A multi-functional approach to assessing species interactions in human-modified tropical landscapes

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

The work in Chapter *2* of the thesis has appeared in publication as follows:
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I was responsible for designing the study with advice from co-authors, and was solely responsible for statistical analysis and interpretation of the data and for writing and structuring the paper. Data were collected by FAE; JF; LKG; WHS; THL. *The contribution of the other authors was* providing logistical support and comments on draft manuscripts.

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A multi-functional approach to assessing species interactions in human-modified tropical landscapes

Abstract

Tropical land-use change via rainforest degradation and agricultural expansion is driving a global extinction crisis. Understanding community dynamics, functional diversity (FD) and species interactions in relation to these land-use changes is essential to both conservation actions and ecological theory. Landscapes are altered at multiple scales, and the changing landscape mosaic impacts biodiversity and in turn potential functional processes and ecosystem services (or dis-services). I use field data combined with functional and modelling statistical approaches, and primarily examine dung beetle communities, but also use bird and ant assemblages to compliment my investigations. I study these communities across a land-use gradient of primary rainforest, selectively logged forest, and adjacent oil palm plantations in Malaysian Borneo.

Logging caused significant shifts in community composition but FD of dung beetles and birds was at similar levels compared to primary rainforest. Along logging roads edge effects penetrated 100m into the logged forest interior, with significant declines in species richness, abundance and biomass with increasing proximity to road edges, and a marked change in species composition. Logged forest communities were predominately randomly assembled across three taxonomic groups, with a strong influence of dispersal assembly for dung beetles. The conversion of forest to oil palm, however lead to a significant reduction in FD, greater influence of habitat filtering in the assembly of dung beetle communities, and significant segregation in dung beetle

and bird community assembly. The extent of forest cover and proximity to forest were not significant predictors of oil palm yield.

Understanding the stability and resilience of FD and the dominant assembly processes emphasises the high value of logged forests as refugia for biodiversity. Nevertheless, better landscape design practices for forestry, specifically road planning, and in-situ habitat conservation within plantations is strongly encouraged. Critically a functional approach to land-use change gives conservation a complete and practical focus.

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Chapter 1: General Introduction

Global biodiversity

The natural world has fascinated human kind for centuries leading to some of the greatest scientific discoveries and the unearthing of iconic natural wonders. Beyond the impressive landscapes it is the incredible biodiversity within these ecosystems that captivates and interests people so intensely. Wilson (1988) first used the term *biodiversity* to describe the assortment of living organisms we see beyond just simply how many species are present, something we would now refer to as diversity. This diversity of life and the interactions between species and their environment influence the fundamental processes and functions within ecosystems (Balvanera *et al.* 2006; Mace, Norris & Fitter 2012). However, our understanding of even the number of species present on Earth is extremely limited, with current estimates of 8.7 million species of eukaryotes (±SE 1.3million) (Mora *et al.* 2011). Biodiversity is greatest in the tropics with a higher concentration of different species (including many more endemic species) in one area compared to a similar area at higher latitudes. Indeed, located between tropic of Cancer and the tropic of Capricorn are 16 of the 25 biodiversity hotspots identified by (Myers *et al.* 2000) for vascular plants and vertebrates. Rainforest ecosystems in particular have exceptional species richness and the mechanisms that permit such hyper-diversity to be maintained are important and fascinating concepts within ecology.

Biodiversity is however vulnerable, over many millennia there have been five global events known as ‘mass extinctions’ where biodiversity has been lost suddenly and at a greater rate than would be expected normally (Barnosky *et al.* 2011). Although many species were lost others adapted and were resilient to the prevailing environmental and subsequent biotic changes. It is suggested we are now in a sixth mass extinction, though this time as a result of anthropogenic pressures (rather than plate tectonics and asteroids) (Barnosky *et al.* 2011), which is resulting in biotic homogenisation (McKinney & Lockwood). The human dominance on Earth has led to accelerated changes in climate, specifically increased greenhouse gases leading to rising temperatures and sea levels, and land-use changes driven by mechanisation and industrialisation. As the human population continues to expand, with estimates of between 9.6 – 12.3 billion people in 2100 (Gerland *et al.* 2014), and a growing wealth and desire for luxuries, the destructive anthropogenic pressures and activities continue to threaten biodiversity and the natural world (Hoegh-Guldberg *et al.* 2007; Newbold *et al.* 2014). It is not just the extent and form of these environmental pressures, but the rate at which change is occurring which distinguishes this ‘mass extinction’ from all others (Pimm *et al.* 1995). How biodiversity has and will continue to respond is unclear.

Concerns over the accelerated environmental changes occurring globally lead to the ‘*Convention on Biological Diversity*’ (United Nations 1992) which brought together countries (now with 193 participating countries) to significantly mitigate against the loss of biodiversity by 2010. Following this, the *strategic plan for biodiversity 2011-2020*, aims to continue and improve efforts on biodiversity conservation and other environmental concerns directly or indirectly related to biodiversity, such as politics, economics and social welfare (United Nations 2010). To succeed with biodiversity conservation we need to improve our understanding of specific individual species preferences, the complex networks of species interactions, and in turn how these influence the stability and resilience of community assemblages (McCann 2007; Reiss *et al.* 2009; Wisz *et al.* 2013). Moreover, we need to assess what the impacts of anthropogenic disturbances are in order to manage and mitigate the severity of future developments to conserve biodiversity.

Functions and species interactions

Individual species are more than just simple numbers, differences in species size, morphology and behaviour are fundamental to their ability to exploit resources, resist environmental stress, and in turn coexist (Caliman *et al.* 2010). Furthermore, it has long been accepted that individual species are not single, isolated entities but rather interconnecting components of communities, and more widely ecosystems. The interactions between species influence the key principles of ecosystems, yet the mechanisms which drive such interactions and permit species coexistence are hotly debated and difficult to discern (Balvanera *et al.* 2006; Weiher *et al.* 2011).

