$), while OG and RSL were similar ($p = 0.344$).

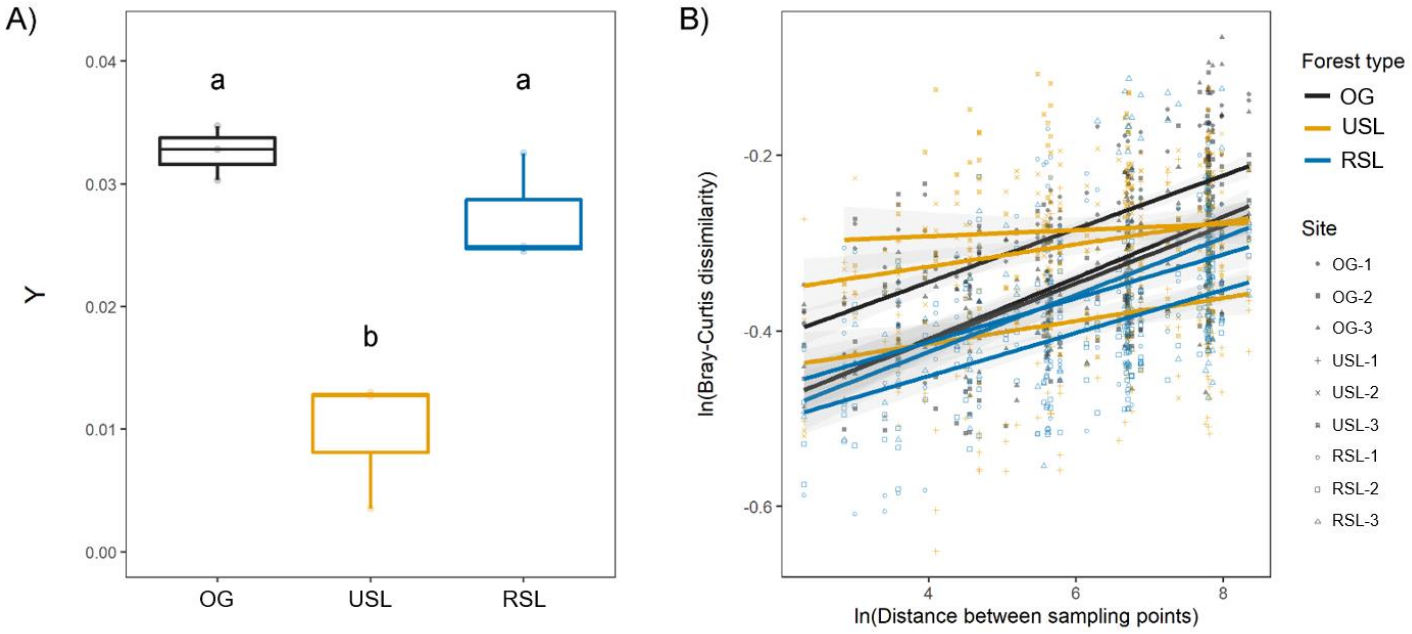

Figure 5.3 *A) Box and whisker plot of differences in rates of spatial turnover of bacterial taxa, distance-decay regression coefficient (Y), corresponding to B) slope of the relationship between log-transformed bacterial community Bray-Curtis dissimilarities and log-transformed geographic distances between sampling points within each site. Lower case letters indicate statistically different or similar groups at the* $p < 0.05$ *level identified by Tukey test after ANOVA.*

5.4.2 Differences in soil microbial community compositions

Analysis of PLFA contents indicated no differences in total microbial, fungal or bacterial biomass or fungal:bacterial ratio between forest types ($p > 0.05$ in overall and pairwise tests). Bray-Curtis community dissimilarities were significantly affected by forest type for all soil microbial groups, with the exception of ectomycorrhizal fungi, which was marginally significant (Fig. 5.4; see Table 5.3 for summary of all PERMANOVA test statistics). Community dissimilarity dispersions were homogenous between all land-use types for all fungal groups (betadisper: $p > 0.05$).

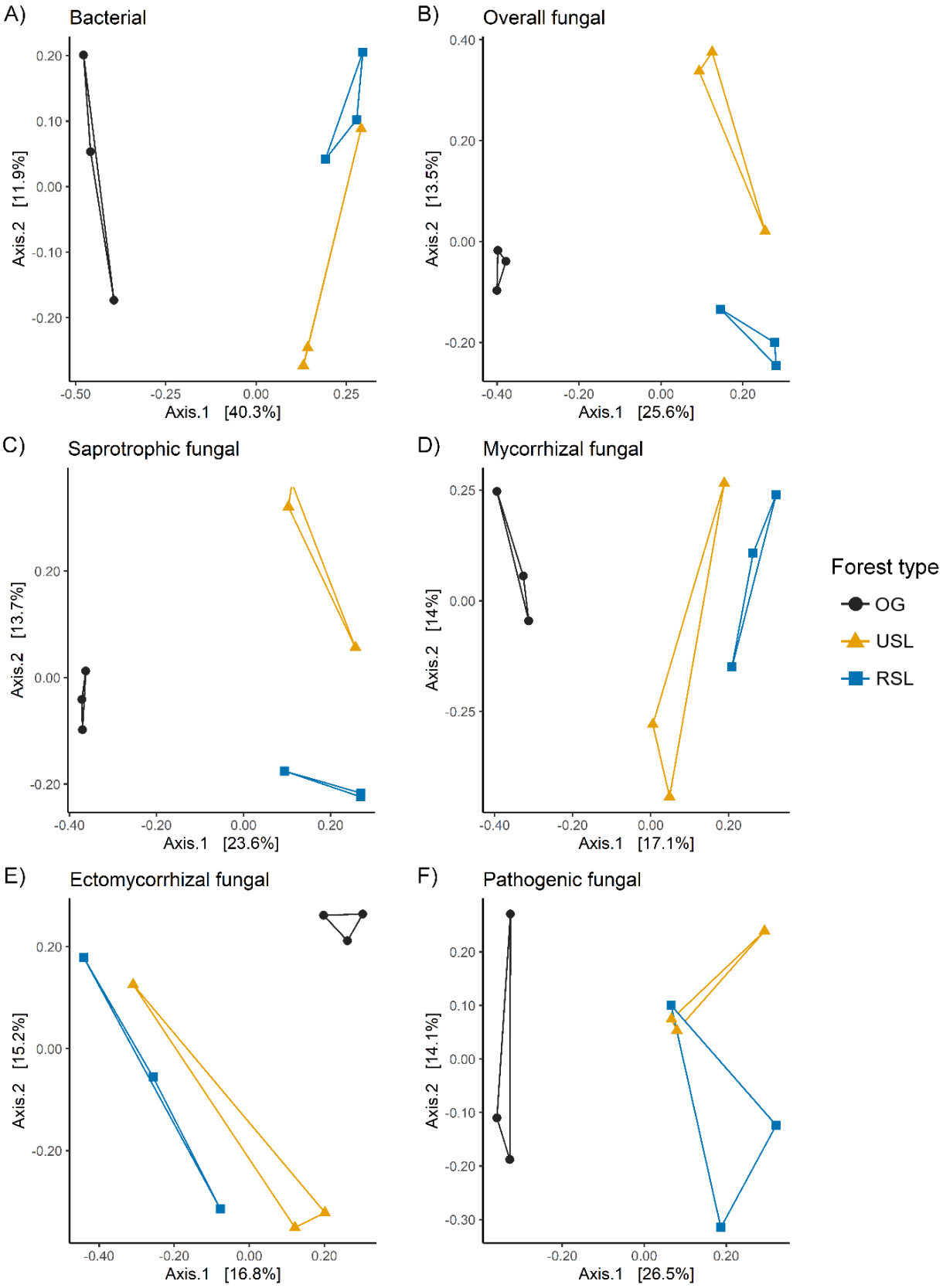

Figure 5.4 *Principle coordinates analysis (PCoA) ordinations of Bray-Curtis dissimilarities for all soil microbial groups across old-growth (OG), logged-unrestored (LU) and logged-restored (LR) forest. Hulls are used to illustrate community dispersion rather than ellipses, due to the low number of replicates within each forest type (3).*

Table 5.3 PERMANOVA test statistics for the effect of forest type on soil microbial community Bray-Curtis dissimilarities. Significant *p*-values ($p < 0.05$) are highlighted in bold.

Soil microbial group	R^2	F	p
Bacteria	0.49	2.90	**0.007**
Overall fungi	0.38	1.85	**0.004**
Saprotrophic fungi	0.36	1.71	**0.004**
Mycorrhizal fungi	0.29	1.25	**0.006**
Ectomycorrhizal fungi	0.28	1.14	0.074
Pathogenic fungi	0.37	1.74	**0.007**

UPGMA hierarchical clustering analysis (Fig. 5.5) identified communities in OG sites to be most dissimilar to those of USL and RSL across all microbial groups, with the exception of EcM fungi (bacteria: 86.50 % dissimilarity; overall fungi: 89.84 %; saprotrophic fungi: 87.46 %; mycorrhizal fungi: 97.27 %; pathogenic fungi: 78.91 %). For EcM, the greatest dissimilarity was found between OG-1 and all other sites (98.44 %), but similarly followed by dissimilarity between OG-2 and OG-3 sites and all others (97.59 % dissimilarity). USL and RSL sites were generally more similar, with USL and RSL sites clustering together over sites of the same forest type in all microbial groups.

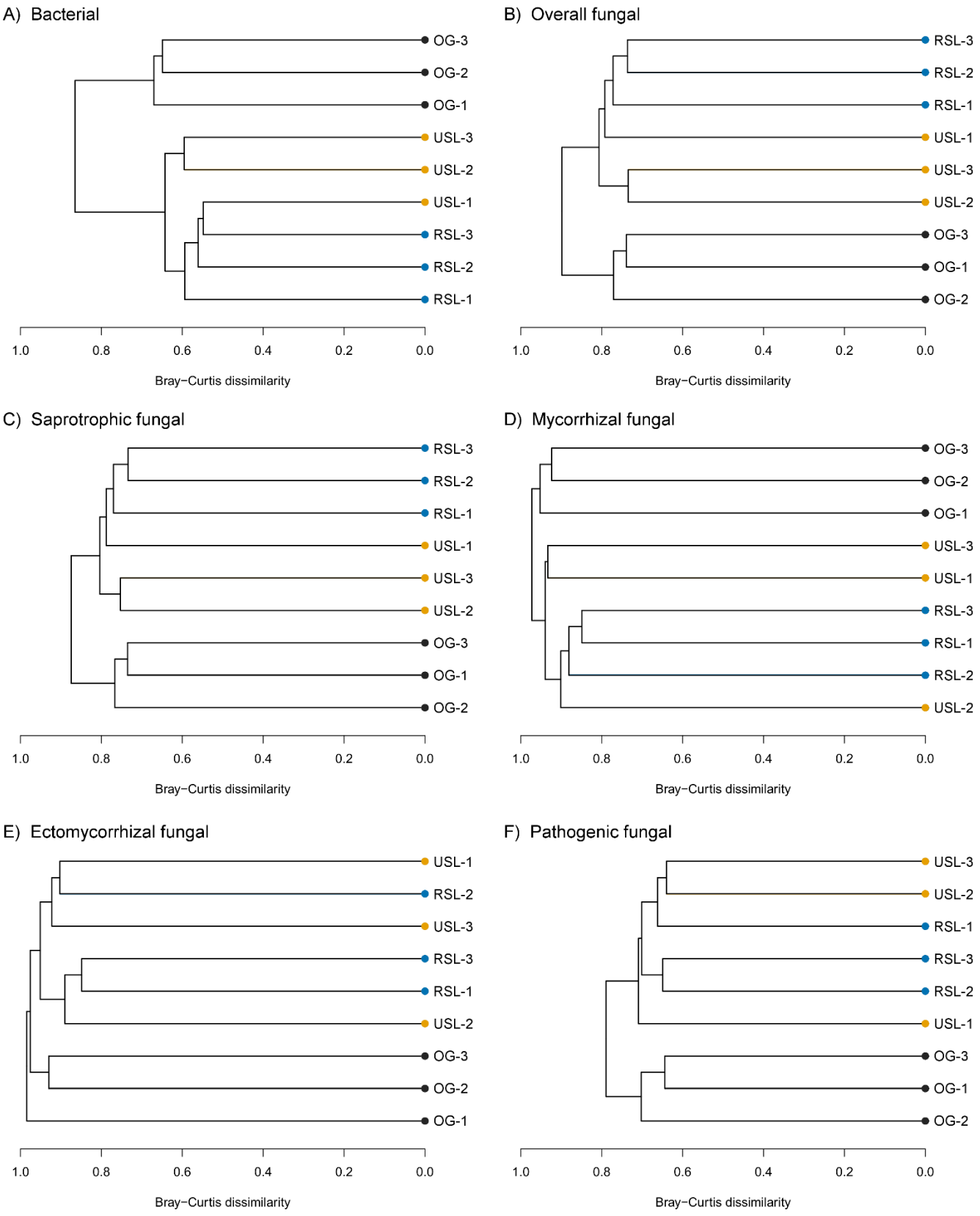

Figure 5.5 *UPGMA (unweighted pair-group method with mathematic average) hierarchical cluster dendrograms illustrating Bray-Curtis dissimilarities between all sites across old-growth (OG), logged-unrestored (LU) and logged-restored forest (LU).*

Fungal guild relative abundances for total pathogens, plant pathogens, animal pathogens and lichens significantly differed by forest type (Fig. 5.6; see Table 5.4 for summary of significant test statistics). Total pathogenic and lichenised fungal relative abundances were significantly higher in OG relative to RSL (USL similar to both OG and RSL forest types for both fungal guilds), while plant pathogenic fungal relative abundance was significantly higher in OG relative to both SL forest types. Animal pathogenic fungal relative abundance was higher in USL relative to RSL (OG similar to both USL and RSL forest types).

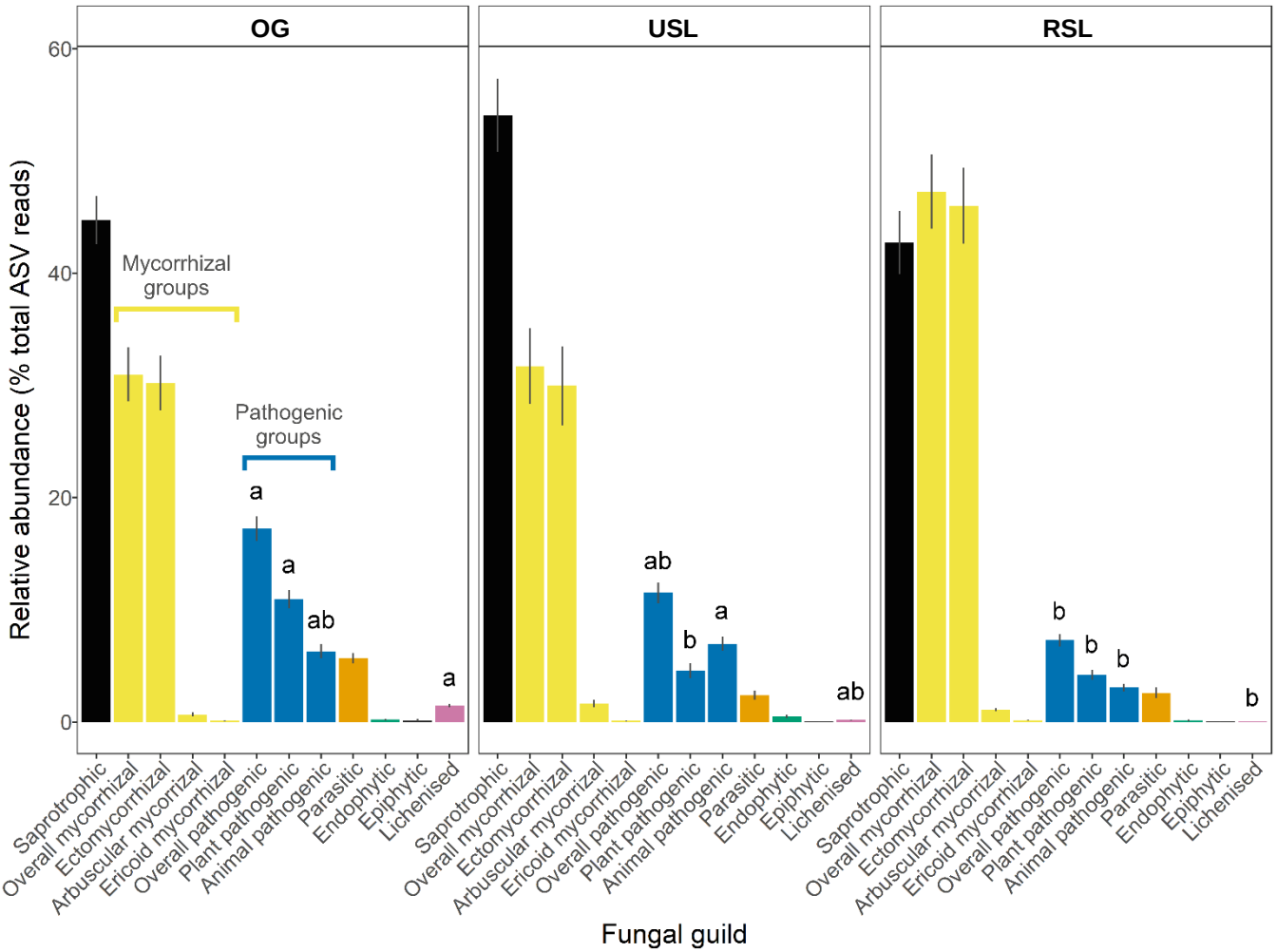

Figure 5.6 *Relative abundances of fungal guilds for old-growth (OG), logged-unrestored (USL) and logged-restored (RSL) forest. Error bars represent standard errors. Lower case letters indicate statistically different or similar groups at the* $p < 0.05$ *level identified in post-hoc tests after linear mixed model or Kruskal-Wallis analysis. Mycorrhizal and pathogenic guilds have been further divided into subtypes as indicated.*

ASVs unique to OG belonged to the Firmicutes in comparison to USL and RSL (Fig 5.7 A).