At any given spatial scale, species are seen to co-occur and often appear to compete directly for the same resources, for example: plants competing for pollinators or light (Goulson 1994). One of the key principles of coexistence is ‘niche theory’ which is based on individual species having a unique set of traits and specific environmental restrictions in which they are competitively advantaged to prevent displacement (Anderson, Peterson & Gomez-Laverde 2002). Intra-specific competition is stronger than inter-specific competition thus limiting the coexistence of similar species (Macarthur & Levins 1967). Species have thus been shown to coexist along a number of niche dimensions such as resource utilisation, morphology and habitat association. For instance, Bumblebees were shown to differentiate by altitudinal preference, as well as flower choice, which is dependent on corolla length, proboscis length and feeding strategy (Pyke 1982). Niche differentiation however, is not always evident, and instead ‘neutral theory’ has been proposed, suggesting that species are competitively equal and in fact random demographic processes determine species coexistence (Hubbell 2005). These theories are not exclusive and rather a balance between assembly processes is likely to influence community structure and diversity (Chave 2004; Leibold & McPeek 2006).

The relative importance of neutral and niche-based mechanisms in structuring assemblages and thus ecological processes remains pivotal in ecology (Weiher *et al.* 2011). Within an ecosystem there are numerous specific interactions that exist between individual species across different dimensions, and this complexity means our understanding of how interactions structure communities is incomplete (Reiss *et al.* 2009). Irrespective of scale, a regional pool of species exists and these species are divided into sub assemblages across a landscape, each representing a different set of interactions and traits. The selection processes that determine these divisions can be thought of as ‘assembly filters’ (Diamond 1975), i.e. the mechanisms which limit an individual species’ presence (or absence) and ‘role’ within an assemblage through abiotic (i.e. climatic conditions) and biotic (i.e. competition) processes (Van der Plas, Anderson & Olff 2012). Consequently, trait variation is altered between and within communities, and this variation can be investigated using different ‘filters’ to assess how species interactions contribute to ecosystem structuring and functioning. For example, larger species of dung beetles are known to be competitively dominant in many assemblages because they can remove dung resources quickly (Doube 1990), and if the predominant dung resource in a community comes from nocturnal mammals then nocturnal dung beetles will have a competitive advantage, in turn influencing how nutrients are recycled within the ecosystem. Moreover, ecosystem processes, such as nutrient recycling or primary production, are based upon the transfer of recourses through an ecosystem, and which if beneficial to humans are termed ecosystem services, i.e. carbon storage or crop pollination (Mace, Norris & Fitter 2012).

In depth exploration of interaction changes across various scales and parameters has been accelerated by advancements in analytical techniques (Weiher *et al.* 2011; de Bello 2012). There is an increasing trend towards using trait based approaches to species identity, to then understand species persistence, resilience, adaptation or extinction in response to habitat variation or change (Koh, Sodhi & Brook 2004; Ockinger *et al.* 2010). For example, functional diversity metrics account for variation of multiple traits (morphological, physiological and behavioural features of a species) across different dimensions and are increasingly considered more valuable when assessing community functioning than just traditional classifications such as species richness or guilds (Petchey & Gaston 2002; Petchey, Hector & Gaston 2004; Villéger, Mason & Mouillot 2008; de Bello 2012). Furthermore, the dominance of species (and the associated traits), or the patterns of specialist and generalist species give insights into the structuring of species assemblages and the potential resilience and recovery of species and associated interactions (Hillebrand, Bennett & Cadotte 2008; Belmaker, Sekercioglu & Jetz 2012). To effectively determine the dominant process of species assembly within a community, the use of null models to compare observed and expected co-occurrence indexes is well known (Gotelli 2000; Gotelli & Ulrich 2010). More recently, research focusing on linking the mechanism of community structure with the specific characteristics and requirements of species, to assess how species interactions and the provision of ecosystem functions relate has gained increasing attention (Best, Stone & Stachowicz 2015; Hoiss, Krauss & Steffan-Dewenter 2015; Griffiths *et al.* 2016). Critically, however it is poorly understood how the disturbance and conversion of natural habitats may impact species interactions and in turn ecosystem processes and services (Morris 2010; Griffiths *et al.* 2016). This is essential as rapid large-scale changes in the terrestrial environment, through logging, mining, agricultural expansion and urbanisation, have occurred over the recent decades and are set to continue.

Drivers of change

Worldwide land-use change continues to occur at an alarming rate (Gibbs *et al.* 2010; FAO 2011; Koh *et al.* 2011; Hansen *et al.* 2013). Land-use change is defined as a significant modification of an area from its previous condition, often leading to a loss or degradation of natural environments, e.g. forest conversion to urban dwellings or mangroves converted to fish ponds. Commercial logging (clear fell and selective) and agricultural expansion (both pasture and crops) are the major contributors to tropical land-use changes (Gibbs *et al.* 2010; Sodhi *et al.* 2010; Newbold *et al.* 2015). Technological advancements, global markets and worldwide demand have seen a transition from local-scale subsistence needs to landscape-scale corporate ventures in resource acquisition and agriculture (Smith *et al.* 2010; van Vliet *et al.* 2012). Consequently, the impacts of land-use change are more widespread and intensive, and the subsequent environmental and ecological effects are magnified, especially as remaining viable land is often in tropical regions which are typically biodiversity rich (Smith *et al.* 2010; Laurance *et al.* 2014). Moreover, the rate and intensity of these changes significantly reduces the ability for natural systems to recover, and in some cases prevents this all together. The magnitude of these changes has also led to a complex network of landscape transformations and novel ecosystems (Hobbs, Higgs & Harris 2009; Hobbs *et al.* 2014).

i) Timber extraction

Logging refers to the removal of all (clear fell) or a selected proportion of the timber (selective logging) resources in a particular area, which can occur on a subsistence scale (e.g. firewood collection) or as a commercial enterprise. The global demand for wood products (including paper, pulp, roundwood, sawnwood, etc) doubled in the six years between 2001 and 2007 (FAO 2010). Although plantation forestry accounts for 3.5% of timber production, a large percentage of current and future global demand for timber products is and will be met from logging activities in tropical nations (FAO 2010; Blaser et al. 2011).