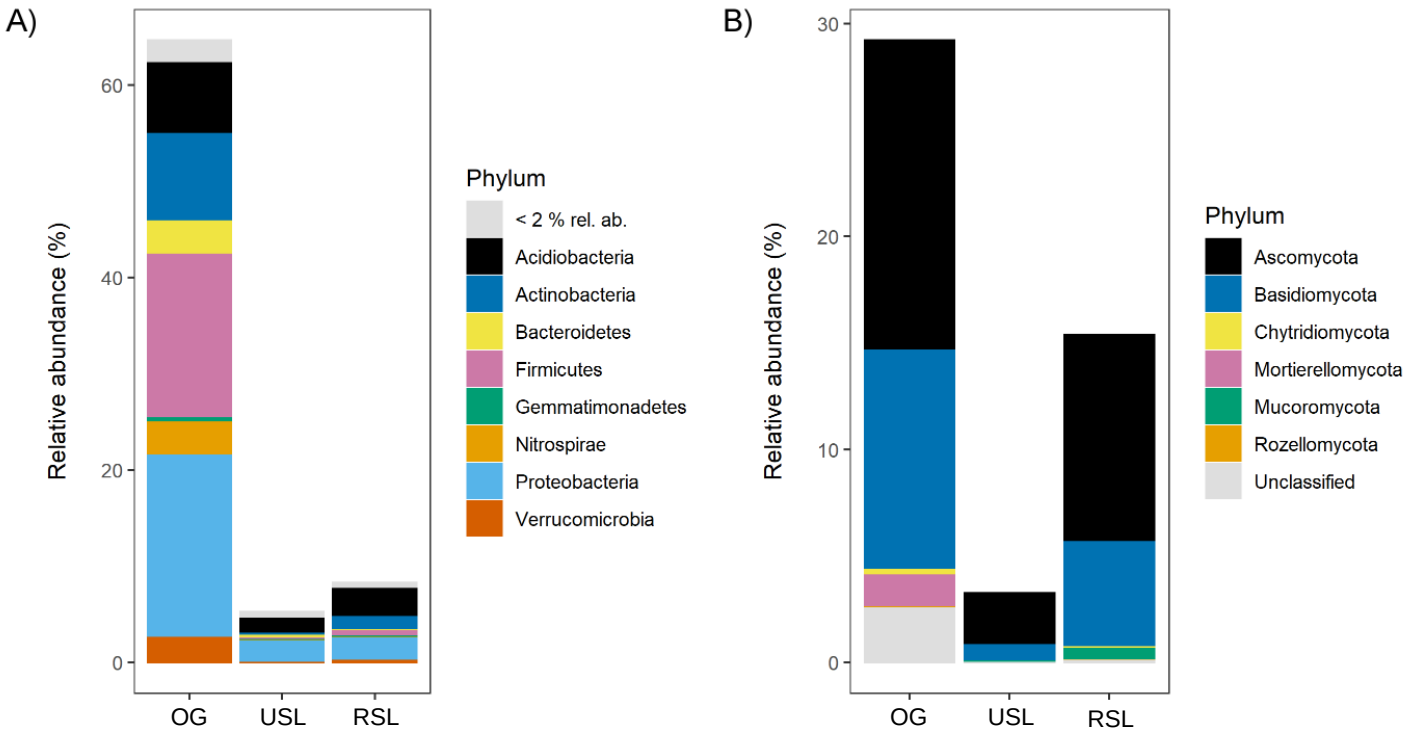

Figure 5.7 *Stacked bar graphs of relative abundances of indicator Amplicon Sequence Variants (ASVs) unique to old-growth (OG), logged-unrestored (LU) and logged restored (LR) forest, grouped at the level of phyla*

For fungal taxa, 205 significant indicator ASVs were identified for OG, 45 for USL and 94 for RSL. Notable differences in composition of phyla was a taxa of the Mortierellomycota occurring mostly only in OG, and taxa of the Mucoromycota mostly only in RSL and USL (Fig 5.7 B).

For significant bacterial indicator ASVs shared between pairs of forest types, only two were identified for OG and RSL together (i.e. indicative of non-USL forest), both belonging to the phylum Firmicutes, class Bacilli (*Alicyclobacillus sp.* and *Bacillus foraminis*). Indicator ASVs for OG and USL belonged to the phyla Proteobacteria, Verrucomicrobia and Acidobacteria. A large number of significant bacterial indicator ASVs were identified for USL and RSL together (472 overall, 314 with maximum

IndVal of 1) representing a large range of phyla. For fungi, a total of four significant indicator ASVs were identified for OG and RSL from the two phyla Ascomycota and Basidiomycota, and two classes Sordariomycetes and Tremellomycetes (*Trichoderma deliquescens*, *Clonostachys rosea*, *Castanediella sp.* and *Saitozyma podzolica*). Indicator ASVs for OG and USL comprised taxa of the Ascomycota and Basidiomycita (also including *Clonostachys rosea*), as did those for USL and RSL, but additionally including taxa of the Mucuromycota, Chytridiomycota, Mortierellomycota and Rozellomycota. The selection of the fungal species *Clonostachys rosea* as an indicator of both OG-USL and OG-RSL, but not USL-RSL forest pairs signified a primary association of this taxon with OG forest.

5.4.4 Differences in soil physicochemical properties, environmental and vegetation characteristics between forest types

Of all the soil physicochemical properties, environmental and vegetation characteristics measured (see Table 5.5 for summary of all variable means by forest type), only soil pH significantly differed between forest types (overall model: $R^2 = 0.83$, $F = 50.56$, $p < 0.001$). Post-hoc tests identified significantly lower soil pH in USL and RSL relative to OG (OG-USL: $p < 0.001$; OG-RSL: $p < 0.001$), while USL and RSL did not significantly differ ($p = 0.693$).

Table 5.5 Means (± 1 SD) of soil physicochemical properties, environmental and vegetation characteristics by forest type for old-growth (OG), logged-unrestored (USL) and logged-restored (RSL) forest. Superscript letters indicate statistically different or similar groups at the $p < 0.05$ level identified in post-hoc tests after linear mixed model analysis.

Group	Parameter	Forest type		
		OG	USL	RSL
Soil	pH	5.57 ± 0.42 [a]	4.02 ± 0.30 [b]	3.89 ± 0.19 [b]
	C (%)	5.87 ± 2.13	5.31 ± 1.67	4.25 ± 1.41
	N (%)	0.44 ± 0.14	0.40 ± 0.11	0.31 ± 0.07
	C : N ratio	13.23 ± 1.49	13.26 ± 1.23	13.52 ± 1.92
	Total P (μg g^{-1})	478.42 ± 142.44	253.39 ± 43.43	348.49 ± 89.32
	Inorganic P (μg g^{-1})	11.65 ± 7.63	14.55 ± 5.22	8.79 ± 4.23
Environmental	PAR (μmol m^{-2} s^{-1})	0.61 ± 0.84	1.44 ± 3.46	0.83 ± 1.95
	Soil temperature (˚C)	26.29 ± 1.10	24.88 ± 0.66	26.37 ± 0.82
	Air temperature (˚C)	26.20 ± 0.69	24.95 ± 0.44	25.86 ± 0.49
Vegetation	Basal area (m^2 ha^{-1})	93.55 ± 42.99	117.92 ± 25.11	141.36 ± 18.00
	Stem density (no. stems DBH ≥ 5 cm)	896.97 ± 98.93	1,336.99 ± 146.88	1,091.60 ± 235.66
	Mean stem diameter (cm)	26.23 ± 4.35	28.61 ± 1.73	27.21 ± 0.19

5.5 Discussion

In this study, we evaluated differences in soil microbial community attributes, soil physicochemical properties, and environmental and vegetation characteristics between OG, USL and RSL forest in Bornean lowland dipterocarp rainforest across different spatial scales. Bacterial community attributes were shown to differ by forest type, including community composition (Fig. 5.4 A), alpha diversity metrics (Fig. 5.2 A) and rates of spatial turnover of taxa (Fig. 5.3), broadly supporting our initial hypothesis (H1). Specifically, results showed higher bacterial alpha diversity and lower rates of

spatial turnover of taxa in USL, in agreement the predictions that forest disturbance increases local bacterial diversity while homogenising communities over larger spatial scales (Rodrigues et al., 2013). Although tropical forest disturbance is often accompanied by declines in both alpha and beta diversity of aboveground organisms (Sodhi et al., 2009; Bierregaard, 2001), this is not necessarily the case for belowground microbial communities where the opposite trend may be seen in local diversity patterns (Petersen et al., 2019). As discussed by Rodrigues et al. (2013), this 'decoupling' of alpha and beta diversity with disturbance may depend on the relative effects of disturbance on ecosystem productivity. For example, alpha diversity in aboveground communities has been shown to increase with disturbance when productivity rates are higher in resulting ecosystems (Smart et al., 2006). In microbial terms, OG rainforests may be characterised by relatively low belowground productivity compared to adjacent open ecosystems created through anthropogenic disturbance (Cenciani et al., 2009; Cerri et al., 2004). In the current study system, increased bacterial alpha diversity with SL may potentially result from changes in vegetation characteristics (e.g. changes in tree community composition, or increasing understorey vegetation through creation of canopy gaps; Denslow, 1995) affecting the quality and quantity of plant inputs to the soil, improving effective resource availability and enhancing microbial growth and turnover (i.e. belowground microbial productivity; Cenciani et al., 2009; Cerri et al., 2004), and simultaneously creating different ecological niches for bacterial communities (Zhang et al., 2018). This observation is congruent with the intermediate disturbance hypothesis, which predicts increases in coupled productivity and diversity with a certain level of disturbance (Zhang et al., 2011; Ferrenberg et al., 2013; Galand et al., 2016; Wilkinson, 1999).

The observed differences in soil bacterial community attributes disagree with previous work in the same region of Borneo that found bacterial communities and diversity to be broadly resilient to SL disturbance (Tripathi et al., 2016; Lee-Cruz et al., 2013). This is likely due to the coarse sampling resolution used in these studies to evaluate alpha and beta diversity (composite samples comprising soil collected up to 200 m apart). As bacterial community structure can vary considerably over metre-and centimetre-scales (O' Brien et al., 2016), sampling resolution of previous surveys may be inappropriate for evaluating bacterial diversity and biogeographical patterns in response to forest ecosystem disturbance. The findings of the present study highlight the need for landscape studies of soil microbial diversity to incorporate fine spatial scale approaches to identify impacts and implications for biogeochemical cycling. Beyond this, although clear differences in alpha diversity and spatial turnover of taxa were detected in USL, findings suggest that restoration of SL forest by enrichment planting can recover these metrics to levels comparable to OG forest. As such, bacterial alpha diversity may even be used as an indicator of rehabilitation of SL forest, with lower values representing ecosystem recovery. This is opposite to the way bacterial alpha diversity may be used to monitor progress of rehabilitation after total forest clearance, which can demonstrate higher values after replanting (Nurulita et al., 2016). This emphasises the importance of disturbance history in identifying appropriate context-specific recovery indicators. Indicator analysis identified a large proportion of bacterial taxa in OG belonging to the Firmicutes, a phylum associated with high soil carbon availability and resilience to environmental (microclimatic) perturbations (Rodrigues et al., 2013; Battistuzzi and Hedges, 2009), that were largely absent from USL and RSL.

The second hypothesis, that fungal community attributes would be affected by forest type with greater similarity between OG and RSL (H2), was only partially

supported. While results broadly agree with the known sensitivity of fungal communities to SL disturbance (Chapter 1; Chapter 2; Elias et al., 2019; Kerfahi et al., 2014; McGuire et al., 2015), the prediction of similarity in community compositions through shared taxa between OG and RSL was not corroborated. Overall, saprotrophic, and fungal communities were shown to differ by forest type (Fig. 5.4 B-F), but were more similar between USL and RSL, with OG appearing more dissimilar to both human-modified forest types (Fig. 5.5 B-F). Notably, *Clonostachys rosea* appeared to be associated with OG forest. This species is known to protect plants by supressing sporulation of other plant-pathogenic fungi and infection of plant-parasitic nematodes, with potential for use as a biological control agent (Zhang et al., 2008). An apparent absence of such microbial taxa beneficial for plant growth and survival may have negative implications for reestablishment of reintroduced species, affecting recovery of ecosystem biodiversity and C storage. There were surprisingly few fungal taxa shared between OG and RSL (420 ASVs; Fig 5.1 B) relative to those shared between USL and RSL (1,334 ASVs), or even OG and USL (659 ASVs) – a pattern even more evident in bacteria (OG-RSL: 409 ASVs; USL-RSL: 2,801; USL-OG: 1,045; Fig 5.1 A). This suggests that there is actually a large amount of taxa lost specifically as a result of restoration practices that are otherwise present in both OG and USL. This is reflected in the lower overall fungal alpha diversity in RSL relative to OG (with richness in RSL similar to USL; Fig 5.2 B & C), which is likely largely driven by lower alpha diversity metrics observed for the saprotrophic fungal group in RSL (Fig 5.2 D & E), as it represented the largest proportion of overall fungal reads (47.17 %). These findings may be potentially related to long-term control of liana species - which have their own soil microbial associations (McGuire et al., 2008; Schnitzer et al., 2005) - and removal of understorey vegetation which is practiced in these study sites, and a common part of

management of enrichment planting programmes employed to ensure maximum survival and productivity of reintroduced tree species (Perumal et al., 2016; Face the Future, 2007). Vegetation removal may alter plant litter inputs, which in turn can affecting resulting microbial decomposer communities (Shi et al., 2019). Further study of the effects of liana and understorey vegetation removal through controlled field experiments (i.e. enrichment planting with and without additional vegetation clearance) is required to unpick the underlying drivers of these observations, and possible role in the impediment of fungal community recovery towards characteristics of OG forest.

Mycorrhizal community composition, relative abundance (including EcM and AM) and alpha diversity did not differ between forest types (although differences in community dissimilarity were marginally non-significant across forest types). This was unexpected, as taxa from this functional group have been identified as some of the most sensitive to SL (Chapter 1; Elias et al., 2019; Kerfahi et al., 2014), likely due to EcM associations of the dominant dipterocarp tree species that are targeted during industrial timber extraction (Taylor and Alexander, 2005; Brearley, 2012; Whitmore, 1984; Appanah and Turnbull, 1998). A lack of a clear effect on mycorrhizal community attributes may owe to the intensity of, and time since, disturbance in the current study system. Here forests were selectively logged only once in 1989, compared to other studies in the region incorporating, for example, extremely degraded forest that has undergone selective logging multiple (up to four) times, with the most recent round in 2008 (Chapter 1; Elias et al., 2019). As such mycorrhizal communities may have recovered over subsequent decades post-disturbance, especially as the mycorrhizal mycelium may be largely retained in SL forest (Chapter1). This is supported by the results of indicator analysis that found fungal indicator taxa of OG and USL forest to belong to pathotrophic and saprotrophic fungal guilds rather than mycorrhizal, as was

initially predicted to result from reintroduction of EcM-associating species. However, it is also important to note that the lack of differences found in community composition and diversity of total mycorrhizal and EcM fungal groups may also have arisen from the low number of reads used for sample normalisation of these subsets (20 and 6 reads per sample for total mycorrhizal and EcM fungi, respectively), increasing variability and therefore limiting sensitivity of analysis.

Surprisingly, no differences were found in indicators of overall microbial biomass between forest types, refuting the hypothesis that overall microbial biomass indicators will be greater in OG than USL, with similar values between OG and RSL (H3). This contrasts with previous studies observing clear reductions in MBC in degraded forest relative to OG (Deng et al., 2010; Nurulita et al., 2016), or higher MBC in restored versus unrestored forest (Daljit Singh et al., 2013). In the present study, it is possible either microbial biomass was unaffected by SL in these forests, or returned to comparable levels with OG in both USL and RSL with natural or managed regeneration during time since disturbance. The small number of samples used for analysis (n = 32) may also have contributes to lack of differences found due to a large amount of within-forest type (and site) variation.

Of all the soil physicochemical properties, environmental and vegetation characteristics measured, only soil pH was affected by forest type (H4) – with more acidic soils found in USL and RSL relative to OG (Table 5.5). Interestingly, bacterial alpha diversity was found to be higher in USL relative to OG despite more acidic soils in USL. This contrasts with studies across multiple biomes as well as Malaysia, which have found bacterial alpha diversity to increase with soil neutrality over land-use gradients (Tripathi et al., 2012; Lauber et al., 2009). This effect may also relate to altered

litter inputs with management of understorey vegetation such as shrubs and climber species, which may be closely associated with soil pH as suggested in previous study of human-made logging gaps (Chapter 2).

In conclusion, these results indicate that restoration by enrichment planting can successfully recover levels of bacterial alpha diversity and spatial turnover of bacterial taxa comparable to OG after approximately 18 years of rehabilitation. Fungal diversity, however, showed slower signs of recovery, largely due to saprotrophic fungal richness and Shannon alpha diversity index remaining similar to USL forest. However, soil microbial community compositions (bacteria and fungi) were generally more similar between USL and RSL, with more relatively more different communities in OG. This indicates recovery of soil microbial communities may be inhibited under current management practices, having implications for biogeochemical cycling in these forests. Few fungal taxa were shared between OG and RSL relative to those shared between other forest types. Soil microbial taxa may potentially be lost through removal of lianas and understorey vegetation, impeding recovery of community attributes towards those characteristic of OG forest. Further study into the effects of liana and understorey vegetation removal through controlled field experiments is required to unpick underlying mechanisms. Contrary to previous studies undertaken at coarser spatial scales, bacterial alpha diversity was found to be greater in USL, while rates of spatial turnover of taxa was lower. This suggests bacterial alpha diversity may be used as an indicator of forest ecosystem rehabilitation following SL disturbance. Findings emphasise the importance of fine spatial scale studies (cm to m) for evaluation of biodiversity patterns in soil microbial communities that may otherwise be overlooked. Overall, these findings suggest impediment to the rehabilitation of soil microbial community attributes under current restoration, with implications for soil functions and

landscape-scale biogeochemical cycling. Changes in current management practices to incorporate the rehabilitation of belowground soil microbial communities may be required for successful ecosystemic recovery of degraded tropical forest and vital ecosystem services, including C storage.

6 General discussion

Tropical forests are vital global reservoirs of biodiversity and carbon (C) (Myers et al., 2000; Pan et al., 2011). Deforestation and degradation of these ecosystems greatly threatens their capacity to provide crucial ecosystem functions and services, including C storage (Baccini et al., 2017), by altering underpinning plant-soil interactions (Wardle et al., 2004; van der Heijden et al., 2008; van Der Putten et al., 2013). Land-use change can have significant impacts on soil microbial communities and the biogeochemical cycles they regulate (Fraterrigo et al., 2006; Bonner et al., 2019; Fichtner et al., 2014; Rodrigues et al., 2013), while potentially affecting sensitivity of soil microbial function to environmental perturbations associated with climate change (Meisner et al., 2018; Bouskill et al., 2016b; Bouskill et al., 2016a).

Human modification of Southeast Asian rainforest resulting from selective logging (SL) and conversion to oil palm plantation (OP) in recent decades has major implications for soil and ecosystem functions (Gaveau et al., 2014; Qie et al., 2017). Potential impacts have only just begun to be elucidated through a small number of studies, which have highlighted sensitivity of key soil microbial groups to these disturbances (Kerfahi et al., 2014; Tripathi et al., 2016; Lee-Cruz et al., 2013; Tripathi et al., 2012). However, understanding of the consequences for soil functioning and the potential for recovery of soil microbial communities is limited. The aim of this thesis was to address knowledge gaps regarding the impacts of tropical forest modification (degradation, conversion and restoration) on soil microbial community attributes and functioning and implications for ecosystem biogeochemical cycling, using lowland dipterocarp rainforest of Borneo as a model study system. The main research questions, key findings, conclusions and implications are summarised in Fig. 6.1.