Commercial selective logging is the extraction of valuable timber above a set diameter or of particular timber species, over a large scale and often with the intention of long-term re-harvesting. Huge areas of the tropics have been transformed and continue to be degraded by such activities with the rate of logging ≈20 times that of forest clearance (Asner *et al.* 2009), and the global area of production forest covering more than 400 million hectares in 2010 (Blaser *et al*. 2011). Indeed, modified tropical and sub-tropical forests, excluding the Amazon, outweigh primary tropical forests in area (Blaser et al. 2011; Laurance, Sayer & Cassman 2014).High timber values and an increasing demand for timber and other wood products ensures these figures are unlikely to reduce in the coming decade (Blaser et al. 2011). Across the tropics logging practices, geographical and political obstacles, and available yields vary greatly, for example, timber extractions rates in Borneo alone were greater than those of all of Latin America and tropical Africa between the late 1980s to the early 2000s (Cleary *et al.* 2007). To meet future (even current) demands, 4 mil km^2 of new logging concessions are planned across the tropics (Bicknell *et al.* 2015), and many more km^2 of tropical forests will be lost through illegal and unreported logging, as well as current protected areas being at risk from downgrading, downsizing or degazettment (Mascia & Pailler 2011; Mascia *et al.* 2014). Furthermore, to gain access to these forests numerous roads will be developed, often at high densities. For instance, in Borneo the average density is 0.48km of road per km^2 (increasing to 0.89km road per km^2 in Sarawak) compared to 0.03km of road per km^2 in Central Africa (Gaveau *et al.* 2014). Biodiversity is frequently negatively associated with roads, which remain in the landscape for decades beyond the last timber extraction and therefore pose a long term issue to biodiversity conservation in production forests. More widely, logging and the associated infrastructure alters the forest structure (Putz *et al.* 2012).

Beyond the initial logging activities natural forest concessions are under threat from secondary encroachment, such as illegal logging, hunting and resettlement as previously inaccessible areas are opened up (Wilkie *et al.* 2000; Peres 2001; Laurance *et al.* 2002); (Clements *et al.* 2014; Kleinschroth, Healey & Gourlet-Fleury 2016). In addition, the threat of re-logging before the original re-harvesting timeframe and thus before sufficient re-growth is commonplace in some regions, causing smaller trees to be extracted and further secondary damage before recovery (van Gardingen *et al.* 2003; Putz *et al.* 2012). Furthermore, misguidance of the value of logged forests has led to their biological worth being dismissed by corporations and governments in favour of economic development on these lands (Edwards *et al.* 2011). Consequently, logging concessions are also threatened by agricultural expansion; indeed 28% of new agricultural land between 1980 and 2000 was developed on such degraded lands (Gibbs *et al.* 2010).

ii) Agricultural expansion replacing forest

Agricultural land cover increased by >100 million ha between 1980 and 2000 (Gibbs et al. 2010) and a further increase of 10^9 hectares in agricultural land area is projected by 2050 to meet the growing demands of the world's human population (Tilman 2001). Of the available global land suitable for agricultural development 1.8 billion ha (90%) occurs in developing countries, mainly concentrated in just seven predominately tropical countries, which are also areas of rich biodiversity (Bruinsma 2009; Laurance, Sayer & Cassman 2014).

One of the principal impacts of forest conversion to agricultural is the homogenisation of the environment as crop plantations and fields are frequently monocultures with a very simplistic uniformed vegetation structure (Fitzherbert *et al.* 2008). In the same way logging has secondary encroachment concerns, agricultural development has a number of detrimental secondary effects after conversion, including soil erosion and water pollution from pesticides and herbicides (Tscharntke *et al.* 2012). In the tropical regions, four main crops (maize, oil palm, soybeans, rice) account for most of the agricultural expansion, though the area of cattle pasture has also increased dramatically (Gibbs *et al.* 2010; FAOSTAT 2012). For example, soy production in Brazil covers ≈20 million hectares (FAOSTAT 2012), while palm oil plantations cover more than 16 million hectares (FAOSTAT 2014). These highly valuable and productive crops provide abundant resources and employment globally but frequently at the expense of tropical rainforest. Globally, more than 80% of new agricultural land developed during the 1980s and 1990s was from forested land (either intact or disturbed), and most of these changes were concentrated across Southeast Asia, Central Africa and Latin America (Gibbs *et al.* 2010). Specifically, development of oil palm plantations during 1990-2010 across Malaysia, Indonesia and Papua New Guinea was mainly on forested land (Gunarso *et al.* 2013; Vijay *et al.* 2016).

Implications of land-use change and biodiversity loss

Land-use change, in particular agricultural expansion is highlighted as one of the biggest drivers of biodiversity loss and increasing extinction risk (Green *et al.* 2005; Gibson *et al.* 2011; Newbold *et al.* 2015), which is particularly evident in the tropics. At a basic level there is an inherent value to biodiversity and natural environments, something that we can enjoy (e.g. wildlife watching or recreation in a national park) and respect (e.g. cultural or spiritual beliefs). The loss of biodiversity results in a loss of this inherent value and in turn can influence human well-being, which is positively linked to exposure to natural environments.

Habitat loss, degradation and fragmentation are the principal negative consequences of logging and agricultural expansion, which disrupt and alter species persistence, interactions and functions within habitats (Wilcove *et al.* 2013; Edwards *et al.* 2014; Laurance, Sayer & Cassman 2014; Lewis, Edwards & Galbraith 2015). More specifically, the residual disturbance of land-use change often alters habitat structure, connectivity and environmental conditions, which in turn can alter niche availability for species, species' competitive ability and their numerical dominance in a community. For example, species' dispersal abilities are frequently limited by monocultures, a modified vegetation structure can encourage competitively superior, invasive and successional species to dominant, and more extreme environmental conditions can breach species' physical tolerances (Freudmann *et al.* 2015). The relationship between land-use change and species interactions depends on multiple factors including species' functional traits, the extent and pattern of the initial disturbance, the area of natural habitat remaining, the time since disturbance and the knock on effects of other species (Sodhi *et al.* 2010; Newbold *et al.* 2015). Communities can often appear robust in degraded habitats, but abundance and compositional changes suggest that there may be hidden species interaction effects (Smith & Knapp 2003). Furthermore, for diversity to be maintained in disturbed habitats there needs to be some level of adaption or resilience which could be overlooked. For example, birds have been found to have higher trophic positions in logged forests, suggesting some degree of dietary flexibility as resources decline or alter in degraded habitats (Edwards *et al.* 2013). Moreover, these altered interactions can have multi-trophic effects, such as disruptions to predator-prey interactions (Van der Plas, Anderson & Olff 2012) or potential mismatch in plant-pollinator communities (Taki & Kevan 2007). Therefore, beyond the inherent value of biodiversity, alterations to ecosystem functions and processes brought about by land-use change could then impact ecosystem services, such as crop pollination or biological pest control (Foley *et al.* 2005; Kremen *et al.* 2007).

Our understanding of logged forests

Although we are increasingly aware of the value of logged forests many unanswered questions remain. Disturbed habitats are indeed valuable reserves for species, which effectively buffer intact forests (Meijaard *et al.* 2005; Berry *et al.* 2010) and maintain greater diversity than the agricultural lands that often replace them (Green 2005; Fitzherbert *et al.* 2008). Recent work has aimed to highlight the biological, economic and conservation value of logged forests in the hope of halting clearance for further agricultural development and demonstrate the ecological value of these degraded forests, especially as a buffer to primary, unlogged forest (Edwards *et* *al.* 2011; Fisher *et al.* 2011b). However, what we lack is an understanding of how resilient specific functions are and what the remaining functional diversity of communities is following tropical disturbance (see chapters 2-3). Furthermore, how species' dominance (i.e. relative abundance) and roles are altered after disturbance influences species interactions and consequently ecological functions (Loreau *et al.* 2001; Smith & Knapp 2003; Hooper *et al.* 2005). Therefore understanding how species co-occurrence is altered with disturbance, and investigating possible functional trait associations with co-occurrence gives a complementary understanding of community assembly structure is disturbed communities (see chapter 4). The increasing emphasis on the functions and services that biodiversity can provide poses new challenges to the conservation of tropical terrestrial biodiversity, and new innovative approaches to landscape design and management are required to meet these changing perspectives (Chazdon *et al.* 2009). For instance, following agricultural expansion, remnant forest fragments and riparian strips could provide reservoirs for biodiversity (Gray *et al.* 2014; Lucey *et al.* 2014) and a means to enhance ecosystem functions and services through positive spill over of biodiversity into the agricultural landscape (Ricketts 2004; Tscharntke *et al.* 2012; Maas, Clough & Tscharntke 2013; Lucey *et al.* 2014). However, whether biodiversity in proximity to oil palm plantations, one of the biggest growing crops globally, can be beneficial to yield is unknown (see chapter 6). Furthermore, an inherent part of logging is the creation of primary and secondary logging roads, leading to extensive networks of highly compressed surfaces with stark contrasting barriers to the natural environment. The consequential long term impacts on biodiversity and the surrounding vegetation is a relatively unknown entity, but understanding these implications is essential for future road planning, as well as conservation efforts within new logging concessions (see chapter 5). In conclusion the ability of biodiversity to buffer against anthropogenic disturbance is not uniformed (Balvanera *et al.* 2006), and it is therefore critical to understand how individual species and community interactions respond over space, time and disturbance regimes (McCann 2007; Lewis 2009; Tylianakis *et al.* 2010; Laufer, Michalski & Peres 2013), in order for us to provide effective conservation.

Focal taxa

In this thesis I primarily focus on dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). These invertebrates are globally widespread, highly abundant and taxonomically well-known across Southeast Asia (Hanski & Cambefort, 1991) making them an ideal model taxonomic group. Furthermore, when investigating ecosystem functions and processes, dung beetles are extremely interesting as they provide a wide range of direct and indirect functions including; dung removal, secondary seed dispersal, soil recycling, and pest suppression (Nichols *et al.* 2008). Moreover, evidence suggests dung beetles are sensitive to environmental change (Nichols *et al.* 2007; Larsen & Forsyth 2005), and as a key indicator group they can provide evidence for the wider condition of biodiversity in an ecosystem, especially mammal populations due to their resource requirements (Gardner *et al.* 2008; Nichols *et al.* 2008). Dung beetles break apart dung piles and distribute the material away from the source, creating dung balls in which larva develop and then feed upon the bacteria within the dung ball (Hanski & Cambefort 1991). There are three distinct guilds of dung beetles which perform this process in different ways; tunnellers (paracoprid) bury dung directly below the dung resource and different species will bury at different depths; rollers (telecoprid) move the dung away, on average up to 1.2m depending on the size of the species (Andresen 1999), from the dung resource before burying it, typically at shallower depths than tunnellers; dwellers (endocoprid) remain within the dung resource and create dung balls within it (Hanski & Cambefort 1991).

I also consider birds and ants which provide a number of important ecosystem processes and are taxonomically well known from the region, providing ideal taxa to complement data on dung beetles. Birds are another key indicator group (Gardner *et al.* 2008), which exhibit a range of morphological and behaviour traits and are essential for pollination, seed dispersal and predation (Sekercioglu 2006; Gray *et al.* 2014; Tscharntke *et al.* 2008). Terrestrial ants have the greatest diversity and density within tropical rainforests (Wilson & Holldobler 2005) and play notable roles in nutrient cycling and seed dispersal (Passos & Oliveira 2002; Underwood & Fisher 2006; Milton & Kaspari 2007) through predation and scavenging.