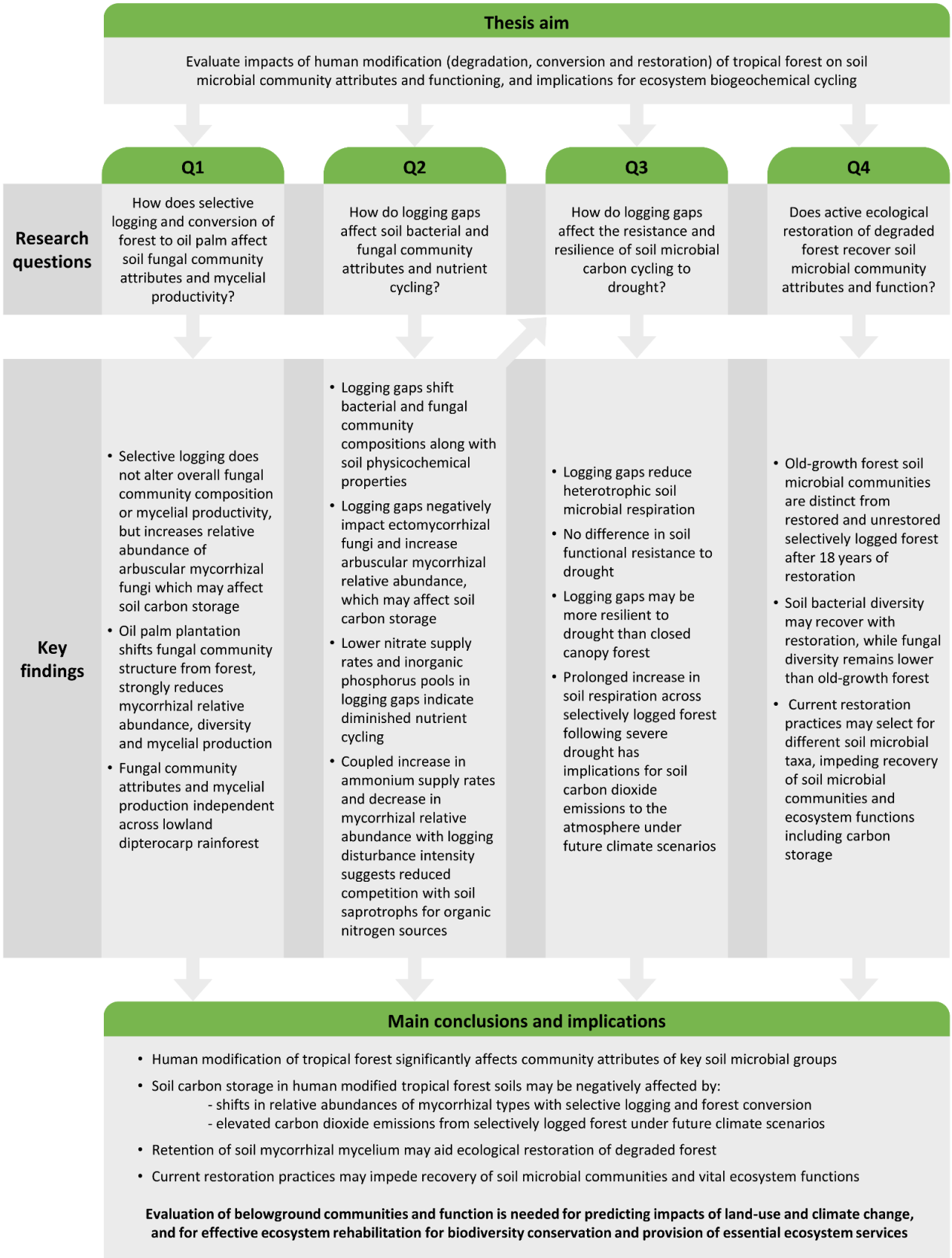

Figure 6.1. *Schematic of thesis structure summarising the main research questions, key findings, conclusions and implications*

The soil mycelium, comprising hyphae produced by actively foraging soil fungi, represents a key component of terrestrial C and nutrient cycles (Cairney, 2012; Finlay, 2008; Johnson et al., 2002). While the mycelium itself provides a C sink and can contribute to accumulation of soil organic matter (Wallander et al., 2013), the extraradical mycelia of mycorrhizal fungi provide a 'functional link' between plants and the soil as pathways of mineral nutrients and C between aboveground vegetation and belowground soil microbial communities (Smith and Read, 2008; Itoo and Reshi, 2013; Chen et al., 2016). While soil fungal communities have shown a sensitivity to SL and forest conversion in Southeast Asia, consequences for fungal functioning have so far been largely unknown. In Chapter 2, the impact of SL and conversion of forest to OP on fungal community characteristics and mycelial productivity was evaluated through a large-scale field survey across a gradient of forest disturbance. The roles of soil and vegetation properties as underlying drivers of mycelial community attributes and production in lowland dipterocarp rainforest were also explored. Conversion of forest to OP had the largest effect on mycelial fungal attributes and productivity. OP significantly reduced mycelial production relative to OG and SL forest, with corresponding shifts in overall, saprotrophic, mycorrhizal and pathogenic fungal community compositions and a reduction in mycorrhizal relative abundance and alpha diversity. As OP now represents a major land-use type across Borneo and Southeast Asia, this may have wide repercussions for nutrient dynamics, plant-soil interactions and potential for ecosystem recovery over large scales. In contrast, SL did not significantly differ in mycelial fungal community structure or productivity from OG forest, indicating potential resilience of mycelial fungal communities and function to forest degradation relative to bulk soil fungi. Findings also suggest the retention of the extramatrical EcM mycelium after SL. This has positive implications for recovery or

restoration of SL lowland dipterocarp forest, benefiting establishment of tree seedlings by providing an existing mycorrhizal inoculum and infrastructure for interplant exchanges of limiting resources through common mycelial networks (CMNs) (Babikova et al., 2013; Nara, 2006; Gorzelak et al., 2015). However, higher relative abundances of arbuscular and ericoid mycorrhizal fungi were associated with SL forest. Alterations in the balance between mycorrhizal types may have consequences for soil C cycling and storage, by reducing competition between ectomycorrhizal and saprotrophic fungi for resources required for the breakdown of soil organic matter (Averill et al., 2014). Across OG and SL forest, mycelial fungal community composition was linked to both vegetation and soil characteristics, while mycelial production was independent of all of these factors (with the exception of a tenuous positive relationship with soil inorganic phosphorous concentrations, potentially relating to proliferation of hyphae in soil mineral nutrient hotspots). This offers new insights into the potentially un-coupled fungal diversity and productivity patterns at the landscape-scale. Taken together, the findings of this chapter demonstrate impacts of land-use change on soil fungi that are likely to influence ecosystem and landscape-scale biogeochemical cycling, as well as the potential for restoration and recovery of vital ecosystem functions that relates to the nature and intensity of forest disturbance.

SL forest is a highly heterogeneous environment, comprising a mosaic of closed canopy forest and open canopy gaps, caused by the removal of large individual trees and creation of logging landings and skid trails (Asner et al., 2004). Canopy gaps can alter vegetation characteristics, soil properties and microclimate (Muscolo et al., 2014; Marthews et al., 2008), significantly affecting biogeochemical cycles regulated by soil microbial communities (Hartmann et al., 2013; Scharenbroch and Bockheim, 2007; 2008a; Saner et al., 2009). In Chapter 3, the impacts of selective logging gaps (SLGs)

on soil microbial community attributes and nutrient cycling were evaluated. This was achieved through a survey of soil microbial communities, soil physicochemical properties, nutrient supply rates and microclimate across in SL forest, in closed canopy forest (CCF) and SLG with varying disturbance intensities (% canopy openness). Results showed significant differences in soil bacterial and fungal community compositions between CCF and SLG. Particularly, lower relative abundances of total mycorrhizal and EcM fungi, and higher relative abundance of AM fungi were found in SLG. These differences were accompanied by significantly higher soil pH, bulk density and maximum soil moisture, and diminished nitrate (NO_3^-) supply rates and inorganic phosphorus (P) pools in SLG relative to CCF. Within SLGs, canopy openness was negatively related to total mycorrhizal and EcM relative abundances, while strongly positively related to supply rates of ammonium (NH_4^+). Overall, these findings indicate reduced nutrient cycling rates in SLG relative to CCF, but with potential enhancement of nitrogen (N) mineralisation with increasing disturbance intensity in SLG by reducing EcM-saprotrophic fungal competition for organic N sources. This provides more evidence of the effects of SL on ecosystem nutrient and C cycling by alterations in relative abundances of mycorrhizal types. These results also highlight SL effects on bacterial communities previously shown to be largely resilient to SL disturbance in studies using broader forest type classifications (i.e. between OG-SL forest) (Tripathi et al., 2016; Lee-Cruz et al., 2013). This emphasises the need for studies at finer spatial scales to evaluate impacts of high environmental heterogeneity resulting from SL on soil microbial communities and functions. The overall findings of this chapter show impacts of SL on key soil microbial groups (bacteria and fungi) that regulate crucial nutrient and C cycles, with the potential to alter biogeochemical functions at the landscape scale. This demonstrates the need for evaluations and predictions of the

impacts of forest degradation (e.g. biodiversity loss and C storage) to include SLG effects on belowground communities and function, which may also influence restoration potential for recovery of biodiversity and ecosystem services in human-modified tropical forest.

Chapter 3 established the impacts of SLG on soil microbial community attributes and soil physicochemical properties. In Chapter 4, the effect of these alterations on soil microbial C cycling, and resistance and resilience of soil function to drought was investigated through controlled laboratory incubations using soil respiration (R_S) as a functional measure. Results showed baseline R_S to be lower in SLG relative to CCF soils. Although reduced R_S has been found in SLGs in SL Bornean forest in a previous field survey, it had not yet been possible to separate the relative contributions of vegetation (i.e. autotrophic root respiration) and soil microbes to overall soil CO_2 efflux, nor account for the confounding microclimatic differences between CCF and SLG (Saner et al., 2009). By controlling for extraneous factors of vegetation, moisture and temperature, these findings highlight the independent impact of SL on heterotrophic soil microbial respiration. Experimental drought and rewetting revealed no differences in resistance of soil microbial function to reduced soil moisture between CCF and SLG. Some evidence was found for greater resilience of SLG soil function relative to CCF, as R_S returned to undisturbed levels faster after milder drought. However, R_S responses of SLG soils to drought and rewetting were highly variable, possibly as a result of varied soil physicochemical and biological characteristics across SLGs studied. Results showed drought can result in prolonged elevation in R_S in both CCF and SLG soils following rewetting. This may result from enhanced microbial growth and turnover (Birch, 1958; Zhou et al., 2016; Blazewicz et al., 2014; Karlowsky et al., 2018) and/or alterations in soil microbial ecophysiological

traits affecting breakdown of more recalcitrant soil C fractions (Bouskill et al., 2016c; Bouskill et al., 2016a). This has major implications for CO_2 release to the atmosphere in response to drought events, which are predicted to increase in intensity and frequency with anthropogenic climate change in the tropics (Coelho and Goddard, 2009; Rifai et al., 2019). The findings of this chapter outline the crucial need to include soil microbial functional responses to land-use and climate change in predictions of land-atmosphere C feedbacks (i.e. climate models), to fully understand and mitigate against impacts of anthropogenic disturbance of tropical forest.

Ecological restoration of degraded tropical forest may recover coupled biodiversity and ecosystem services, including C storage (Aronson and Alexander, 2013; Benayas et al., 2009; Face the Future, 2007), through re-establishment of vegetation communities and soil microbial attributes (Deng et al., 2010; Nurulita et al., 2016). However, most studies of restoration of SL forest in Southeast Asia have focussed on vegetation rather than soil microbial dynamics, potentially limiting rehabilitation success (Perumal et al., 2016). In Chapter 5, the effects of forest restoration by enrichment planting on soil microbial community attributes was evaluated through a survey of soil, vegetation and environmental characteristics across OG forest, restored SL (RSL) and unrestored SL forest (USL). Results showed RSL and USL bacterial and fungal communities to be relatively similar, while those of OG were distinct even after 18 years of restoration. Surprisingly, less soil microbial taxa were shared between OG and RSL across all groups compared to between OG and USL, and RSL and USL. Nevertheless, bacterial alpha and beta diversity indices appeared to successfully recover to levels representative of OG with enrichment planting. Additionally, further evidence was found for sensitivity of bacterial communities to forest disturbance, contradicting current understanding of bacterial community

resilience to SL (Tripathi et al., 2016; Lee-Cruz et al., 2013). Overall fungal alpha diversity was shown to recover more slowly, potentially driven by persistence of lower saprotrophic fungal alpha diversity in RSL comparable to USL. Findings indicate that current restoration management practices may be selecting for different soil microbial taxa in RSL than in OG and USL forest, which include liana and understorey vegetation removal. An apparent absence in human-modified forest of specific fungal taxa which may suppress plant pathogens (fungi and nematodes) with restoration may have negative consequences for reestablishment of planted species. Restoration practices may be impeding rehabilitation of soil microbial (particularly fungal) attributes, with implications for soil functioning. This is of vital importance considering the increased pressure now on remaining Bornean forest to provide essential ecosystem services, the vast majority of which is heavily degraded through SL (Gaveau et al., 2014). Overall, the findings of this chapter show that changes in current management practices to include consideration of the rehabilitation of belowground communities are required to effectively achieve ecosystemic recovery for biodiversity conservation and provision of vital ecosystem services, including C storage.

There are several caveats regarding approaches taken and conclusions drawn in this thesis, and further research is required to confirm or unpick underlying mechanisms. For example, the effects of mycorrhizal types on soil C accumulation by altering mycorrhizal-saprotrophic competition for mineral nutrients remains a subject of contention in current research (Zak et al., 2019), with potential links made through correlative studies that cannot separate effects of climate (Averill et al., 2014). In the context of modified tropical forest, field manipulations of mycorrhizal abundances, for example using fungal hyphal and fine root exclusion cores (Johnson et al., 2001; Langley et al., 2006), along with analysis of soil C and nutrient cycling processes are

needed. For evaluation of SLG impacts on resistance and resilience of soil function to climate perturbations, incorporation of different classes of SLG according to soil biological and physicochemical properties in future analysis may help to explain the high variability observed in RS responses to drought and rewetting. Repeated and longer duration incubation studies of drought-rewetting cycles in conjunction with pre- and post-disturbance analyses of soil microbial community attributes are needed to clarify whether prolonged elevated R_S following drought in SL forest soils represents a temporary burst in microbial activity, or a persistent shift in microbial communities and ecophysiological traits (Bouskill et al., 2016). Substrate addition experiments are also required to identify differences in soil microbial C cycling capabilities between SLG and CCF (Whitaker et al., 2014a; Whitaker et al., 2014b). Finally, further study is required to corroborate the effects of current forest restoration practices on soil microbial community recovery and confirm impacts on soil function. Controlled liana and understorey vegetation removal experiments alongside *in situ* monitoring of nutrient and C cycling processes will help elucidate consequences for ecosystem functions. Survey of restored forests of differing management regimes, ages and locations will also help confirm underlying patterns in belowground biodiversity and functions.

This thesis has demonstrated impacts of human modification of tropical rainforest (degradation, conversion and restoration) on soil microbial community attributes, and highlighted potential consequences for crucial soil functions. Overall, the main findings may have implications for large-scale soil nutrient cycling and C storage, through shifts in relative abundances of mycorrhizal types relating to breakdown of soil organic matter, and prolonged elevation of soil CO_2 emissions in SL forest in response to drought. This calls into question the capacity of remaining degraded forest to offset

anthropogenic C emissions, especially under future climate scenarios. An apparent retention of the soil mycorrhizal mycelium in SL forest may aid restoration by providing key limiting nutrients for establishment of dipterocarp seedlings, although results indicate potential selection of different soil microbial taxa by current restoration practices. This may inhibit recovery of soil microbial communities and ecosystem C sequestration in these biodiversity and degradation hotspots. Improved understanding of the impacts of degradation and restoration is required to ensure protection of globally critical tropical forest ecosystems. Evaluation of belowground communities and function is needed for predicting impacts of land-use and climate change, as well as effective ecosystem rehabilitation for biodiversity conservation and provision of essential ecosystem services by these vital, hyperdiverse environments.

7 References

Adachi, M., Bekku, Y. S., Rashidah, W., Okuda, T. & Koizumi, H. 2006. Differences in Soil Respiration between Different Tropical Ecosystems. *Applied Soil Ecology,* 34(2)**,** 258-265.

Alexander, A. 2012. Soil Compaction on Skid Trails after Selective Logging in Moist Evergreen Forest of Ghana. *ABJNA,* 3(6)**,** 262-264.

Allen, S. E. 1989. *Chemical Analysis of Ecological Materials*: Blackwell Scientific.

Allison, S. D. & Martiny, J. B. H. 2008. Resistance, Resilience, and Redundancy in Microbial Communities. *Proceedings of the National Academy of Sciences of the United States of America,* 105**,** 11512-11519.

Alroy, J. 2017. Effects of Habitat Disturbance on Tropical Forest Biodiversity. *Proceedings of the National Academy of Sciences of the United States of America,* 114(23)**,** 6056.

Anderson, J. M. & Ingram, J. S. I. 1993. *Tropical Soil Biology and Fertility : A Handbook of Methods,* Wallingford: CAB International.

Appanah, S. & Turnbull, J. M. 1998. *A Review of Dipterocarps: Taxonomy, Ecology and Silviculture* [Online]. Available: http://www.cifor.org/publications/pdf_files/Books/Dipterocarps.pdf [Accessed 22nd August 2019].

Aronson, E., Allison, S. & Helliker, B. 2013. Environmental Impacts on the Diversity of Methane-Cycling Microbes and Their Resultant Function. *Frontiers in Microbiology,* 4**,** 225.

Aronson, J. & Alexander, S. 2013. Ecosystem Restoration Is Now a Global Priority: Time to Roll up Our Sleeves. *Restoration Ecology,* 21(3)**,** 293-296.

Arunachalam, A. & Arunachalam, K. 2000. Influence of Gap Size and Soil Properties on Microbial Biomass in a Subtropical Humid Forest of North-East India. *An International Journal on Plant-Soil Relationships,* 223(1)**,** 187-195.

Asner, G. P., Brodrick, P. G., Philipson, C., Vaughn, N. R., Martin, R. E., Knapp, D. E., Heckler, J., Evans, L. J., Jucker, T., Goossens, B., Stark, D. J., Reynolds, G., Ong, R., Renneboog, N., Kugan, F. & Coomes, D. A. 2018. Mapped Aboveground Carbon Stocks to Advance Forest Conservation and Recovery in Malaysian Borneo. *Biological Conservation,* 217(C)**,** 289-310.