Study location

This thesis is based in Sabah, Malaysian Borneo, within Southeast Asia an endemic hotspot. Southeast Asia represents one of the key biodiversity rich regions on earth, yet it is also highly threatened (Myers *et al.* 2000; Brooks *et al.* 2002; Hoffmann *et al.* 2010). Forest cover in Southeast Asia declined by 0.9 million ha per year between 2000 and 2010, down from 1980-1990's figures but still the greatest loss in the Asian region (FAO 2010). The island of Borneo, in particular has suffered substantial degradation from selective logging and forest conversion to agriculture (principally oil palm) (Fitzherbert *et al.* 2008; Gaveau *et al.* 2014), with forest cover loss nearly double the rate of the rest of the humid tropics (Gaveau *et al.* 2014). However, 80% of the remaining forest in Southeast Asia occurs within Malaysia and Indonesia, and a large percentage of this is in Borneo (FAO 2010), therefore providing an ideal location to study the land-use gradient from primary rainforest, selective logging and forest conversion to agriculture.

My study sites are located within the Yayasan Sabah (YS) logging concession and adjacent oil palm plantations (Appendix 1). The YS logging concession includes a core area of 45,200 ha of primary lowland rainforest, dominated by highly valuable Dipterocarpaceae species (Fisher *et al.* 2011a). Surrounding this is 238,000 ha of selectively logged forest (Ulu Segama-Malua Forest Reserve - US-MFR), 41% has undergone a single rotation of timber extraction (once-logged forest), while the remaining 59% has undergone two rotations of logging (twice-logged forest). Selective logging in the region has been some of the highest globally (Cleary *et al.* 2007), the first rotation of logging which took place between 1987 and 1991 extracted a yield ≈115 m3 of timber per ha, where all commercially viable stems >0.6 m diameter were cut (Fisher *et al.* 2011a). During the re-logging phase (between 2001 and 2007) an additional 15 – 72 m3 of timber per ha (Edwards *et al.* 2011; Fisher *et al.* 2011a) was removed by reducing the minimum extractable stem diameter to >0.4m. The re-logging phase occurred considerably before the prescribed 70 year recovery period leading to extensive disturbance and large areas without mature trees (i.e. canopy of <10m compared to a minimum of 40m in primary forest) (Reynolds *et al.* 2011, pers observ).These logged forests are structurally altered compared to primary forest, with increased ground and understory vegetation cover, lower tree density, a more open canopy, and an increase in climbing bamboos, invasive grasses, herbs, and pioneer species (such as Macaranga) (Willott *et al.* 2000; Berry *et al.* 2008; Ansell, Edwards & Hamer 2011; Edwards *et al.* 2011).

Beyond the YS concession are vast oil palm plantations, which cover ≈19% of the land area in Sabah (Reynolds *et al.* 2011). The global market for palm oil is extensive, with Malaysia and Indonesia accounting for more than 80% of the global palm oil production (FAO 2010). Oil palm (*Elaeis guineensis*), a native West African palm grows exceptionally well across Southeast Asia and is a highly valuable crop (>$500 USD per metric ton) which can be harvested multiple times a year and yield up to 6 tonnes ha-1 per year (Donough et al. 2009; FAO 2016). Palms are planted at a density of ≈100 palms ha-1 (Edwards *et al.* 2010) and take ≈5 years to produce a valuable crop, but can be continually harvested for ≈25 years afterwards. All of my study sites where biodiversity was sampled were restricted to areas where palms were mature (≈15-20 years old).

Thesis outline

In this thesis I aim to investigate how anthropogenic land-use change impacts species interactions across functional, environmental and spatial filters in tropical invertebrate and avian assemblages. I will do so across a logging and agricultural disturbance gradient in Sabah, Malaysian Borneo, and I will combine field-based data collection with functional and spatial analytical techniques.

In Chapter 2, I compare avian functional diversity in primary forest, logged forest (through two rotations) and oil palm in Malaysian Borneo.

In Chapter 3, I compare dung beetle taxonomic richness and community composition across a forest (primary and logged) to agriculture (oil palm) land-use gradient in Malaysian Borneo. I also explore how functional diversity changes across this same gradient.

In Chapter 4, I compare species co-occurrences in primary forest, logged forest (through two rotations) and oil palm in Malaysian Borneo, using three key indicator taxonomic groups (dung beetles, birds and ants). I also investigate the impact of scale and whether functional traits can explain observed patterns of co-occurrence.

In Chapter 5, I determine the magnitude and spatial extent of edge effects alongside logging roads in Sabah, Malaysian Borneo. To do so I focus on dung beetle community and functional composition.

In Chapter 6, I investigate the value of remnant forest patches, within the oil palm landscape, directly on palm oil yield.

In Chapter 7, I discuss the results from Chapters 2–6 in the context of the wider literature, and how future research might be directed.

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Chapter 2: Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland

The following paper, *F. A. Edwards, D. P. Edwards, K. C.Hamer, & R. G. Davies (2013). Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. Ibis, 155:313-326,* is a modified version of this chapter.

FAE designed the study with advice from co-authors and was solely responsible for statistical analysis and interpretation of the data, and for writing and structuring the paper. Field data (point-counts of birds) were obtained by DPE and all co-authors provided comments on draft manuscripts.

Abstract

Sundaland in Southeast Asia is a hotspot of imperilled biodiversity due to intensive selective logging and subsequent conversion of degraded forest to oil palm. Our understanding of the impacts of these disturbances and the resulting local extinctions on the functional roles performed by the remaining species is limited. I address this issue by examining functional diversity (FD), which quantifies a range of traits that affect a species' ecological role in a community as a single continuous metric. I calculate FD for birds across a gradient of disturbance in Borneo, from primary forest through intensively logged forest to oil palm plantations on previously forested land. Logged rainforest retained similar levels of FD to unlogged rainforest, even after two logging rotations, but the conversion of logged forest to oil palm resulted in dramatic reductions in FD. The few remaining species in oil palm filled a disproportionately wide range of functional roles but showed very little clustering in terms of functional traits, suggesting that any further extinctions from oil palm would reduce FD even further. Determining to what extent the changes I recorded were due to under-utilisation of resources within oil palm or a reduction in the resources present is an important next step. Nonetheless this study improves our understanding of the stability and resilience of functional diversity in these ecosystems, and of the implications of land-use changes for ecosystem functioning.

Introduction

Sundaland in Southeast Asia is among the hottest ‘hotspots’ of imperilled biodiversity (Myers *et al.* 2000; Butchart *et al.* 2004). This stems from widespread habitat degradation via intensive selective logging (Laurance 2007; Edwards *et al.* 2011b) and one of the highest global rates of forest conversion to agriculture (Hansen *et al.* 2008; Gibbs *et al.* 2010). Timber concessions account for over half of Sundaland’s remaining lowland forest cover (ITTO 2005), with both primary and logged forests under pressure from further logging (Edwards *et al.* 2011b, 2012a; Sloan *et al.* 2012). In addition, the total area of lowland dipterocarp forest that remains in Sundaland is dwindling (WWF-Indonesia 2010; Fisher *et al.* 2011a), with a large area of forest having being converted to oil palm agriculture and other plantation crops (Gibbs *et al.* 2010).

Given the extent of logged forests and their frequently imminent threat of conversion to agriculture, understanding the biological value of these degraded lands is of critical importance to conservation in Sundaland. Studies from across Sundaland have highlighted the changing patterns of bird species richness, diversity and community composition across gradients of disturbance from primary forest to logged forest to agriculture (e.g., Lambert 1992; Johns 1996; Berry *et al.* 2010; Edwards *et al.* 2010b, 2011b; Styring *et al.* 2011). These studies consistently reveal that selective logging has a surprisingly limited impact on species richness but more marked effects on species composition, and that conversion of forest to agriculture drives far higher levels of species loss and causes dramatic shifts in community composition.

Our understanding of the impacts of disturbance on the functional roles performed by species, and thus on ecosystem functioning, is much more limited

(Gardner *et al.* 2009) and is based mainly on the changes in the abundance of species in different feeding-foraging guilds or of different body sizes (Gray *et al.* 2007; Edwards *et al.* 2009). These approaches have indicated that predators, frugivores, insectivores, sallying foragers, and larger-bodied species often decline after logging, and that frugivores and insectivores decline further still after the conversion of logged forests to oil palm. In turn, these changes in the abundance of individual functional traits have potential implications for food-web stability and seed dispersal (Terborgh *et al.* 2001; Duffy 2003; Borrvall & Ebenman 2006). However, analyses at the level of coarse functional categories (e.g., 'insectivores') assume that species within these prescribed groups are highly similar, although this assumption is seldom tested and may rarely be met (Tilman 2001). Such approaches have also not considered the variation in functional impacts derived from other traits, such as bill morphology (influencing food type and size) and wing length (influencing aerial agility and flight distance), that can vary within prescribed groups.

An alternative approach to evaluating the effects of habitat degradation and conversion on the functional roles performed by species is to examine functional diversity (FD; Tilman 2001; Petchey & Gaston 2002). This metric quantifies the distribution of a range of functional traits within multi-dimensional niche space, typically focusing on those morphological, physiological, and behavioural traits that define a species' ecological role in a community (Petchey & Gaston 2006; Villéger *et al.* 2008) and yielding a single continuous measure (Petchey & Gaston 2002). Having done so, this metric permits an assessment of whether a species is functionally unique or functionally redundant within a community. Functional redundancy is important for the stability and resilience of ecological communities to disturbance (Chapin et al. 1997; Elmqvist et al. 2003). At the same time, we are also able to assess (i) functional evenness (FEve), which describes how regularly species are distributed within functional space, weighted by relative abundances, and (ii) functional divergence (FDiv), which describes how the relative abundance of species are distributed within functional space, relative to the centre of gravity (Villéger et al. 2008). Functional assessments further simple guild classifications, because they account for variation of multiple traits within prescribed groups and because FD tends to explain more about community functioning than does traditional classification (Petchey *et al.* 2004). Assessing FD can thus have important consequences for our understanding of the effects of disturbance on ecosystem functioning, particularly in the context of conservation of tropical biodiversity (Laliberte *et al.* 2010).

In this study, I investigate changes in avian functional diversity across a gradient of increasing habitat degradation on the island of Borneo, within the Sundaland biodiversity hotspot, where habitat modification has resulted in large-scale local extinctions of species (Sodhi *et al.* 2010). Specifically, the gradient I study comprises primary rainforest, once- and twice-logged rainforests, to forest cleared and converted to oil palm plantation. Birds are a functionally diverse group spanning a wide range of dietary, foraging and microhabitat niches, and performing important functional roles, such as pollination, seed dispersal, and predation (Sekercioglu *et al.* 2006; Gray *et al.* 2007; Tscharntke *et al.* 2008).

In this paper, I test the hypothesis that both logging and conversion of forest to oil palm in Southeast Asia will negatively impact the functioning of the avian community. Previous works from the Neotropics and Africa have shown that communities of vertebrates and plants within modified landscapes have significantly lower functional diversity compared to those in intact primary habitats (Ernst *et al.* 2006; Flynn *et al.* 2009 Loiola *et al.* 2010; Hidasi-Neto *et al.* 2012). To do this I evaluate the extent and pattern of changes in FD along our land-use gradient, (i) for the entire community, and (ii) across different spatial scales (habitats, transects and sampling points), because there can be non-random effects of spatial scale when measuring the patterns of change following disturbance (Hill & Hamer 2004; Hamer & Hill 2000). To complement these analyses I also measure functional evenness (FEve) and functional divergence (FDiv). To determine whether different habitats support higher or lower levels of functional diversity, and thus a set of species showing greater or less niche complementarity, I also compare the observed patterns of functional diversity with those expected if communities along our disturbance gradient were assembled at random from the regional species pool (i.e. all species recorded in this study). Finally, to examine which functional traits were associated with particular habitats, and whether changes in species composition following disturbance resulted in functionally distinct communities, I also consider the distribution of species within functional trait space using RLQ analysis.