Asner, G. P., Keller, M. & Silva, J. N. M. 2004. Spatial and Temporal Dynamics of Forest Canopy Gaps Following Selective Logging in the Eastern Amazon. *Global Change Biology,* 10(5)**,** 765-783.

Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R. & Emerson, R. 2009. A Contemporary Assessment of Change in Humid Tropical Forests. *Conservation Biology,* 23(6)**,** 1386-1395.

Auffret, M. D., Karhu, K., Khachane, A., Dungait, J. A. J., Fraser, F., Hopkins, D. W., Wookey, P. A., Singh, B. K., Freitag, T. E., Hartley, I. P. & Prosser, J. I. 2016. The Role of Microbial Community Composition in Controlling Soil Respiration Responses to Temperature. *PLoS ONE,* 11(10)**,** e0165448.

Averill, C., Turner, B. L. & Finzi, A. C. 2014. Mycorrhiza- Mediated Competition between Plants and Decomposers Drives Soil Carbon Storage. *Nature,* 505(7484)**,** 543.

Aydin, M., Yang, S. L., Kurt, N. & Yano, T. 2005. Test of a Simple Model for Estimating Evaporation from Bare Soils in Different Environments. *Ecological Modelling,* 182(1)**,** 91-105.

Bååth, E. & Anderson, T. H. 2003. Comparison of Soil Fungal/Bacterial Ratios in a Ph Gradient Using Physiological and Plfa-Based Techniques. *Soil Biology and Biochemistry,* 35(7)**,** 955-963.

Babikova, Z., Gilbert, L., Bruce, T. J. A., Birkett, M., Caulfield, J. C., Woodcock, C., Pickett, J. A. & Johnson, D. 2013. Underground Signals Carried through Common Mycelial Networks Warn Neighbouring Plants of Aphid Attack. *Ecology Letters,* 16(7)**,** 835-843.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D. & Houghton, R. A. 2017. Tropical Forests Are a Net Carbon Source Based on Aboveground Measurements of Gain and Loss. *Science (New York, N.Y.),* 358(6360)**,** 230.

Bahram, M., Peay, K. G. & Tedersoo, L. 2015. Local-Scale Biogeography and Spatiotemporal Variability in Communities of Mycorrhizal Fungi.

Bakker, M., Delerue, F., Andreasson, F., Ngao, J., Dannoura, M., Zeller, B. & Epron, D. 2015. Hyphal Growth in Ingrowth Mesh Bags in Fagus Sylvatica, Quercus Petraea and Pinus Pinaster Stands in France. *European Journal Of Soil Biology,* 70**,** 111-117.

Banin, L., Lewis, S. L., Lopez-Gonzalez, G., Baker, T. R., Quesada, C. A., Chao, K. J., Burslem, D. F. R. P., Nilus, R., Abu Salim, K., Keeling, H. C., Tan, S., Davies, S. J., Monteagudo Mendoza, A., Vásquez, R., Lloyd, J., Neill, D. A., Pitman, N. & Phillips, O. L. 2014. Tropical Forest Wood Production: A Cross-Continental Comparison. *Journal of Ecology,* 102(4)**,** 1025-1037.

Banning, N. C., Gleeson, D. B., Grigg, A. H., Grant, C. D., Andersen, G. L., Brodie, E. L. & Murphy, D. V. 2011. Soil Microbial Community Successional Patterns During Forest Ecosystem Restoration. *Applied and environmental microbiology,* 77(17)**,** 6158.

Barberán, A., Mcguire, K. L., Wolf, J. A., Jones, F. A., Wright, S. J., Turner, B. L., Essene, A., Hubbell, S. P., Faircloth, B. C. & Fierer, N. 2015. Relating Belowground Microbial Composition to the Taxonomic, Phylogenetic, and Functional Trait Distributions of Trees in a Tropical Forest. *Ecology Letters,* 18(12)**,** 1397-1405.

Barreto, D. P., Conrad, R., Klose, M., Claus, P. & Enrich-Prast, A. 2014. Distance-Decay and Taxa-Area Relationships for Bacteria, Archaea and Methanogenic Archaea in a Tropical Lake Sediment. *PLoS ONE,* 9(10)**,** e110128.

Barriuso, J., Valverde, J. R. & Mellado, R. P. 2011. Estimation of Bacterial Diversity Using Next Generation Sequencing of 16s Rdna: A Comparison of Different Workflows. *BMC Bioinformatics,* 12(1)**,** 473-473.

Barto, E. K., Weidenhamer, J. D., Cipollini, D. & Rillig, M. C. 2012. Fungal Superhighways: Do Common Mycorrhizal Networks Enhance Below Ground Communication? *Trends in Plant Science,* 17(11)**,** 633-637.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using Lme4. *Journal of Statistical Software,* 67(1)**,** 1-48.

Battistuzzi, F. U. & Hedges, S. B. 2009. A Major Clade of Prokaryotes with Ancient Adaptations to Life on Land. *Molecular Biology and Evolution,* 26(2)**,** 335-343.

Benayas, J. M. R., Newton, A. C., Diaz, A. & Bullock, J. M. 2009. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. *Science,* 325(5944)**,** 1121-1124.

Berenguer, E., Ferreira, J., Gardner, T. A., Aragão, L. E. O. C., De Camargo, P. B., Cerri, C. E., Durigan, M., Oliveira, R. C. D., Vieira, I. C. G. & Barlow, J. 2014. A Large- Scale Field Assessment of Carbon Stocks in Human- Modified Tropical Forests. *Global Change Biology,* 20(12)**,** 3713-3726.

Berga, M., Székely, A. J. & Langenheder, S. 2012. Effects of Disturbance Intensity and Frequency on Bacterial Community Composition and Function. *PloS one,* 7(5)**,** e36959-e36959.

Berruti, A., Desirò, A., Visentin, S., Zecca, O. & Bonfante, P. 2017. ITS Fungal Barcoding Primers Versus 18s Amf-Specific Primers Reveal Similar Amf-Based Diversity Patterns in Roots and Soils of Three Mountain Vineyards. *Environmental Microbiology Reports,* 9(5)**,** 658-667.

Bever, J. D., Dickie, I. A., Facelli, E., Facelli, J. M., Klironomos, J., Moora, M., Rillig, M. C., Stock, W. D., Tibbett, M. & Zobel, M. 2010. Rooting Theories of Plant Community Ecology in Microbial Interactions. *Trends in Ecology & Evolution,* 25(8)**,** 468-478.

Bierregaard, R. O. 2001. Lessons from Amazonia : The Ecology and Conservation of a Fragmented Forest, New Haven ; London: Yale University Press.

Birch, H. F. 1958. The Effect of Soil Drying on Humus Decomposition and Nitrogen Availability. *Plant and Soil,* 10(1)**,** 9-31.

Blanchet, F. G., Legendre, P. & Borcard, D. 2008. Forward Selection of Explanatory Variables. *Ecology,* 89(9)**,** 2623-2632.

Blazewicz, S. J., Schwartz, E. & Firestone, M. K. 2014. Growth and Death of Bacteria and Fungi Underlie Rainfall-Induced Carbon Dioxide Pulses from Seasonally Dried Soil. *Ecology,* 95(5)**,** 1162-1172.

Boddington, C. L., Bassett, E. E., Jakobsen, I. & Dodd, J. C. 1999. Comparison of Techniques for the Extraction and Quantification of Extra-Radical Mycelium of Arbuscular Mycorrhizal Fungi in Soils. *Soil Biology and Biochemistry,* 31(3)**,** 479-482.

Bonner, M. T. L., Allen, D. E., Brackin, R., Smith, T. E., Lewis, T., Shoo, L. P. & Schmidt, S. 2019. Tropical Rainforest Restoration Plantations Are Slow to Restore the Soil Biological and Organic Carbon Characteristics of Old Growth Rainforest. *Microbial Ecology*.

Bossel, H. & Krieger, H. 1991. Simulation Model of Natural Tropical Forest Dynamics. *Ecological Modelling,* 59(1-2)**,** 37-71.

Both, S., Elias, D. M. O., Kritzler, U. H., Ostle, N. J. & Johnson, D. 2017. Land Use Not Litter Quality Is a Stronger Driver of Decomposition in Hyperdiverse Tropical Forest. *Ecology and Evolution,* 7(22)**,** 9307-9318.

Both, S., Riutta, T., Paine, C. E. T., Elias, D. M. O., Cruz, R. S., Jain, A., Johnson, D., Kritzler, U. H., Kuntz, M., Majalap-Lee, N., Mielke, N., Montoya Pillco, M. X., Ostle, N. J., Arn Teh, Y., Malhi, Y. & Burslem, D. F. R. P. 2019. Logging and Soil Nutrients Independently Explain Plant Trait Expression in Tropical Forests. *The New phytologist,* 221(4)**,** 1853.

Bouskill, N. J., Wood, T. E., Baran, R., Hao, Z., Ye, Z., Bowen, B. P., Lim, H. C., Nico, P. S., Holman, H.-Y., Gilbert, B., Silver, W. L., Northen, T. R. & Brodie, E. L. 2016a. Belowground Response to Drought in a Tropical Forest Soil. II. Change in Microbial Function Impacts Carbon Composition. *Frontiers in Microbiology,* 7**,** 323.

Bouskill, N. J., Wood, T. E., Baran, R., Ye, Z., Bowen, B. P., Lim, H., Zhou, J., Nostrand, J. D. V., Nico, P., Northen, T. R., Silver, W. L. & Brodie, E. L. 2016b. Belowground Response to Drought in a Tropical Forest Soil. I. Changes in Microbial Functional Potential and Metabolism. *Frontiers in Microbiology,* 7**,** 525.

Box, J. E. & Taylor, S. A. 1962. Influence of Soil Bulk Density on Matric Potential1. *Soil Science Society of America Journal,* 26**,** 119-122.

Bradshaw, C. J., Sodhi, N. S. & Brook, B. W. 2009. Tropical Turmoil: A Biodiversity Tragedy in Progress.

Brancalion, P. H., Viani, R. A., Calmon, M., Carrascosa, H. & Rodrigues, R. R. 2013. How to Organize a Large-Scale Ecological Restoration Program? The Framework Developed by the Atlantic Forest Restoration Pact in Brazil. *Journal of Sustainable Forestry,* 32(7)**,** 728-744.

Bray, R. H. & Kurtz, L. T. 1945. Determination of Total Organic and Available Forms of Phosphorus in Soils. *Soil Science,* 59(1)**,** 39-46.

Brearley, F. Q. 2012. Ectomycorrhizal Associations of the Dipterocarpaceae. *Biotropica,* 44(5)**,** 637-648.

Briones, M. J. I., Mcnamara, N. P., Poskitt, J., Crow, S. E. & Ostle, N. J. 2014. Interactive Biotic and Abiotic Regulators of Soil Carbon Cycling: Evidence from Controlled Climate Experiments on Peatland and Boreal Soils. *Global Change Biology,* 20(9)**,** 2971-2982.

Brookes, P. C., Kragt, J. F., Powlson, D. S. & Jenkinson, D. S. 1985. Chloroform Fumigation and the Release of Soil Nitrogen: The Effects of Fumigation Time and Temperature. *Soil Biology and Biochemistry,* 17(6)**,** 831-835.

Brundrett, M. C. 2002. Coevolution of Roots and Mycorrhizas of Land Plants. Oxford, UK.

Bryan, J. E., Shearman, P. L., Asner, G. P., Knapp, D. E., Aoro, G. & Lokes, B. 2013. Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei. *PloS one,* 8(7)**,** e69679.

Cairney, J. W. G. 2012. Extramatrical Mycelia of Ectomycorrhizal Fungi as Moderators of Carbon Dynamics in Forest Soil. *Soil Biology and Biochemistry,* 47**,** 198-208.

Callahan, B. J., Mcmurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A. & Holmes, S. P. 2016. Dada2: High-Resolution Sample Inference from Illumina Amplicon Data. *Nature Methods,* 13(7).

Camenzind, T., Hättenschwiler, S., Treseder, K. K., Lehmann, A. & Rillig, M. C. 2018. Nutrient Limitation of Soil Microbial Processes in Tropical Forests. *Ecological Monographs,* 88(1)**,** 4-21.

Camenzind, T., Papathanasiou, H. J., Forster, A., Dietrich, K., Hertel, D., Homeier, J., Oelmann, Y., Olsson, P. A., Suarez, J. P. & Rillig, M. C. 2016. Increases in Soil Aggregation Following Phosphorus Additions in a Tropical Premontane Forest Are Not Driven by Root and Arbuscular Mycorrhizal Fungal Abundances. *Frontiers in Earth Science,* 3.

Canarini, A., Kiær, L. P. & Dijkstra, F. A. 2017. Soil Carbon Loss Regulated by Drought Intensity and Available Substrate: A Meta-Analysis. *Soil Biology and Biochemistry,* 112**,** 90-99.

Carlson, K., M., Curran, L., M., Asner, G., P., Pittman, A. M., Trigg, S., N. & Adeney, J. M. 2012. Carbon Emissions from Forest Conversion by Kalimantan Oil Palm Plantations. *Nature Climate Change,* 3(3)**,** 283.

Caspermeyer, J. 2017. Diversity without Limits: New Insights from the Most Comprehensive Tree of Prokaryotic Life Assembled to Date. *Molecular Biology and Evolution,* 34(2)**,** 507-507.

Cassman, K. G. & Munns, D. N. 1980. Nitrogen Mineralization as Affected by Soil Moisture, Temperature, and Depth. Soil Science Society of America Journal, 44(6), 1233-1237.

Celis, G. & Jose, S. 2011. Restoring Abandoned Pasture Land with Native Tree Species in Costa Rica: Effects of Exotic Grass Competition and Light. *For. Ecol. Manage.,* 261(10)**,** 1598-1604.

Cenciani, K., Lambais, M. R., Cerri, C. C., Azevedo, L. C. B. D. & Feigl, B. J. 2009. Bacteria Diversity and Microbial Biomass in Forest, Pasture and Fallow Soils in the Southwestern Amazon Basin. Revista brasileira de ciência do solo, 33(4), 907-916.

Cerri, C. E. P., Paustian, K., Bernoux, M., Victoria, R. L., Melillo, J. M. & Cerri, C. C. 2004. Modeling Changes in Soil Organic Matter in Amazon Forest to Pasture Conversion with the Century Model. Global change biology, 10(5), 815-832.

Cerullo, G. R., Edwards, F. A., Mills, S. C. & Edwards, D. P. 2019. Tropical Forest Subjected to Intensive Post-Logging Silviculture Maintains Functionally Diverse Dung Beetle Communities. *Forest Ecology and Management,* 444**,** 318-326.

Chaer, G., Fernandes, M., Myrold, D. & Bottomley, P. 2009. Comparative Resistance and Resilience of Soil Microbial Communities and Enzyme Activities in Adjacent Native Forest and Agricultural Soils. *Microbial Ecology,* 58(2)**,** 414-424.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N., M., Gerber, J., S., West, P., C., Mandle, L., Engstrom, P., Baccini, A., Sim, S., Mueller, C. & King, H. 2015. Degradation in Carbon Stocks near Tropical Forest Edges. *Nature Communications,* 6.

Chazdon, R. L. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. *Science,* 320(5882)**,** 1458-1460.

Chen, W., Koide, R. T., Adams, T. S., Deforest, J. L., Cheng, L. & Eissenstat, D. M. 2016. Root Morphology and Mycorrhizal Symbioses Together Shape Nutrient Foraging Strategies of Temperate Trees. *Proceedings of the National Academy of Sciences of the United States of America,* 113(31)**,** 8741.

Chen, W., Simpson, J. & Levesque, C. A. 2018. Ram: r for amplicon-Sequencing-Based Microbial-Ecology [Online]. Available: https://cran.r-project.org/package=ram [Accessed 27th January 2020].

Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A. & Lindahl, B. D. 2015. Carbon Sequestration Is Related to Mycorrhizal Fungal Community Shifts During Long-Term Succession in Boreal Forests. *New Phytologist,* 205(4)**,** 1525-1536.

Cleveland, C. C., Wieder, W. R., Reed, S. C. & Townsend, A. R. 2010. Experimental Drought in a Tropical Rain Forest Increases Soil Carbon Dioxide Losses to the Atmosphere. *Ecology,* 91(8)**,** 2313-2323.

Cochrane, M. A. 2001. Synergistic Interactions between Habitat Fragmentation and Fire in Evergreen Tropical Forests. *Conservation Biology,* 15(6)**,** 1515-1521.

Coelho, C. A. S. & Goddard, L. 2009. El Niño–Induced Tropical Droughts in Climate Change Projections. *Journal of Climate,* 22(23)**,** 6456-6476.

Corley, R. H. V. 2009. How Much Palm Oil Do We Need? *Environmental Science & Policy,* 12(2)**,** 134-139.

Cortois, R., Schröder-Georgi, T., Weigelt, A., van der Putten, W. H. & de Deyn, G. B. 2016. Plant–Soil Feedbacks: Role of Plant Functional Group and Plant Traits. *Journal of Ecology,* 104(6)**,** 1608-1617.

Curran, L. M., Trigg, S. N., Mcdonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., Caniago, I. & Kasischke, E. 2004. Lowland Forest Loss in Protected Areas of Indonesian Borneo. *Science,* 303(5660)**,** 1000-1003.

Curtis, T. P., Sloan, W. T. & Scannell, J. W. 2002. Estimating Prokaryotic Diversity and Its Limits.(Abstract). *Proceedings of the National Academy of Sciences of the United States,* 99(16)**,** 10494.

Daisuke, H., Tanaka, K., Joseph Jawa, K., Ikuo, N. & Katsutoshi, S. 2013. Rehabilitation of Degraded Tropical Rainforest Using Dipterocarp Trees in Sarawak, Malaysia. *International Journal of Forestry Research,* 2013(2013).

Daljit Singh, K. S., Arifin, A., Radziah, O., Shamshuddin, J., Hazandy, A. H., Majid, N. M., Aiza-Shaliha, J., Rui, T. X. & Keeren, S. R. 2013. Status of Soil Microbial Population, Enzymatic Activity and Biomass of Selected Natural, Secondary and Rehabilitated Forests. *American Journal of Environmental Science,* 9(4)**,** 301-309.