Material and methods

Study site

The study was based around the one million hectare Yayasan Sabah (YS) logging concession in eastern Sabah, Malaysian Borneo. Within the YS concession is the Danum Valley Conservation Area and Palum Tambun Watershed Reserve, comprising a combined area of 45 200 ha of unlogged (primary) lowland dry Dipterocarp rainforest, which is dominated by valuable timber species of the Dipterocarpaceae (Fisher *et al.* 2011a). Contiguous with this primary forest is the 238 000 ha Ulu Segama-Malua Forest Reserve (US-MFR; again part of the YS concession), which includes selectively logged forests that have undergone either one (41 % of US-MFR) or two rotations (59 % of US-MFR) of timber extraction. Sampled locations in once-logged forest were logged between 1987 and 1991 using a modified uniform system in which all commercial stems > 0.6 m diameter were removed (yielding an average of 120 m^3 of timber per ha, Fisher et al. 2011a). Our twice-logged locations were logged using the same methods during the first rotation, and again between 2001-2007, employing the same logging techniques but with the minimum tree diameter reduced to > 0.4 m (> 0.25 m in some cases) and resulting in an additional 15–72 m^3 of timber extracted per ha (Edwards *et al.* 2011b; Fisher et al. 2011a). For a summary of tree species and volumes harvested see Fisher *et al.* (2011a). Logged forests show significant structural differences compared to unlogged forests, including increased ground and understory vegetation cover, lower tree density, a more open canopy, and an increase in climbing bamboos (Berry *et al*. 2008; Ansell *et al*. 2011; Edwards *et al.* 2011b), as well as incursion by a labyrinth of skid trails, roads and logging dumps (Pinard *et al.* 2000; see also Laporte *et al.* 2007). To the north, east and south of the US-MFR are oil palm plantations spanning >1 million hectares in area. The sampled sites had mature palms (20-30 years old) at a density of 100 trees per ha (Edwards *et al.* 2010b).

Avifaunal sampling

Fieldwork was conducted from May to September 2008 and May to June 2009. Four widely spaced sampling sites were created in each of the four habitats, using a space-for-time substitution as an alternative to following land-use change over decades (Pickett 1989). Within a habitat, sites were located ≥ 2 km apart (mean ± SE=32.5 ± 4.86), and between habitats, sites were separated by 1–92 km (32.5 ± 4.9). Distances ranged from 1.1 to 21.3 km (once-logged: 3.9 ± 1.5, twice-logged: 14.4 ±

2.7) between logged sites and the nearest primary forest edge, and from 2.8 to ≈ 50 km (20.3 ± 9.2) between oil palm sites and primary forest (Appendix 1). However, previous work has revealed no impact of distance from primary forest edge on metrics of biodiversity in these logged forests (Fisher *et al.* 2011b) and of distance from logged forest edge on metrics of biodiversity in these oil palm estates (Edwards *et al.* 2010b).

Birds were sampled using unlimited-radius point counts, which we considered more appropriate than distance sampling in our densely forested and topographically varied study sites (see Lees & Peres 2006; Edwards *et al.* 2010b, 2011b). At each site, 12 count stations were established at 250 m intervals (192 stations in total) along a line transect, and each station was visited for 15 min on three consecutive days between 05:45 and 10:00. Given that many tropical birds show high site fidelity, the final count for a particular species at a station was taken as the highest number of individuals recorded on any of the three visits. Studies in tropical forests have indicated that bird census points separated by more than 200 m can be considered to be statistically independent (see Hill & Hamer 2004 and references therein). Moreover, the point counts revealed abundance trends for understorey birds that are broadly similar to those obtained from mist nets in the same sample locations (Edwards *et al.* 2011b).

Functional trait matrix

Avian functional diversity was assessed with respect to resource use, using traits highlighted as being functionally important in previous studies (Petchey *et al.* 2007; Flynn *et al.* 2009; Luck *et al.* 2012). I thus considered three broad categories: feeding (determined as foraging guild), morphological (measured as size, weight, wing length, bill shape, bill index and tarsus length); and behavioural (determined as foraging strategy and foraging substrate) (Table 2.1). Foraging guild, foraging strategy and foraging substrate included categorical traits, for which each category (level) was considered to be an independent trait. In cases where such traits were not mutually exclusive they were split into binary traits; for instance, a species might be a frugivore and insectivore but not a predator and detritivore (Petchey *et al.* 2007). Information to populate the matrix was drawn from the literature for each bird species (Smythies 1960; Del Hoyo *et al.* 1992, 1994, 1997, 1999, 2001, 2002, 2003, 2005, 2006, 2007, 2008, 2009; Madge & Burn 1994; Kemp 1995; Feare & Craig 1998; Wells 1999; Ferguson-Lees & Christie 2000; Kennedy *et al.* 2000; Cheke *et al.* 2001; Juniper & Parr 2003; Wells 2003; Robson 2009).

Table 2.1: List of broad resource-use categories and the 22 resource-use traits. Scale indicates how traits are measured, and traits are categorised as being feeding, behavioural or morphological (i.e. physical attributes). Functional Significance indicates the value of these traits for service and functional provision. Superscripts denote: [t] Bill index calculated as bill length/bill depth; [§] Bill shape categorised as decurved=1, hooked=2, straight=3.

Resource-use Category	Resource-use Trait	Scale	Functional Significance
Feeding	1. Insectivore	Binary	Transfer of genetic material - degree of pollination & seed dispersal. Trophic processes - population & pest control. Dietary specialisation. Nurient recycling & rate of resource removal. Nurient deposition - transfer between aquatic & terrestrial systems.
	2. Frugivore	Binary	
	3. Granivore	Binary	
	4. Nectarivore	Binary	
	5. Piscivore	Binary	
	6. Predator	Binary	
	7. Carrion	Binary	
Behavioural	8. Gleaning	Binary	Resource use - type of resources & rate of consumption. Habitat specialisation.
	9. Sallying	Binary	
	10. Probing/digging	Binary	
	11. Pursuit	Binary	
	12. Water	Binary	
	13. Air	Binary	
	14. Vegetation	Binary	
	15. Aboreal bark	Binary	
	16. Ground	Binary	
Morphological	18. Tarsus length (mm)	Continuous	Foraging behaviour
	19. Wing length (mm)	Continuous	Aerial agility & flight distance, effectiveness of seed dispersal, and resource use.
	17. Length of body (cm)	Continuous	Rate of resource consumption, foraging behaviour, and territory size.
	20. Weight (g)	Continuous	
	21. Bill index[t]	Continuous	The selection of fruits & seeds, the effectivenness of pollination, and foraging mode.
	22. Bill shape[§]	Nominal	

Functional measure

The chosen measure of functional diversity was the FD index (Petchey & Gaston 2002, 2006), which is defined as the total branch lengths of a functional dendrogram in which there are as many branch tips as species. The approach starts with a species-by-trait matrix, which is then converted to a distance matrix, which is in turn converted to a dendrogram using a clustering method. I computed the dendrogram for all 188 species recorded within the study, and calculated FD from the total branch lengths connecting the subset of species present at a given sampling site (or pooled set of sites).