Day, P. R. 1965. *Particle Fractionation and Particle-Size Analysis,* Madison, Wisconsin, USA: American Society of Agronomy.

de Bruyn, M., Stelbrink, B., Morley, R. J., Hall, R., Carvalho, G. R., Cannon, C. H., Van Den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L., Maiorano, L., Shoup, R. & Von Rintelen, T. 2014. Borneo and Indochina Are Major Evolutionary Hotspots for Southeast Asian Biodiversity. *Systematic Biology,* 63(6)**,** 879-901.

de Caceres, M. & Legendre, P. 2009. Associations between Species and Groups of Sites: Indices and Statistical Inference [Online]. Available: http://sites.google.com/site/miqueldecaceres/ [Accessed 27th January 2020].

de Carvalho, T. S., Jesus, E. D. C., Barlow, J., Gardner, T. A., Soares, I. C., Tiedje, J. M. & Moreira, F. M. D. S. 2016. Land Use Intensification in the Humid Tropics Increased Both Alpha and Beta Diversity of Soil Bacteria. Ecology (Durham), 97(10), 2760-2771.

de Deyn, G. B., Shiel, R. S., Ostle, N. J., Mcnamara, N. P., Oakley, S., Young, I., Freeman, C., Fenner, N., Quirk, H. & Bardgett, R. D. 2011. Additional Carbon Sequestration Benefits of Grassland Diversity Restoration. *Journal of Applied Ecology,* 48(3)**,** 600-608.

de Nijs, E. A., Hicks, L. C., Leizeaga, A., Tietema, A. & Rousk, J. 2019. Soil Microbial Moisture Dependences and Responses to Drying–Rewetting: The Legacy of 18 Years Drought. *Global Change Biology,* 25(3)**,** 1005-1015.

de Sy, V., Herold, M., Achard, F., Avitabile, V., Baccini, A., Carter, S., Clevers, J. G. P. W., Lindquist, E., Pereira, M. & Verchot, L. 2019. Tropical Deforestation Drivers and Associated Carbon Emission Factors Derived from Remote Sensing Data. *Environmental Research Letters,* 14(9)**,** 094022.

Defries, R. S., Houghton, R. A., Hansen, M. C., Field, C. B., Skole, D. & Townshend, J. 2002. Carbon Emissions from Tropical Deforestation and Regrowth Based on Satellite Observations for the 1980s and 1990s. *Proc. Natl. Acad. Sci. U. S. A.,* 99(22)**,** 14256-14261.

Deng, H., Zhang, B., Yin, R., Wang, H.-L., Mitchell, S., Griffiths, B. & Daniell, T. 2010. Long-Term Effect of Re-Vegetation on the Microbial Community of a Severely Eroded Soil in Sub-Tropical China. *An International Journal on Plant-Soil Relationships,* 328(1)**,** 447-458.

Deng, Q., Zhang, D., Han, X., Chu, G., Zhang, Q. & Hui, D. 2018. Changing Rainfall Frequency Rather Than Drought Rapidly Alters Annual Soil Respiration in a Tropical Forest. Soil biology & biochemistry, 121, 8-15.

Denslow, J. S. 1995. Disturbance and Diversity in Tropical Rain Forests: The Density Effect. Ecological applications, 5(4), 962-968.

Denslow, J. S., Ellison, A. M. & Sanford, R. E. 1998. Treefall Gap Size Effects on above- and Below- Ground Processes in a Tropical Wet Forest. *Journal of Ecology,* 86(4)**,** 597-609.

Dickie, I., Koele, N., Blum, J. D., Gleason, J. D. & Mcglone, M. S. 2014. Mycorrhizas in Changing Ecosystems. *Botany,* 92(2)**,** 149-160.

Dirzo, R. & Raven, P. H. 2003. Global State of Biodiversity and Loss. *Annu. Rev. Environ. Resour.,* 28**,** 137-167.

Don, A., Schumacher, J. & Freibauer, A. 2011. Impact of Tropical Land-Use Change on Soil Organic Carbon Stocks - a Meta-Analysis. *Glob. Change Biol.*

Drigo, B., Anderson, I. C., Kannangara, G. S. K., Cairney, J. W. G. & Johnson, D. 2012. Rapid Incorporation of Carbon from Ectomycorrhizal Mycelial Necromass into Soil Fungal Communities. *Soil Biology and Biochemistry,* 49**,** 4-10.

Dufrêne, M. & Legendre, P. 1997. Species Assemblages and Indicator Species:The Need for a Flexible Asymmetrical Approach. *Ecological Monographs,* 67(3)**,** 345-366.

Dupont, A. Ö. C., Griffiths, R. I., Bell, T. & Bass, D. 2016. Differences in Soil Micro-Eukaryotic Communities over Soil Ph Gradients Are Strongly Driven by Parasites and Saprotrophs. *Environmental Microbiology,* 18(6)**,** 2010-2024.

Eaton, W. D., Mcgee, K. M., Alderfer, K., Jimenez, A. R. & Hajibabaei, M. 2020. Increase in Abundance and Decrease in Richness of Soil Microbes Following Hurricane Otto in Three Primary Forest Types in the Northern Zone of Costa Rica. PloS one, 15(7), e0231187.

Ek, H., Sjögren, M., Arnebrant, K. & Söderström, B. 1994. Extramatrical Mycelial Growth, Biomass Allocation and Nitrogen Uptake in Ectomycorrhizal Systems in Response to Collembolan Grazing. *Applied Soil Ecology,* 1(2)**,** 155-169.

Ekblad, A., Wallander, H., Godbold, D., Cruz, C., Johnson, D., Baldrian, P., Björk, R., Epron, D., Kieliszewska-Rokicka, B., Kjøller, R., Kraigher, H., Matzner, E., Neumann, J. & Plassard, C. 2013. The Production and Turnover of Extramatrical Mycelium of Ectomycorrhizal Fungi in Forest Soils: Role in Carbon Cycling. *Plant Soil,* 366(1)**,** 1-27.

Elias, D. M. O., Both, S., Goodall, T., Robinson, S., Ostle, N. J., Mcnamara, N. P., Burslem, D. F. R. P., Riutta, T., Malhi, Y., Griffiths, R., Johnson, D. & Majalap-Lee, N. 2019. Linkages between Soil Microbial Diversity, Plant Functional Traits and Soil Properties across Primary and Human Modified Tropical Forests. Unpublished Manuscript.

Elias, D. M. O., McNamara, N. P., Ostle, N. J. & Majalap-Lee, N. 2018. Soil Properties across Primary Forest, Logged Forest and Oil Palm Plantation in Sabah, Malaysia. Nerc Environmental Information Data Centre [Online dataset]. Available: https://doi.org/10.5285/7e046092-8405-41b8-9e38-67a844bb9e7d [Accessed 9th September 2019].

Ellis, P., Griscom, B., Walker, W., Gonçalves, F. & Cormier, T. 2016. Mapping Selective Logging Impacts in Borneo with Gps and Airborne Lidar. *Forest Ecology and Management,* 365**,** 184-196.

Emmett, B. A., Frogbrook, Z. L., Chamberlain, P. M., Griffiths, R., Pickup, R., Poskitt, J., Reynolds, B., Rowe, E., Rowland, P., Spurgeon, D., Wilson, J. & Wood, C. M. 2008. Countryside Survey Technical Report No.03/07. Available: http://www.countrysidesurvey.org.uk/sites/default/files/CS_UK_2007_TR3%20-%20Soils%20Manual.pdf [Accessed 19/11/2019].

Epron, D., Nouvellon, Y., Deleporte, P., Ifo, S., Kazotti, G. U. Y., Thongo M'bou, A., Mouvondy, W., Andre, L. S., Roupsard, O., Jourdan, C. & Hamel, O. 2006. Soil Carbon Balance in a Clonal Eucalyptus Plantation in Congo: Effects of Logging on Carbon Inputs and Soil Co2 Efflux. Global change biology, 12(6), 1021-1031.

Essene, A. L., Shek, K. L., Lewis, J. D., Peay, K. G. & Mcguire, K. L. 2017. Soil Type Has a Stronger Role Than Dipterocarp Host Species in Shaping the Ectomycorrhizal Fungal Community in a Bornean Lowland Tropical Rain Forest. *Frontiers in Plant Science,* 8.

Evans, S. E. & Wallenstein, M. D. 2011. Soil Microbial Community Response to Drying and Rewetting Stress: Does Historical Precipitation Regime Matter? Biogeochemistry, 109(1-3), 101-116.

Evans, S. E. & Wallenstein, M. D. 2012. Soil Microbial Community Response to Drying and Rewetting Stress: Does Historical Precipitation Regime Matter? *Biogeochemistry,* 109(1)**,** 101-116.

Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J. L. & Turner, E. C. 2011. A Large-Scale Forest Fragmentation Experiment: The Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B,* 366(1582)**,** 3292-3302.

Face the Future 2007. INFAPRO Rehabilitation of Logged-over Dipterocarp Forest in Sabah, Malaysia [Online]. Available: http://theredddesk.org/sites/default/files/verified_carbon_standard_project_document.pdf [Accessed 12th April 2017].

Face the Future. 2020. *Infapro Restoration of Tropical Rainforest: Sabah, Malaysia* [Online]. Available: https://facethefuture.com/projects/sabah-maleisie-bosherstel-en-bescherming [Accessed 11th February 2020].

Ferraz, A., Saatchi, S., Xu, L., Hagen, S., Chave, J., Yu, Y., Meyer, V., Garcia, M., Silva, C., Roswintiart, O., Samboko, A., Sist, P., Walker, S., Pearson, T., Wijaya, A., Sullivan, F., Rutishauser, E., Hoekman, D. & Ganguly, S. 2018. Carbon Storage Potential in Degraded Forests of Kalimantan, Indonesia. *Environ. Res. Lett.,* 13(9).

Ferraz, S., Ferraz, K., Cassiano, C., Brancalion, P., Luz, D., Azevedo, T., Tambosi, L. & Metzger, J. 2014. How Good Are Tropical Forest Patches for Ecosystem Services Provisioning? *Landscape Ecol,* 29(2)**,** 187-200.

Ferrenberg, Apos, Neill, Knelman, Todd, Duggan & Bradley 2013. Changes in Assembly Processes in Soil Bacterial Communities Following a Wildfire Disturbance. *The ISME journal.,* 7**,** 1102-1111.

Fichtner, A., Von Oheimb, G., Härdtle, W., Wilken, C. & Gutknecht, J. L. M. 2014. Effects of Anthropogenic Disturbances on Soil Microbial Communities in Oak Forests Persist for More Than 100 Years. *Soil Biology and Biochemistry,* 70(C)**,** 79-87.

Fierer, N. & Schimel, J. P. 2002. Effects of Drying–Rewetting Frequency on Soil Carbon and Nitrogen Transformations. *Soil Biology and Biochemistry,* 34(6)**,** 777-787.

Finlay, R. D. 2008. Ecological Aspects of Mycorrhizal Symbiosis: With Special Emphasis on the Functional Diversity of Interactions Involving the Extraradical Mycelium. *Journal of Experimental Botany,* 59(5)**,** 1115-1126.

Fisher, B., Edwards, D. P., Giam, X. & Wilcove, D. S. 2011. The High Costs of Conserving Southeast Asia's Lowland Rainforests. *Frontiers in Ecology and the Environment,* 9(6)**,** 329-334.

Fisher, J., Malhi, Y., Torres, I., Metcalfe, D., Van De Weg, M., Meir, P., Silva-Espejo, J. & Huasco, W. 2013. Nutrient Limitation in Rainforests and Cloud Forests Along a 3,000-M Elevation Gradient in the Peruvian Andes. *Oecologia,* 172(3)**,** 889-902.

Franco, A. L. C., Sobral, B. W., Silva, A. L. C. & Wall, D. H. 2019. Amazonian Deforestation and Soil Biodiversity. Conserv Biol, 33(3), 590-600.

Fraterrigo, J. M., Balser, T. C. & Turner, M. G. 2006. Microbial Community Variation and Its Relationship with Nitrogen Mineralization in Historically Altered Forests. *Ecology,* 87(3)**,** 570-579.

Frazer, G. W., Fournier, R. A., Trofymow, J. A. & Hall, R. J. 2001. A Comparison of Digital and Film Fisheye Photography for Analysis of Forest Canopy Structure and Gap Light Transmission. *Agricultural and Forest Meteorology,* 109(4)**,** 249-263.

Gagen, M. 2019. *The World's Tallest Known Tropical Tree Has Been Found—and Climbed* [Online]. National Geographic Society. Available: https://www.nationalgeographic.com/environment/2019/04/worlds-tallest-tropical-tree-discovered-climbed-borneo/?cmpid=org=ngp::mc=social::src=facebook::cmp=editorial::add=fb20190403env-tallesttropicaltree::rid=&sf210363218=1&fbclid=IwAR1hFk6sdt_3liAzmRHoy6D5-Qg97CTjVJwoaFZiEJDmUC55sxbW3V1-zTQ [Accessed 10th February 2020].

Galand, P. E., Lucas, S., Fagervold, S. K., Peru, E., Pruski, A. M., Vétion, G., Dupuy, C. & Guizien, K. 2016. Disturbance Increases Microbial Community Diversity and Production in Marine Sediments. *Frontiers in microbiology,* 7**,** 1950-1950.

García De León, D., Neuenkamp, L., Moora, M., Öpik, M., Davison, J., Peña-Venegas, C. P., Vasar, M., Jairus, T. & Zobel, M. 2018. Arbuscular Mycorrhizal Fungal Communities in Tropical Rain Forest Are Resilient to Slash-and-Burn Agriculture. J. Trop. Ecol, 34(3), 186-199.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A. & Sodhi, N. S. 2009. Prospects for Tropical Forest Biodiversity in a Human-Modified World. Oxford, UK.

Gaveau, D. L. A., Sheil, D., Husnayaen, Salim, M. A., Arjasakusuma, S., Ancrenaz, M., Pacheco, P. & Meijaard, E. 2016. Rapid Conversions and Avoided Deforestation: Examining Four Decades of Industrial Plantation Expansion in Borneo. *Scientific Reports,* 6(1).

Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N. & Meijaard, E. 2014. Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PloS one,* 9(7)**,** e101654.

Giam, X. 2017. Global Biodiversity Loss from Tropical Deforestation. *Proceedings of the National Academy of Sciences of the United States of America,* 114(23)**,** 5775.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. & Sodhi, N., S 2011. Primary Forests Are Irreplaceable for Sustaining Tropical Biodiversity. *Nature,* 478(7369)**,** 378.

Gorzelak, M. A., Asay, A. K., Pickles, B. J. & Simard, S. W. 2015. Inter-Plant Communication through Mycorrhizal Networks Mediates Complex Adaptive Behaviour in Plant Communities. *AoB PLANTS,* 7(1).

Green, J. L., Holmes, A. J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M. & Beattie, A. J. 2004. Spatial Scaling of Microbial Eukaryote Diversity. *Nature,* 432(7018)**,** 747.

Griffiths, B. S. & Philippot, L. 2013. Insights into the Resistance and Resilience of the Soil Microbial Community. *FEMS Microbiology Reviews,* 37(2)**,** 112-129.

Griffiths, B. S., Ritz, K., Bardgett, R. D., Cook, R., Christensen, S., Ekelund, F., Sørensen, S. J., Bååth, E., Bloem, J., De Ruiter, P. C., Dolfing, J. & Nicolardot, B. 2000. Ecosystem Response of Pasture Soil Communities to Fumigation-Induced Microbial Diversity Reductions: An Examination of the Biodiversity–Ecosystem Function Relationship. *Oikos,* 90(2)**,** 279-294.

Grigal, D. F. 2000. Effects of Extensive Forest Management on Soil Productivity. *Forest Ecology and Management,* 138(1-3)**,** 167-185.

Grządziel, J. 2017. Functional Redundancy of Soil Microbiota – Does More Always Mean Better? *Polish Journal of Soil Science; Vol 50, No 1 (2017)DO - 10.17951/pjss.2017.50.1.75*.

Guillaume, T., Damris, M. & Kuzyakov, Y. 2015. Losses of Soil Carbon by Converting Tropical Forest to Plantations: Erosion and Decomposition Estimated by Δ13c. *Global Change Biology,* 21(9)**,** 3548-3560.

Haack, S. K., Garchow, H., Odelson, D. A., Forney, L. J. & Klug, M. J. 1994. Accuracy, Reproducibility, and Interpretation of Fatty Acid Methyl Ester Profiles of Model Bacterial Communities. *Applied and environmental microbiology,* 60(7)**,** 2483.

Hagenbo, A., Kyaschenko, J., Clemmensen, K. E., Lindahl, B. D. & Fransson, P. 2018. Fungal Community Shifts Underpin Declining Mycelial Production and Turnover across a Pinus Sylvestris Chronosequence. *Journal of Ecology,* 106(2)**,** 490-501.

Hagerberg, D., Thelin, G. & Wallander, H. 2003. The Production of Ectomycorrhizal Mycelium in Forests: Relation between Forest Nutrient Status and Local Mineral Sources. *Plant and Soil,* 252(2)**,** 279-290.

Han, M. & Zhu, B. *forthcoming*. Changes in Soil Greenhouse Gas Fluxes by Land Use Change from Primary Forest. *Global Change Biology*.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O. & Townshend, J. R. G. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science,* 342(6160)**,** 850.

Hanssen, J. F., Thingstad, T. F. & Goksøyr, J. 1974. Evaluation of Hyphal Lengths and Fungal Biomass in Soil by a Membrane Filter Technique. *Oikos,* 25(1)**,** 102-107.

Hart, M. M., Aleklett, K., Chagnon, P. L., Egan, C., Ghignone, S., Helgason, T., Lekberg, Y., Öpik, M., Pickles, B. J. & Waller, L. 2015. Navigating the Labyrinth: A Guide to Sequence-Based, Community Ecology of Arbuscular Mycorrhizal Fungi. *New Phytologist,* 207(1)**,** 235-247.

Hartmann, M., Howes, C. G., Vaninsberghe, D., Yu, H., Bachar, D., Christen, R., Nilsson, R. H., Hallam, S. J. & Mohn, W. W. 2012. Significant and Persistent Impact of Timber Harvesting on Soil Microbial Communities in Northern Coniferous Forests. *The ISME Journal,* 6(12)**,** 2320.

Hartmann, M., Niklaus, P. A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., Lüscher, P., Widmer, F. & Frey, B. 2013. Resistance and Resilience of the Forest Soil Microbiome to Logging-Associated Compaction. *The ISME Journal,* 8(1)**,** 226.

Hazebroek, H. P., Adlin, T. Z. & Sinun, W. 2004. Maliau Basin: Sabah's Lost World. Kota Kinabalu, Malaysia: Natural History Publications (Borneo).

Horner-Devine, C. M., Leibold, M. A., Smith, V. H. & Bohannan, B. J. M. 2003. Bacterial Diversity Patterns Along a Gradient of Primary Productivity. *Ecology Letters,* 6(7)**,** 613-622.

Hu, B., Yang, B., Pang, X., Bao, W. & Tian, G. 2016. Responses of Soil Phosphorus Fractions to Gap Size in a Reforested Spruce Forest. *Geoderma,* 279**,** 61-69.

Hu, L., Gong, Z., Li, J. & Zhu, J. 2009. Estimation of Canopy Gap Size and Gap Shape Using a Hemispherical Photograph. *Trees,* 23(5)**,** 1101-1108.

Hueso, S., García, C. & Hernández, T. 2012. Severe Drought Conditions Modify the Microbial Community Structure, Size and Activity in Amended and Unamended Soils. Soil biology & biochemistry, 50, 167-173.

Hughes, A. C. 2017. Understanding the Drivers of Southeast Asian Biodiversity Loss. *Ecosphere,* 8(1)**,** n/a-n/a.

Humphreys, C. P., Franks, P. J., Rees, M., Bidartondo, M. I., Leake, J. R. & Beerling, D. J. 2010. Mutualistic Mycorrhiza-Like Symbiosis in the Most Ancient Group of Land Plants. *Nature Communications,* 1(8)**,** 103.

Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L. & Schwinning, S. 2004. Precipitation Pulses and Carbon Fluxes in Semiarid and Arid Ecosystems. *Oecologia,* 141(2)**,** 254-268.

Ihrmark, K., Bodeker, I. T. M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandstrom-Durling, M., Clemmensen, K. E. & Lindahl, B. D. 2012. New Primers to Amplify the Fungal Its2 Region - Evaluation by 454-Sequencing of Artificial and Natural Communities. *Fems Microbiology Ecology,* 82(3)**,** 666-677.

International Timber Trade Organisation (ITTO) 2012. Annual Review and Assessment of the World Tropical Timber Situation. International Timber Trade Organisation.

Itoo, Z. & Reshi, Z. 2013. The Multifunctional Role of Ectomycorrhizal Associations in Forest Ecosystem Processes. *Bot. Rev.,* 79(3)**,** 371-400.

Jenkins, M. & Schaap, B. 2018. Untapped Potential: Forest Ecosystem Services for Achieving Sdg 15. background Study Prepared for the Thirteenth Session of the United Nations Forum on Forests.

Jesus, E., Da C, Marsh, T., L, Tiedje, J., M & Moreira, F., M, De S 2009. Changes in Land Use Alter the Structure of Bacterial Communities in Western Amazon Soils. *The ISME Journal,* 3(9)**,** 1004.

Johnson, D., Leake, J. R. & Read, D. J. 2001. Novel in- Growth Core System Enables Functional Studies of Grassland Mycorrhizal Mycelial Networks. *New Phytologist,* 152(3)**,** 555-562.

Johnson, D., Leake, J. R., Ostle, N., Ineson, P. & Read, D. J. 2002. In Situ 13 Co 2 Pulse-Labelling of Upland Grassland Demonstrates a Rapid Pathway of Carbon Flux from Arbuscular Mycorrhizal Mycelia to the Soil. *New Phytologist,* 153(2)**,** 327-334.

Karlowsky, S., Augusti, A., Ingrisch, J., Akanda, M. K. U., Bahn, M. & Gleixner, G. 2018. Drought-Induced Accumulation of Root Exudates Supports Post-Drought Recovery of Microbes in Mountain Grassland. *Frontiers in Plant Science,* 9**,** 1593.

Keenan, R. J., Reams, G. A., Achard, F., De Freitas, J. V., Grainger, A. & Lindquist, E. 2015. Dynamics of Global Forest Area: Results from the Fao Global Forest Resources Assessment 2015. *Forest Ecology and Management,* 352(C)**,** 9-20.

Kerfahi, D., Tripathi, B. M., Lee, J., Edwards, D. P. & Adams, J. M. 2014. The Impact of Selective-Logging and Forest Clearance for Oil Palm on Fungal Communities in Borneo. *PLoS ONE,* 9(11).

Kjøller, R. 2006. Disproportionate Abundance between Ectomycorrhizal Root Tips and Their Associated Mycelia. *FEMS Microbiology Ecology,* 58(2)**,** 214-224.

Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K. & Schloss, P. D. 2013. Development of a Dual-Index Sequencing Strategy and Curation Pipeline for Analyzing Amplicon Sequence Data on the Miseq Illumina Sequencing Platform. *Applied and environmental microbiology,* 79(17)**,** 5112.

Kumagai, T. O. & Porporato, A. 2012. Drought-Induced Mortality of a Bornean Tropical Rain Forest Amplified by Climate Change. *Journal of Geophysical Research: Biogeosciences,* 117(G2).

Kuypers, M. M. M., Marchant, H. K. & Kartal, B. 2018. The Microbial Nitrogen-Cycling Network. *Nature Reviews Microbiology,* 16(5)**,** 263-276.

Kyaschenko, J., Clemmensen, K. E., Karltun, E. & Lindahl, B. D. 2017. Below-Ground Organic Matter Accumulation Along a Boreal Forest Fertility Gradient Relates to Guild Interaction within Fungal Communities. *Ecology Letters,* 20(12)**,** 1546-1555.

Lambers, H., Raven, J. A., Shaver, G. R. & Smith, S. E. 2008. Plant Nutrient-Acquisition Strategies Change with Soil Age. *Trends in Ecology & Evolution,* 23(2)**,** 95-103.

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J. & Veneklaas, E. J. 2006. Root Structure and Functioning for Efficient Acquisition of Phosphorus: Matching Morphological and Physiological Traits. *Annals of Botany,* 98(4)**,** 693-713.

Lambin, E. F., Geist, H. J. & Lepers, E. 2003. Dynamics of Land-Use and Land-Cover Change in Tropical Regions. *Annu. Rev. Environ. Resour.,* 28(1)**,** 205-241.

Landeweert, R., Hoffland, E., Finlay, R. D., Kuyper, T. W. & Van Breemen, N. 2001. Linking Plants to Rocks: Ectomycorrhizal Fungi Mobilize Nutrients from Minerals. *Trends in ecology & evolution,* 16(5)**,** 248.

Landon, J. R. 1984. Booker Tropical Soil Manual : A Handbook for Soil Survey and Agricultural Land Evaluation in the Tropics and Subtropics, London: Booker Agriculture International.

Langley, J. A., Chapman, S. K. & Hungate, B. A. 2006. Ectomycorrhizal Colonization Slows Root Decomposition: The Post- Mortem Fungal Legacy. *Ecology Letters,* 9(8)**,** 955-959.

Lauber, C. L., Hamady, M., Knight, R. & Fierer, N. 2009. Pyrosequencing-Based Assessment of Soil pH as a Predictor of Soil Bacterial Community Structure at the Continental Scale. *Applied and Environmental Microbiology,* 75(15)**,** 5111.

Lauber, C. L., Strickland, M. S., Bradford, M. A. & Fierer, N. 2008. The Influence of Soil Properties on the Structure of Bacterial and Fungal Communities across Land-Use Types. *Soil Biology and Biochemistry,* 40(9)**,** 2407-2415.

Laurance, W. F. 1999. Reflections on the Tropical Deforestation Crisis. *Biological Conservation,* 91(2-3)**,** 109-117.

Laurance, W. F. 2007a. Forest Destruction in Tropical Asia. *Current Science,* 93(11)**,** 1544-1550.

Laurance, W. F. 2007b. Have We Overstated the Tropical Biodiversity Crisis? *Trends in Ecology & Evolution,* 22(2)**,** 65-70.

Laurance, W. F., Sayer, J. & Cassman, K. G. 2014. Agricultural Expansion and Its Impacts on Tropical Nature. *Trends in ecology & evolution,* 29(2)**,** 107.

Leake, J., Johnson, D., Donnelly, D., Muckle, G., Boddy, L. & Read, D. 2004. Networks of Power and Influence: The Role of Mycorrhizal Mycelium in Controlling Plant Communities and Agroecosystem Functioning. *Canadian Journal of Botany,* 82(8)**,** 1016-1045.

Lechevalier, H. & Lechevalier, M. P. 1988. Chemotaxonomic Use of Lipids - an Overview. *In:* RATLEDGE, C. & WILKINSON, S. G. (eds.) *Microbial Lipids.* London: Academic Press.

Lee-Cruz, L., Edwards, D. P., Tripathi, B. M. & Adams, J. M. 2013. Impact of Logging and Forest Conversion to Oil Palm Plantations on Soil Bacterial Communities in Borneo. *Applied and environmental microbiology,* 79(23)**,** 7290.

Legendre, P. & Borcard, D. 2018. Box–Cox-Chord Transformations for Community Composition Data Prior to Beta Diversity Analysis. *Ecography,* 41(11)**,** 1820-1824.

Lekberg, Y., Vasar, M., Bullington, L. S., Sepp, S. K., Antunes, P. M., Bunn, R., Larkin, Beau g. & Öpik, M. 2018. More Bang for the Buck? Can Arbuscular Mycorrhizal Fungal Communities Be Characterized Adequately Alongside Other Fungi Using General Fungal Primers? *New Phytologist,* 220(4)**,** 971-976.

Lennon, J. T., Muscarella, M. E., Placella, S. A. & Lehmkuhl, B. K. 2018. How, When, and Where Relic Dna Affects Microbial Diversity. *mBio,* 9(3)**,** e00637-18.

Lenth, R. S., Henrik, Love, J., Buerkner, P. & Herve, M. 2019. Estimated Marginal Means, Aka Least-Squares Means [Online]. Available: https://cran.r-project.org/package=emmeans [Accessed 28th September 2020].

Li, D., Li, X., Su, Y., Li, X., Yin, H., Li, X., Guo, M. & He, Y. 2019. Forest Gaps Influence Fungal Community Assembly in a Weeping Cypress Forest. *Applied Microbiology and Biotechnology,* 103(7)**,** 3215-3224.

Liang, C., Amelung, W., Lehmann, J. & Kästner, M. 2019. Quantitative Assessment of Microbial Necromass Contribution to Soil Organic Matter. *Global Change Biology,* 25(11)**,** 3578-3590.

Lin, N., Bartsch, N., Heinrichs, S. & Vor, T. 2015. Long-Term Effects of Canopy Opening and Liming on Leaf Litter Production, and on Leaf Litter and Fine-Root Decomposition in a European Beech (Fagus Sylvatica L.) Forest. *Forest Ecology and Management,* 338**,** 183-190.

Lindahl, B. D. & Tunlid, A. 2015. Ectomycorrhizal Fungi – Potential Organic Matter Decomposers, yet Not Saprotrophs.

Lindahl, B. D., Ihrmark, K., Boberg, J., Trumbore, S. E., Högberg, P., Stenlid, J. & Finlay, R. D. 2007. Spatial Separation of Litter Decomposition and Mycorrhizal Nitrogen Uptake in a Boreal Forest. *New Phytologist,* 173(3)**,** 611-620.

Liu, X., Burslem, D. F. R. P., Taylor, J. D., Taylor, A. F. S., Khoo, E., Majalap-Lee, N., Helgason, T. & Johnson, D. 2018. Partitioning of Soil Phosphorus among Arbuscular and Ectomycorrhizal Trees in Tropical and Subtropical Forests. *Ecology Letters,* 21(5)**,** 713-723.

Lu, S., Katahata, S., Naramoto, M., Mizunaga, H. & Wang, Q. 2014. Controlling Factors of Temporal Variation of Soil Respiration in a Natural Beech Forest as Revealed by Natural Incubation Experiments. *Ecol Res,* 29(5)**,** 789-799.

Luizão, F. J., Proctor, J., Thompson, J., Luizão, R. C. C., Marrs, R. H., Scott, D. A. & Viana, V. 1998. Rain Forest on Maracá Island, Roraima, Brazil: Soil and Litter Process Response to Artificial Gaps. *Forest Ecology and Management,* 102(2)**,** 291-303.

Luke, S. 2017. Evaluating Significance in Linear Mixed-Effects Models in R. *Behavior Research Methods,* 49(4)**,** 1494-1502.

Majdi, H., Truus, L., Johansson, U., Nylund, J.-E. & Wallander, H. 2008. Effects of Slash Retention and Wood Ash Addition on Fine Root Biomass and Production and Fungal Mycelium in a Norway Spruce Stand in Sw Sweden. *Forest Ecology and Management,* 255(7)**,** 2109-2117.

Malhi, Y. & Phillips, O. L. 2004. Tropical Forests and Global Atmospheric Change: A Synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 359(1443)**,** 549-555.

Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C. I., Fiore, A. D., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Montoya, L. M. M., Monteagudo, A., Neill, D. A., Vargas, P. N., Patiño, S., Pitman, N. C. A., Quesada, C. A., Salomão, R., Silva, J. N. M., Lezama, A. T., Martínez, R. V., Terborgh, J., Vinceti, B. & Lloyd, J. 2004. The above- Ground Coarse Wood Productivity of 104 Neotropical Forest Plots. *Global Change Biology,* 10(5)**,** 563-591.

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., Aguila-Pasquel, J., Aragão, L. E. O. C., Araujo-Murakami, A., Brando, P., Costa, A. C. L., Silva-Espejo, J. E., Farfán Amézquita, F., Galbraith, D. R., Quesada, C. A., Rocha, W., Salinas-Revilla, N., Silvério, D., Meir, P. & Phillips, O. L. 2015. The Linkages between Photosynthesis, Productivity, Growth and Biomass in Lowland Amazonian Forests. *Global Change Biology,* 21(6)**,** 2283-2295.

Malik, A. A., Puissant, J., Buckeridge, K. M., Goodall, T., Jehmlich, N., Chowdhury, S., Gweon, H. S., Peyton, J. M., Mason, K. E., Van Agtmaal, M., Blaud, A., Clark, I. M., Whitaker, J., Pywell, R. F., Ostle, N., Gleixner, G. & Griffiths, R. I. 2018. Land Use Driven Change in Soil pH Affects Microbial Carbon Cycling Processes. *Nature Communications,* 9(1)**,** 3591.

Malmer, A. & Grip, H. 1990. Soil Disturbance and Loss of Infiltrability Caused by Mechanized and Manual Extraction of Tropical Rainforest in Sabah, Malaysia. *Forest Ecology and Management,* 38(1)**,** 1-12.

Manzoni, S., Schimel, J. P. & Porporato, A. 2012. Responses of Soil Microbial Communities to Water Stress: Results from a Meta-Analysis. Ecology, 93(4), 930-938.

Marsh, C. W. & Greer, A. G. 1992. Forest Land-Use in Sabah, Malaysia: An Introduction to Danum Valley. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 335(1275)**,** 331-339.

Marshall, V. G. 2000. Impacts of Forest Harvesting on Biological Processes in Northern Forest Soils. *Forest Ecology and Management,* 133(1)**,** 43-60.

Marthews, T, Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Ruiz Jaén, M., Girardin, C., Butt, N, Cain, R. & Networks, A. C. F. T. R. A. G. 2014. Measuring Tropical Forest Carbon Allocation and Cycling: A Rainfor-Gem Field Manual for Intensive Census Plots. Version 3.0. Manual. Global Ecosystems Monitoring Network [Online]. http:gem.tropicalforests.ox.ac.uk [Accessed 28th September 2020].

Marthews, T. R., Burslem, D. F. R. P., Paton, S. R., Yangüez, F. & Mullins, C. E. 2008. Soil Drying in a Tropical Forest: Three Distinct Environments Controlled by Gap Size. *Ecological Modelling,* 216(3)**,** 369-384.

Martinez Arbizu, P. 2019. Pairwiseadonis: Pairwise Multilevel Comparison Using Adonis. R Package Version 0.3 [Online]. Available: https://github.com/pmartinezarbizu/pairwiseadonis [Accessed 28th September 2020].

Martiny, J. B. H., Bohannan, B. J. M., Brown, J. H., Colwell, R. K., Fuhrman, J. A., Green, J. L., Horner-Devine, M. C., Kane, M., Krumins, J. A., Kuske, C. R., Morin, P. J., Naeem, S., Ovreås, L., Reysenbach, A.-L., Smith, V. H. & Staley, J. T. 2006. Microbial Biogeography: Putting Microorganisms on the Map. *Nature reviews. Microbiology,* 4(2)**,** 102.

Matricardi, E. A. T., Skole, D. L., Pedlowski, M. A. & Chomentowski, W. 2013. Assessment of Forest Disturbances by Selective Logging and Forest Fires in the Brazilian Amazon Using Landsat Data. *International Journal of Remote Sensing,* 34(4)**,** 1057-1086.

Maxwell Stevens, B., Propster, J., Wilson, G. W. T., Abraham, A., Ridenour, C., Doughty, C. & Collins Johnson, N. 2018. Mycorrhizal Symbioses Influence the Trophic Structure of the Serengeti. *Journal of Ecology,* 106(2)**,** 536-546.

Mcguire, K., D'angelo, H., Brearley, F., Gedallovich, S., Babar, N., Yang, N., Gillikin, C., Gradoville, R., Bateman, C., Turner, B., Mansor, P., Leff, J. & Fierer, N. 2015. Responses of Soil Fungi to Logging and Oil Palm Agriculture in Southeast Asian Tropical Forests. *Microbial Ecology,* 69(4)**,** 733-747.

Mcguire, K., Henkel, T., Granzow De La Cerda, I., Villa, G., Edmund, F. & Andrew, C. 2008. Dual Mycorrhizal Colonization of Forest-Dominating Tropical Trees and the Mycorrhizal Status of Non-Dominant Tree and Liana Species. *Mycorrhiza,* 18(4)**,** 217-222.

Mcmurdie, P. J. & Holmes, S. 2013. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS ONE,* 8(4)**,** e61217.

Meir, P., Wood, T. E., Galbraith, D. R., Brando, P. M., Da Costa, A. C. L., Rowland, L. & Ferreira, L. V. 2015. Threshold Responses to Soil Moisture Deficit by Trees and Soil in Tropical Rain Forests: Insights from Field Experiments. Bioscience, 65(9), 882-892.

Meisner, A., Jacquiod, S., Snoek, B. L., Ten Hooven, F. C. & van der Putten, W. H. 2018. Drought Legacy Effects on the Composition of Soil Fungal and Prokaryote Communities. *Frontiers in Microbiology,* 9**,** 294.

Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M. & Tabarelli, M. 2013. On the Hope for Biodiversity-Friendly Tropical Landscapes. *Trends in Ecology & Evolution,* 28(8)**,** 462-468.

Melvin, K. K. K., Japar, S. B., Osumanu, H. A., Nik, M. A. M., Roland, K. J. H. & Silvester, J. 2011. Comparison of Carbon and Selected Macronutrients in Forest-Floor Litter of Rehabilitated and Secondary Forests. *American Journal of Applied Sciences,* 8(10)**,** 967.

Mendes, L. W., De Lima Brossi, M. J., Kuramae, E. E. & Tsai, S. M. 2015a. Land-Use System Shapes Soil Bacterial Communities in Southeastern Amazon Region. Applied soil ecology : a section of Agriculture, ecosystems & environment, 95, 151-160.

Mendes, L. W., Tsai, S. M., Navarrete, A. A., De Hollander, M., Van Veen, J. A. & Kuramae, E. E. 2015b. Soil-Borne Microbiome: Linking Diversity to Function. Microb Ecol, 70(1), 255-265.

Miller, W. P. & Miller, D. M. 1987. A Micro-Pipette Method for Soil Mechanical Analysis. *Communications in Soil Science and Plant Analysis,* 18(1)**,** 1-15.

Mohanty, R. B. & Panda, T. 2011. Soil Respiration and Microbial Population in a Tropical Deciduous Forest Soil of Orissa, India. Flora. Morphologie, Geobotanik, Oekophysiologie, 206(12), 1040-1044.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J. L. 2008. A General Framework for the Distance–Decay of Similarity in Ecological Communities. *Ecology Letters,* 11(9)**,** 904-917.

Moyano, F. E., Manzoni, S. & Chenu, C. 2013. Responses of Soil Heterotrophic Respiration to Moisture Availability: An Exploration of Processes and Models. Soil biology & biochemistry, 59, 72-85.

Mueller, R. C., Rodrigues, J. L. M., Nüsslein, K. & Bohannan, B. J. M. 2016. Land Use Change in the Amazon Rain Forest Favours Generalist Fungi. *Functional Ecology,* 30(11)**,** 1845-1853.

Muscolo, A., Bagnato, S., Sidari, M. & Mercurio, R. 2014. A Review of the Roles of Forest Canopy Gaps. *Journal of Forestry Research,* 25(4)**,** 725-736.

Muscolo, A., Settineri, G., Bagnato, S., Mercurio, R. & Sidari, M. 2017. Use of Canopy Gap Openings to Restore Coniferous Stands in Mediterranean Environment. *iForest - Biogeosciences and Forestry,* 10(1)**,** 322-327.

Muscolo, A., Sidari, M. & Mercurio, R. 2007a. Influence of Gap Size on Organic Matter Decomposition, Microbial Biomass and Nutrient Cycle in Calabrian Pine (Pinus Laricio, Poiret) Stands. *Forest Ecology and Management,* 242(2)**,** 412-418.

Muscolo, A., Sidari, M. & Mercurio, R. 2007b. Variations in Soil Chemical Properties and Microbial Biomass in Artificial Gaps in Silver Fir Stands. *European Journal of Forest Research,* 126(1)**,** 59-65.

Muscolo, A., Sidari, M., Bagnato, S., Mallamaci, C. & Mercurio, R. 2010. Gap Size Effects on above- and Below-Ground Processes in a Silver Fir Stand. *European Journal of Forest Research,* 129(3)**,** 355-365.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. 2000. Biodiversity Hotspots for Conservation Priorities. *Nature,* 403(6772)**,** 853.

Nannipieri, P., Ascher, J., Ceccherini, M. T., Landi, L., Pietramellara, G. & Renella, G. 2017. Microbial Diversity and Soil Functions. *European Journal of Soil Science,* 68(1)**,** 12-26.

Nara, K. 2006. Ectomycorrhizal Networks and Seedling Establishment During Early Primary Succession. *New Phytologist,* 169(1)**,** 169-178.

Nasto, M. K., Alvarez-Clare, S., Lekberg, Y., Sullivan, B. W., Townsend, A. R. & Cleveland, C. C. 2014. Interactions among Nitrogen Fixation and Soil Phosphorus Acquisition Strategies in Lowland Tropical Rain Forests. *Ecology letters,* 17(10)**,** 1282.

Navarrete, A. A., Tsai, S. M., Mendes, L. W., Faust, K., De Hollander, M., Cassman, N. A., Raes, J., Van Veen, J. A. & Kuramae, E. E. 2015. Soil Microbiome Responses to the Short-Term Effects of Amazonian Deforestation. Mol Ecol, 24(10), 2433-2448.

Nazaries, L., Tottey, W., Robinson, L., Khachane, A., Al-Soud, W. A., Sørensen, S. & Singh, B. K. 2015. Shifts in the Microbial Community Structure Explain the Response of Soil Respiration to Land-Use Change but Not to Climate Warming. *Soil Biology and Biochemistry,* 89**,** 123-134.

Nekola, J. C. & White, P. S. 1999. The Distance Decay of Similarity in Biogeography and Ecology. *Journal of Biogeography,* 26(4)**,** 867-878.

Nema, V. 2019. Chapter 34 - the Role and Future Possibilities of Next-Generation Sequencing in Studying Microbial Diversity. *In:* DAS, S. & DASH, H. R. (eds.) *Microbial Diversity in the Genomic Era.* Academic Press.

Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S. & Kennedy, P. G. 2016. Funguild: An Open Annotation Tool for Parsing Fungal Community Datasets by Ecological Guild. *Fungal Ecology,* 20**,** 241-248.

Nilsson, L. O. & Wallander, H. 2003. Production of External Mycelium by Ectomycorrhizal Fungi in a Norway Spruce Forest Was Reduced in Response to Nitrogen Fertilization. *New Phytologist,* 158(2)**,** 409-416.

Nottingham, A. T., Turner, B. L., Winter, K., Chamberlain, P. M., Stott, A. & Tanner, E. V. J. 2013. Root and Arbuscular Mycorrhizal Mycelial Interactions with Soil Microorganisms in Lowland Tropical Forest. *FEMS Microbiology Ecology,* 85(1)**,** 37-50.

Nurulita, Y., Adetutu, E. M., Gunawan, H., Zul, D. & Ball, A. S. 2016. Restoration of Tropical Peat Soils: The Application of Soil Microbiology for Monitoring the Success of the Restoration Process. *Agriculture, Ecosystems and Environment,* 216**,** 293-303.

O' Brien, S. L., Gibbons, S. M., Owens, S. M., Hampton-Marcell, J., Johnston, E. R., Jastrow, J. D., Gilbert, J. A., Meyer, F. & Antonopoulos, D. A. 2016. Spatial Scale Drives Patterns in Soil Bacterial Diversity. *Environmental Microbiology,* 18(6)**,** 2039-2051.

O'Connell, C. S., Ruan, L. & Silver, W. L. 2018. Drought Drives Rapid Shifts in Tropical Rainforest Soil Biogeochemistry and Greenhouse Gas Emissions. Nat Commun, 9(1), 1348-9.

Öhlinger, R. 1995. Methods in Soil Physics: Maximum Water Holding Capacity. *In:* SCHINNER, F., ÖHLINGER, R., KANDELER, E. & MARGESIN, R. (eds.) *Methods in Soil Biology.* Berlin ; London: Springer.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. 2019. Vegan: Community Ecology Package [Online]. Available: https://cran.r-project.org/package=vegan [Accessed 28th September 2020].

O'leary, W. M. & Wilkinson, S. G. 1988. Gram-Positive Bacteria. *In:* RATLEDGE, C. & WILKINSON, S. G. (eds.) *Microbial Lipids.* London: Academic Press.

Orwin, K. H., Kirschbaum, M. U. F., St John, M. G. & Dickie, I. A. 2011. Organic Nutrient Uptake by Mycorrhizal Fungi Enhances Ecosystem Carbon Storage: A Model-Based Assessment. *Ecology Letters,* 14(5)**,** 493-502.

Orwin, K. H., Kirschbaum, M. U. F., St John, M. G. & Dickie, I. A. 2011. Organic Nutrient Uptake by Mycorrhizal Fungi Enhances Ecosystem Carbon Storage: A Model-Based Assessment. *Ecology Letters,* 14(5)**,** 493-502.

Ostertag, R. 1998. Belowground Effects of Canopy Gaps in a Tropical Wet Forest. *Ecology,* 79(4)**,** 1294-130.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., Mcguire, A. D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science,* 333(6045)**,** 988-993.

Paul, M., Catterall, C. P., Pollard, P. C. & Kanowski, J. 2010. Recovery of Soil Properties and Functions in Different Rainforest Restoration Pathways. *Forest Ecology and Management,* 259(10)**,** 2083-2092.

Paz, C. P., Goosem, M., Bird, M., Preece, N., Goosem, S., Fensham, R. & Laurance, S. 2016. Soil Types Influence Predictions of Soil Carbon Stock Recovery in Tropical Secondary Forests. *Forest Ecology and Management,* 376**,** 74-83.

Perumal, M., Wasli, M. E. & Lat, J. 2016. Effects of Enrichment Planting on the Soil Physicochemical Properties at Reforestation Sites Planted with *Shorea Macrophylla De Vriese* in Sampadi Forest Reserve, Sarawak, Malaysia. *Proceedings of the Symposium "Frontier in Tropical Forest Research: Progress in Joint Projects between the Forest Department Sarawak and the Japan Research Consortium for Tropical Forests in Sarawak".* Kyoto.

Petersen, I. A. B., Meyer, K. M. & Bohannan, B. J. M. 2019. Meta-Analysis Reveals Consistent Bacterial Responses to Land Use Change across the Tropics. Frontiers in ecology and evolution, 7.

Phosri, C., Rodriguez, A., Sanders, I. R. & Jeffries, P. 2010. The Role of Mycorrhizas in More Sustainable Oil Palm Cultivation. *Agriculture, Ecosystems and Environment,* 135(3)**,** 187-193.

Potila, H., Wallander, H. & Sarjala, T. 2009. Growth of Ectomycorrhizal Fungi in Drained Peatland Forests with Variable P and K Availability. *An International Journal on Plant-Soil Relationships,* 316(1)**,** 139-150.

Powers, R. P. & Jetz, W. 2019. Global Habitat Loss and Extinction Risk of Terrestrial Vertebrates under Future Land-Use-Change Scenarios. *Nature Climate Change,* 9(4)**,** 323-329.

Qian, P. & Schoenau, J. J. 2002. Practical Applications of Ion Exchange Resins in Agricultural and Environmental Soil Research. *Canadian Journal of Soil Science.*

Qie, L., Lewis, S., Sullivan, M., Lopez-Gonzalez, G., Pickavance, G., Sunderland, T., Ashton, P., Hubau, W., Abu Salim, K., Aiba, S.-I., Banin, L., Berry, N., Brearley, F., Burslem, D., Dančák, M., Davies, S., Fredriksson, G., Hamer, K., Hédl, R., Kho, L., Kitayama, K., Krisnawati, H., Lhota, S., Malhi, Y., Maycock, C., Metali, F., Mirmanto, E., Nagy, L., Nilus, R., Ong, R., Pendry, C., Poulsen, A., Primack, R., Rutishauser, E., Samsoedin, I., Saragih, B., Sist, P., Slik, J., Sukri, R., Svátek, M., Tan, S., Tjoa, A., Van Nieuwstadt, M., Vernimmen, R., Yassir, I., Kidd, P., Fitriadi, M., Ideris, N. K., Serudin, R., Abdullah Lim, L., Saparudin, M. & Phillips, O. 2017. Long-Term Carbon Sink in Borneo's Forests Halted by Drought and Vulnerable to Edge Effects. *Nat Commun,* 8(1)**,** 1966-1966.

R Core Team 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria [Online]. Available: http://www.r-project.org/ [Accessed 9th July 2019].

R Core Team 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria [Online]. Available: http://www.r-project.org/ [Accessed 24th January 2020].

Raes, N., Roos, M. C., Slik, J. W. F., Van Loon, E. E. & Steege, H. T. 2009. Botanical Richness and Endemicity Patterns of Borneo Derived from Species Distribution Models. *Ecography,* 32(1)**,** 180-192.

Raynaud, X. & Nunan, N. 2014. Spatial Ecology of Bacteria at the Microscale in Soil.(Research Article). *PLoS ONE,* 9(1)**,** e87217.

Redecker, D., Kodner, R. & Graham, L. E. 2000. Glomalean Fungi from the Ordovician. *Science,* 289(5486)**,** 1920-1921.

Reynolds, G., Payne, J., Sinun, W., Mosigil, G. & Walsh, R. P. D. 2011. Changes in Forest Land Use and Management in Sabah, Malaysian Borneo, 1990–2010, with a Focus on the Danum Valley Region. *Philosophical Transactions of the Royal Society B,* 366(1582)**,** 3168-3176.

Rifai, S. W., Li, S. & Malhi, Y. 2019. Coupling of El Niño Events and Long-Term Warming Leads to Pervasive Climate Extremes in the Terrestrial Tropics. *Environmental Research Letters,* 14(10)**,** 105002.

Rillig, M. C. & Mummey, D. L. 2006. Mycorrhizas and Soil Structure.

Rillig, M. C., Aguilar-Trigueros, C. A., Bergmann, J., Verbruggen, E., Veresoglou, S. D. & Lehmann, A. 2015. Plant Root and Mycorrhizal Fungal Traits for Understanding Soil Aggregation. *New Phytologist,* 174(1)**,** 1385-1388.

Rinnan, R. & Bååth, E. 2009. Differential Utilization of Carbon Substrates by Bacteria and Fungi in Tundra Soil. *Applied and Environmental Microbiology,* 75(11)**,** 3611-3620.

Ritter, E. 2005. Litter Decomposition and Nitrogen Mineralization in Newly Formed Gaps in a Danish Beech (Fagus Sylvatica) Forest. *Soil Biology and Biochemistry,* 37(7)**,** 1237-1247.

Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M., Tan, S., Turner, E., Reynolds, G., Both, S., Burslem, D. F. R. P., Teh, Y. A., Vairappan, C. S., Majalap, N. & Ewers, R. M. 2018. Logging Disturbance Shifts Net Primary Productivity and Its Allocation in Bornean Tropical Forests. *Global Change Biology,* 24(7)**,** 2913-2928.

Roberts, D. W. 2016. Ordination and Multivariate Analysis for Ecology [Online]. Available: http://ecology.msu.montana.edu/labdsv/r [Accessed 23rd July 2019].

Robinson, S., Berg, E., Meirelles, G. & Ostle, N. 2015. Factors Influencing Early Secondary Succession and Ecosystem Carbon Stocks in Brazilian Atlantic Forest. *Biodiversity and Conservation,* 24(9)**,** 2273-2291.

Rodrigues, J. L. M., Pellizari, V. H., Mueller, R., Baek, K., Jesus, E. D. C., Paula, F. S., Mirza, B., Hamaoui, G. S., Jr., Tsai, S. M., Feigl, B., Tiedje, J. M., Bohannan, B. J. M. & Nusslein, K. 2013. Conversion of the Amazon Rainforest to Agriculture Results in Biotic Homogenization of Soil Bacterial Communities. *Proceedings of the National Academy of Sciences of the United States,* 110(3)**,** 988.

Rodrigues, R., Lima, R., Gandolfi, S. & Nave, A. 2009. On the Restoration of High Diversity Forests: 30 Years of Experience in the Brazilian Atlantic Forest. *Biological Conservation,* 142(6)**,** 1242-1251.

Roesch, L. F. W., Fulthorpe, R. R., Riva, A., Casella, G., Hadwin, A. K. M., Kent, A. D., Daroub, S. H., Camargo, F. A. O., Farmerie, W. G. & Triplett, E. W. 2007. Pyrosequencing Enumerates and Contrasts Soil Microbial Diversity. *The ISME Journal,* 1(4)**,** 283.

Roos, M. C., Keßler, P. J. A., Robbert Gradstein, S. & Baas, P. 2004. Species Diversity and Endemism of Five Major Malesian Islands: Diversity–Area Relationships. *Journal of Biogeography,* 31(12)**,** 1893-1908.

Rousk, J., Bååth, E., Brookes, P., C, Lauber, C., L, Lozupone, C., Caporaso, J. G., Knight, R. & Fierer, N. 2010. Soil Bacterial and Fungal Communities across a Ph Gradient in an Arable Soil. *The ISME Journal,* 4(10)**,** 1340.

Runting, R. K., Meijaard, E., Abram, N. K., Wells, J. A., Gaveau, D. L. A., Ancrenaz, M., Possingham, H. P., Wich, S. A., Ardiansyah, F., Gumal, M. T., Ambu, L. N. & Wilson, K. A. 2015. Alternative Futures for Borneo Show the Value of Integrating Economic and Conservation Targets across Borders. *Nature communications,* 6(1)**,** 6819.

Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. 2011. Benchmark Map of Forest Carbon Stocks in Tropical Regions across Three Continents. *Proceedings of the National Academy of Sciences of the United States of America,* 108(24)**,** 9899.

Sahani, U. & Behera, N. 2001. Impact of Deforestation on Soil Physicochemical Characteristics, Microbial Biomass and Microbial Activity of Tropical Soil. Land degradation & development, 12(2), 93-105.

Sanderman, J., Hengl, T. & Fiske, G. J. 2017. Soil Carbon Debt of 12,000 Years of Human Land Use. *Proceedings of the National Academy of Sciences,* 114(36)**,** 9575.

Saner, P., Lim, R., Burla, B., Ong, R. C., Scherer-Lorenzen, M. & Hector, A. 2009. Reduced Soil Respiration in Gaps in Logged Lowland Dipterocarp Forests. *Forest Ecology and Management,* 258(9)**,** 2007-2012.

Saner, P., Loh, Y. Y., Ong, R. C. & Hector, A. 2012. Carbon Stocks and Fluxes in Tropical Lowland Dipterocarp Rainforests in Sabah, Malaysian Borneo (Carbon Stocks and Fluxes in Tropical Logged Forest). *PLoS ONE,* 7(1)**,** e29642.

Scharenbroch, B. & Bockheim, J. 2007. Impacts of Forest Gaps on Soil Properties and Processes in Old Growth Northern Hardwood- Hemlock Forests. *An International Journal on Plant-Soil Relationships,* 294(1)**,** 219-233.

Scharenbroch, B. & Bockheim, J. 2008a. Gaps and Soil C Dynamics in Old Growth Northern Hardwood–Hemlock Forests. *Ecosystems,* 11(3)**,** 426-441.

Scharenbroch, B. & Bockheim, J. 2008b. The Effects of Gap Disturbance on Nitrogen Cycling and Retention in Late- Successional Northern Hardwood– Hemlock Forests. *An International Journal,* 87(3)**,** 231-245.

Schimel, J. P. & Bennett, J. 2004. Nitrogen Mineralization: Challenges of a Changing Paradigm. *Ecology,* 85(3)**,** 591-602.

Schimel, J. P. & Schaeffer, S. M. 2012. Microbial Control over Carbon Cycling in Soil. *Front. Microbiol.*

Schjønning, P., Thomsen, I. K., Moldrup, P. & Christensen, B. T. 2003. Linking Soil Microbial Activity to Water- and Air-Phase Contents and Diffusivities. Soil Science Society of America journal, 67(1), 156-165.

Schliemann, S. A. & Bockheim, J. G. 2011. Methods for Studying Treefall Gaps: A Review. *Forest Ecology and Management,* 261(7)**,** 1143-1151.

Schliemann, S. A. & Bockheim, J. G. 2014. Influence of Gap Size on Carbon and Nitrogen Biogeochemical Cycling in Northern Hardwood Forests of the Upper Peninsula, Michigan. *Plant and Soil,* 377(1-2)**,** 323-335.

Schloss, P. D. & Handelsman, J. 2006. Toward a Census of Bacteria in Soil (Bacterial Census in Soil). *PLoS Computational Biology,* 2(7)**,** e92.

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. 2012. Nih Image to Imagej: 25 Years of Image Analysis. *Nature Methods,* 9(7)**,** 671.

Schnitzer, S. A., Kuzee, M. E. & Bongers, F. 2005. Disentangling above- and Below-Ground Competition between Lianas and Trees in a Tropical Forest. *Journal of Ecology,* 93(6)**,** 1115-1125.

Setälä, H., Kulmala, P., Mikola, J. & Markkola, A. M. 1999. Influence of Ectomycorrhiza on the Structure of Detrital Food Webs in Pine Rhizosphere. *Oikos,* 87(1)**,** 113-122.

Shade, A., Peter, H., Allison, S. D., Baho, D. L., Berga, M., Bürgmann, H., Huber, D. H., Langenheder, S., Lennon, J. T., Martiny, J. B. H., Matulich, K. L., Schmidt, T. M. & Handelsman, J. 2012. Fundamentals of Microbial Community Resistance and Resilience.

Sheldon, F. H., Lim, H. C. & Moyle, R. G. 2015. Return to the Malay Archipelago: The Biogeography of Sundaic Rainforest Birds. *Journal of Ornithology,* 156(1)**,** 91-113.

Shen, Q., Kirschbaum, M. U. F., Hedley, M. J. & Camps Arbestain, M. 2016. Testing an Alternative Method for Estimating the Length of Fungal Hyphae Using Photomicrography and Image Processing.(Report). 11(6).

Shi, L., Dossa, G. G. O., Paudel, E., Zang, H., Xu, J. & Harrison, R. D. 2019. Changes in Fungal Communities across a Forest Disturbance Gradient. *Applied and environmental microbiology,* 85(12).

Shi, L., Dossa, G. G. O., Paudel, E., Zang, H., Xu, J. & Harrison, R. D. 2019. Changes in Fungal Communities across a Forest Disturbance Gradient. Applied and environmental microbiology, 85(12).

Shoo, L. P., Freebody, K., Kanowski, J. & Catterall, C. P. 2016. Slow Recovery of Tropical Old-Field Rainforest Regrowth and the Value and Limitations of Active Restoration. *Conservation Biology,* 30(1)**,** 121-132.

Simpson, G. L., R Core Team, Bates, D. M. & Oksanen, J. 2019. Functions for Generating Restricted Permutations of Data [Online]. Available: https://github.com/gavinsimpson/permute [Accessed 28th September 2020].

Singh, B. K., Bardgett, R. D., Smith, P. & Reay, D. S. 2010. Microorganisms and Climate Change: Terrestrial Feedbacks and Mitigation Options. *Nature Reviews Microbiology,* 8(11)**,** 779.

Singh, V., Tewari, A., Kushwaha, S. P. S. & Dadhwal, V. K. 2011. Formulating Allometric Equations for Estimating Biomass and Carbon Stock in Small Diameter Trees. *Forest Ecology and Management,* 261(11)**,** 1945-1949.

Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C. & Firbank, L. G. 2006. Biotic Homogenization and Changes in Species Diversity across Human-Modified Ecosystems. Proc Biol Sci, 273(1601), 2659-2665.

Smith, S. E. & Read, D. J. 2008. *Mycorrhizal Symbiosis,* Amsterdam ; London: Academic.

Sodhi, N. S., Lee, T. M., Koh, L. P. & Brook, B. W. 2009. A Meta-Analysis of the Impact of Anthropogenic Forest Disturbance on Southeast Asia's Biotas. Biotropica, 41(1), 103-109.

Soininen, J., Mcdonald, R. & Hillebrand, H. 2007. The Distance Decay of Similarity in Ecological Communities. *Ecography,* 30(1)**,** 3-12.

Soliman, T., Yang, S.-Y., Yamazaki, T., Jenke-Kodama, H. & Riesgo-Escovar, J. 2017. Profiling Soil Microbial Communities with Next-Generation Sequencing: The Influence of Dna Kit Selection and Technician Technical Expertise. *PeerJ,* 5(12).

Song, X., Zhu, J., He, N., Huang, J., Tian, J., Zhao, X., Liu, Y. & Wang, C. 2017. Asynchronous Pulse Responses of Soil Carbon and Nitrogen Mineralization to Rewetting Events at a Short-Term: Regulation by Microbes. *Scientific Reports,* 7(1)**,** 7492.

Stark, J. M. & Firestone, M. K. 1995. Mechanisms for Soil Moisture Effects on Activity of Nitrifying Bacteria. Appl Environ Microbiol, 61(1), 218-221.

Stockmann, U., Adams, M. A., Crawford, J. W., Field, D. J., Henakaarchchi, N., Jenkins, M., Minasny, B., Mcbratney, A. B., Courcelles, V. D. R. D., Singh, K., Wheeler, I., Abbott, L., Angers, D. A., Baldock, J., Bird, M., Brookes, P. C., Chenu, C., Jastrow, J. D., Lal, R., Lehmann, J., O'donnell, A. G., Parton, W. J., Whitehead, D. & Zimmermann, M. 2013. The Knowns, Known Unknowns and Unknowns of Sequestration of Soil Organic Carbon. *Agriculture, Ecosystems and Environment,* 164**,** 80-99.

Strickland, M. S., Callaham, M. A., Gardiner, E. S., Stanturf, J. A., Leff, J. W., Fierer, N. & Bradford, M. A. 2017. Response of Soil Microbial Community Composition and Function to a Bottomland Forest Restoration Intensity Gradient. *Applied Soil Ecology,* 119(C)**,** 317-326.

Taylor, A. F. S. & Alexander, I. 2005. The Ectomycorrhizal Symbiosis: Life in the Real World. *Mycologist,* 19(3)**,** 102-112.

Tecon, R. & Or, D. 2017. Biophysical Processes Supporting the Diversity of Microbial Life in Soil. FEMS Microbiol Rev, 41(5), 599-623.

Tennant, D. 1975. A Test of a Modified Line Intersect Method of Estimating Root Length. *Journal of Ecology,* 63(3)**,** 995-1001.

Tripathi, B. M., Edwards, D. P., Mendes, L. W., Kim, M., Dong, K., Kim, H. & Adams, J. M. 2016. The Impact of Tropical Forest Logging and Oil Palm Agriculture on the Soil Microbiome. *Molecular Ecology,* 25(10)**,** 2244-2257.

Tripathi, B., Kim, M., Singh, D., Lee-Cruz, L., Lai-Hoe, A., Ainuddin, A., Go, R., Rahim, R., Husni, M., Chun, J. & Adams, J. 2012. Tropical Soil Bacterial Communities in Malaysia:pH Dominates in the Equatorial Tropics Too. *Microb Ecol,* 64(2)**,** 474-484.

Trivedi, P., Delgado-Baquerizo, M., Trivedi, C., Hu, H., Anderson, I. C., Jeffries, T. C., Zhou, J. & Singh, B. K. 2016. Microbial Regulation of the Soil Carbon Cycle: Evidence from Gene–Enzyme Relationships. *The ISME Journal,* 10(11)**,** 2593-2604.

Unite Community 2017. Unite General Fasta Release. Version 01.12.2017 [Online]. Available: https://doi.org/10.15156/bio/587475 [Accessed 13th September 2019].

van der Heijden, M. G. A., Bardgett, R. D. & Van Straalen, N. M. 2008. The Unseen Majority: Soil Microbes as Drivers of Plant Diversity and Productivity in Terrestrial Ecosystems.

van der Putten, W., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B., Fukami, T., Kardol, P., Klironomos, J., Kulmatiski, A., Schweitzer, J., Suding, K., Van De Voorde, T. & Wardle, D. 2013. Plant-Soil Feedbacks: The Past, the Present and Future Challenges. *J. Ecol.,* 101(2)**,** 265-276.

van Meeteren, M. J. M., Tietema, A., Van Loon, E. E. & Verstraten, J. M. 2008. Microbial Dynamics and Litter Decomposition under a Changed Climate in a Dutch Heathland. Applied soil ecology : a section of Agriculture, ecosystems & environment, 38(2), 119-127.

van Straaten, O., Veldkamp, E. & Corre, M. D. 2011. Simulated Drought Reduces Soil Co2 Efflux and Production in a Tropical Forest in Sulawesi, Indonesia. Ecosphere (Washington, D.C), 2(10), 1-22.

Vance, E. D., Brookes, P. C. & Jenkinson, D. S. 1987. An Extraction Method for Measuring Soil Microbial Biomass C. *Soil Biology and Biochemistry,* 19(6)**,** 703-707.

Vet, R., Artz, R. S., Carou, S., Shaw, M., Ro, C.-U., Aas, W., Baker, A., Bowersox, V. C., Dentener, F., Galy-Lacaux, C., Hou, A., Pienaar, J. J., Gillett, R., Forti, M. C., Gromov, S., Hara, H., Khodzher, T., Mahowald, N. M., Nickovic, S., Rao, P. S. P. & Reid, N. W. 2014. A Global Assessment of Precipitation Chemistry and Deposition of Sulfur, Nitrogen, Sea Salt, Base Cations, Organic Acids, Acidity and Ph, and Phosphorus. *Atmospheric Environment,* 93**,** 3-100.

Vitousek, P., Cassman, K., Cleveland, C., Crews, T., Field, C., Grimm, N., Howarth, R. W., Marino, R., Martinelli, L., Rastetter, E. & Sprent, J. 2002. Towards an Ecological Understanding of Biological Nitrogen Fixation. *Biogeochemistry,* 57(1)**,** 1-45.

Waksman, S. A. & Gerretsen, F. C. 1931. Influence of Temperature and Moisture Upon the Nature and Extent of Decomposition of Plant Residues by Microorganisms. Ecology (Durham), 12(1), 33-60.

Wallander, H., Ekblad, A., Godbold, D. L., Johnson, D., Bahr, A., Baldrian, P., Björk, R. G., Kieliszewska-Rokicka, B., Kjøller, R., Kraigher, H., Plassard, C. & Rudawska, M. 2013. Evaluation of Methods to Estimate Production, Biomass and Turnover of Ectomycorrhizal Mycelium in Forests Soils – a Review. *Soil Biology and Biochemistry,* 57(C)**,** 1034-1047.

Wallander, H., Nilsson, L. O., Hagerberg, D. & Bååth, E. 2001. Estimation of the Biomass and Seasonal Growth of External Mycelium of Ectomycorrhizal Fungi in the Field. *New Phytologist,* 151(3)**,** 753-760.

Walsh, R. P. D. & Newbery, D. M. 1999. The Ecoclimatology of Danum, Sabah, in the Context of the World's Rainforest Regions, with Particular Reference to Dry Periods and Their Impact. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 354(1391)**,** 1869-1883.

Wardle, D., Bardgett, R. D., Klironomos, J., Setala, H., van der Putten, W. & Wall, D. 2004. Ecological Linkages between Aboveground and Belowground Biota. *Science.*

Waring, B. G. & Hawkes, C. V. 2014. Short-Term Precipitation Exclusion Alters Microbial Responses to Soil Moisture in a Wet Tropical Forest. Microb Ecol, 69(4), 843-854.

Weemstra, M., Mommer, L., Visser, E. J. W., Ruijven, J., Kuyper, T. W., Mohren, G. M. J. & Sterck, F. J. 2016. Towards a Multidimensional Root Trait Framework: A Tree Root Review.(Report). *New Phytologist,* 211(4)**,** 1159.

Wei, T. & Simko, V. 2017. R Package "Corrplot": Visualization of a Correlation Matrix [Online]. Available: https://github.com/taiyun/corrplot [Accessed 3rd December 2019].

Wei, X., Shao, M., Gale, W. & Li, L. 2014. Global Pattern of Soil Carbon Losses Due to the Conversion of Forests to Agricultural Land. *Scientific Reports,* 4(1).

Whitaker, J., Ostle, N., Mcnamara, N. P., Nottingham, A. T., Stott, A. W., Bardgett, R. D., Salinas, N., Ccahuana, A. J. Q. & Meir, P. 2014a. Microbial Carbon Mineralization in Tropical Lowland and Montane Forest Soils of Peru. *Frontiers in microbiology,* 5**,** 720.

Whitaker, J., Ostle, N., Nottingham, A. T., Ccahuana, A., Salinas, N., Bardgett, R. D., Meir, P. & Mcnamara, N. P. 2014b. Microbial Community Composition Explains Soil Respiration Responses to Changing Carbon Inputs Along an a Ndes-to- a Mazon Elevation Gradient. *Journal of Ecology,* 102(4)**,** 1058-1071.

White, D., Davis, W., Nickels, J., King, J. & Bobbie, R. 1979. Determination of the Sedimentary Microbial Biomass by Extractible Lipid Phosphate. *Oecologia,* 40(1)**,** 51-62.

Whitman, W. B., Coleman, D. C. & Wiebe, W. J. 1998. Prokaryotes: The Unseen Majority. *Proceedings of the National Academy of Sciences of the United States of America,* 95(12)**,** 6578.

Whitmore, T. C. 1984. *Tropical Rain Forests of the Far East,* Oxford: Clarendon Press.

Wickham, H. 2016. *Ggplot2: Elegant Graphics for Data Analysis,* Cham: Cham: Springer International Publishing.

Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B. & Koh, L. P. 2013. Navjot's Nightmare Revisited: Logging, Agriculture, and Biodiversity in Southeast Asia. *Trends in Ecology & Evolution,* 28(9)**,** 531-540.

Wilkinson, D. M. 1999. The Disturbing History of Intermediate Disturbance. *Oikos,* 84(1)**,** 145-147.

Wilson, G. W. T., Rice, C. W., Rillig, M. C., Springer, A. & Hartnett, D. C. 2009. Soil Aggregation and Carbon Sequestration Are Tightly Correlated with the Abundance of Arbuscular Mycorrhizal Fungi: Results from Long-Term Field Experiments. *Ecology Letters,* 12(5)**,** 452-461.

Woodruff, D. 2010. Biogeography and Conservation in Southeast Asia: How 2.7 Million Years of Repeated Environmental Fluctuations Affect Today's Patterns and the Future of the Remaining Refugial-Phase Biodiversity. *Biodiversity and Conservation,* 19(4)**,** 919-941.

Wright, S. J. 2010. The Future of Tropical Forests. *Annals of the New York Academy of Sciences,* 11951(1)**,** 1-27.

Wurzburger, N. & Clemmensen, K. E. 2018. From Mycorrhizal Fungal Traits to Ecosystem Properties – and Back Again. *Journal of Ecology,* 106(2)**,** 463-467.

Xu, H., Li, Y., Liu, S., Zang, R., He, F. & Spence, J. R. 2015. Partial Recovery of a Tropical Rain Forest a Half-Century after Clear-Cut and Selective Logging. *Journal of Applied Ecology,* 52(4)**,** 1044-1052.

Xuan, Y., Lin, Y., Shixuan, F., Zitong, M., Ruqian, H. & Zhong, Z. 2018. Effect of Soil Layer and Plant–Soil Interaction on Soil Microbial Diversity and Function after Canopy Gap Disturbance. *Forests,* 9(11)**,** 680.

Yamada, T., Hosaka, T., Okuda, T. & Kassim, A. R. 2013. Effects of 50years of Selective Logging on Demography of Trees in a Malaysian Lowland Forest. *Forest Ecology and Management,* 310**,** 531.

Yamanaka, T., Takeda, A. & Shimada, J. 1998. Evaporation beneath the Soil Surface: Some Observational Evidence and Numerical Experiments. *Hydrological Processes,* 12(13-14)**,** 2193-2203.

Yang, B., Pang, X., Hu, B., Bao, W. & Tian, G. 2017a. Does Thinning-Induced Gap Size Result in Altered Soil Microbial Community in Pine Plantation in Eastern Tibetan Plateau? *Ecology and Evolution,* 7(9)**,** 2986-2993.

Yang, Y., Geng, Y., Zhou, H., Zhao, G. & Wang, L. 2017b. Effects of Gaps in the Forest Canopy on Soil Microbial Communities and Enzyme Activity in a Chinese Pine Forest. *Pedobiologia - Journal of Soil Ecology,* 61**,** 51-60.

Yuste, C. J., Janssens, I. A., Carrara, A. & Ceulemans, R. 2004. Annual Q 10 of Soil Respiration Reflects Plant Phenological Patterns as Well as Temperature Sensitivity. *Global Change Biology,* 10(2)**,** 161-169.

Zak, D. R., Pellitier, P. T., Argiroff, W., Castillo, B., James, T. Y., Nave, L. E., Averill, C., Beidler, K. V., Bhatnagar, J., Blesh, J., Classen, A. T., Craig, M., Fernandez, C. W., Gundersen, P., Johansen, R., Koide, R. T., Lilleskov, E. A., Lindahl, B. D., Nadelhoffer, K. J., Phillips, R. P. & Tunlid, A. 2019. Exploring the Role of Ectomycorrhizal Fungi in Soil Carbon Dynamics. *New Phytologist,* 223(1)**,** 33-39.

Zarin, D. J. 2012. Carbon from Tropical Deforestation. *Science,* 336(6088)**,** 1518-1519.

Zelles, L. 1999. Fatty Acid Patterns of Phospholipids and Lipopolysaccharides in the Characterisation of Microbial Communities in Soil: A Review. *Biology and Fertility of Soils,* 29(2)**,** 111-129.

Zhang, L., Yang, J., Niu, Q., Zhao, X., Ye, F., Liang, L. & Zhang, K.-Q. 2008. Investigation on the Infection Mechanism of the Fungus Clonostachys Rosea against Nematodes Using the Green Fluorescent Protein. *Applied Microbiology and Biotechnology,* 78(6)**,** 983-990.

Zhang, X., Johnston, E. R., Barberán, A., Ren, Y., Wang, Z. & Han, X. 2018. Effect of Intermediate Disturbance on Soil Microbial Functional Diversity Depends on the Amount of Effective Resources. *Environmental Microbiology,* 20(10)**,** 3862-3875.

Zhang, X., Liu, W. E. I., Bai, Y., Zhang, G. & Han, X. 2011. Nitrogen Deposition Mediates the Effects and Importance of Chance in Changing Biodiversity. *Molecular Ecology,* 20(2)**,** 429-438.

Zhou, X., Fornara, D., Ikenaga, M., Akagi, I., Zhang, R. & Jia, Z. 2016. The Resilience of Microbial Community under Drying and Rewetting Cycles of Three Forest Soils. *Frontiers in microbiology,* 7**,** 1101-1101.

Zhu, J., Lu, D. & Zhang, W. 2014. Effects of Gaps on Regeneration of Woody Plants: A Meta-Analysis. *Journal of Forestry Research,* 25(3)**,** 501.

Zhu, J.-J., Matsuzaki, T., Lee, F.-Q. & Gonda, Y. 2003. Effect of Gap Size Created by Thinning on Seedling Emergency, Survival and Establishment in a Coastal Pine Forest. *Forest Ecology and Management,* 182(1)**,** 339-354.

Zirlewagen, D. & Von Wilpert, K. 2001. Modeling Water and Ion Fluxes in a Highly Structured, Mixed-Species Stand. *Forest Ecology and Management,* 143(1-3)**,** 27-37.