To produce the functional dendrogram, I used a combination of the extended Gower distance measure as described by Pavoine *et al.* 2009 (dist.ktab function in ade4 package, Dray & Dufour 2007), which can accommodate a combination of categorical, binary and continuous variables and allows for multi-choice nominal variables (where a single species can occupy several levels) to be selected (Podani & Schmera 2006), and an unweighted pair-group arithmetic average (UPGMA) clustering, which gave the highest cophenetic correlation coefficient (0.90). This high correlation suggests the difference between our trait and phenetic distances was minimal and that I can be confident that our dendrogram represents a realistic depiction of natural variation (Petchey & Gaston 2006 and references therein). FD scores were standardized by the FD of the complete dendrogram of all 188 species recorded during the study, giving a range of 0 to 1 (Petchey & Gaston 2006). FD does have the limitation that it can be highly correlated to species richness, a limitation that should be considered when interpreting our results (Pavoine & Bonsall 2011).

Because FD does not account for species abundances, rare species may, by chance, have been sampled only in one or another type of forest: Species rarely recorded in unlogged forest might not be reliant on primary habitat, whereas rarely recorded species in logged forest might not represent viable populations (Barlow et al. 2010). Such rare species could artificially elevate FD assessments, obscuring patterns between habitats. To account for rarity I repeated the FD analysis at the overall habitat scale, first by removing those species that occurred once (1), and then again by removing those that occurred twice (1+2) in a particular habitat. FD scores were again standardized by the FD of the complete dendrogram of 165 species with singletons removed and 154 species with singletons+doubletons removed (Petchey & Gaston 2006).

I also calculate functional evenness (FEve) and divergence (FDiv) using the convex hull methodology of Villéger *et al.* (2008). This technique uses a multidimensional convex hull to position species in functional trait space, where traits act as coordinates (Villéger *et al.* 2008). Firstly, a distance matrix was calculated using the extended Gower distance measure (as described above), then a principal coordinates analysis (PCoA) was run to calculate a new trait matrix of transformed coordinates (Villéger *et al.* 2008), and finally these PCoA axes (n = 6) were used to calculate the functional metrics. Functional traits were given equal weighting and weighted by their relative abundance.

To examine how the observed patterns of change following habitat disturbance were affected by spatial scale we calculated FD separately for each habitat, and then using summed data for each transect (4 per habitat) and for each sampling point (48 per habitat). At the smaller spatial scales of transect and sampling point, we compared FD between habitats using a general linear model for transects and a linear mixed-effect model for sampling points (lme function within nlme package (Pinheiro *et al.* 2011), with transect as a random effect). These same models were used for testing the significance of species richness at the transect- and sample-scale. To test whether our transect level results may have been influenced by spatial autocorrelation we conducted a Moran's I test using model residuals.

Observed and expected functional diversity within habitats

I determined whether habitats exhibit a higher or lower level of functional diversity, and thus a more or less functionally complementary set of species, than expected by a process of random assembly from the overall regional species pool (all species found during the study). To do this I calculated the standardised effect size (SES=[observed FD - mean expected FD]/standard deviation of expected FD) using the ses.pd function in the picante package of R (Kembel *et al.* 2010). An independent-swap algorithm was used to maintain species richness and species frequency occurrence (Gotelli 2000), and 1000 random communities were drawn. To test whether the SES was significantly different from zero, for each habitat I used a one-sample t-test with $\mu = 0$.

Species composition and variation in functional traits

Changes in functional diversity can be caused by shifts in species composition and by the loss or gain of functional groups. I used RLQ analysis (ade4 package, Chessel *et al.* 2004) to investigate the relationship between habitat type and species functional traits, while accounting for species' abundances across the site locations. RLQ analysis compares three matrices: R - environmental parameter(s) at each site (sites x environment); L - species' abundances at each site (sites x species); and Q - functional traits for each species (species x traits; Dolédec *et al.* 1996). Firstly, individual ordinations were performed on the three matrices: a correspondence analysis (CA) was run on our species abundance matrix; and principal components (PCA) analyses using the Hill and Smith method (Hill and Smith 1976), which allows for a mix of continuous and factor variables, were run on the environmental and the trait matrices. These PCA analyses used site and species scores from the CA analysis as row and column weightings (respectively) to link the R (by site) and Q (by species) matrices with the L matrix. Secondly, these ordinations were combined to perform the RLQ analysis, a form of co-inertia analysis which aims to maximise the co-variance between the R and Q variables (Dolédec *et al.* 1996; Ribera *et al.* 2001). Finally, I calculated a Monte-Carlo permutation test, with 1000 repetitions to test the significance of the relationship between the environmental and trait data. All analyses were run in R v.2.14.1 (R Development Core Team 2011).

Results

Functional measures

Across the four habitats, 6892 observations were made comprising 188 species, from which I created the functional dendrogram to describe the functional relationships between species (Fig. 2.1). The dendrogram contained a number of clusters of species indicating an overlap in resource-use traits, and other isolated species exhibiting distinctive sets of traits. Those species that occurred in oil palm showed little clustering, being spread across the dendrogram and indicating a wide range of functional traits (Fig. 2.1, species denoted by + and ++).

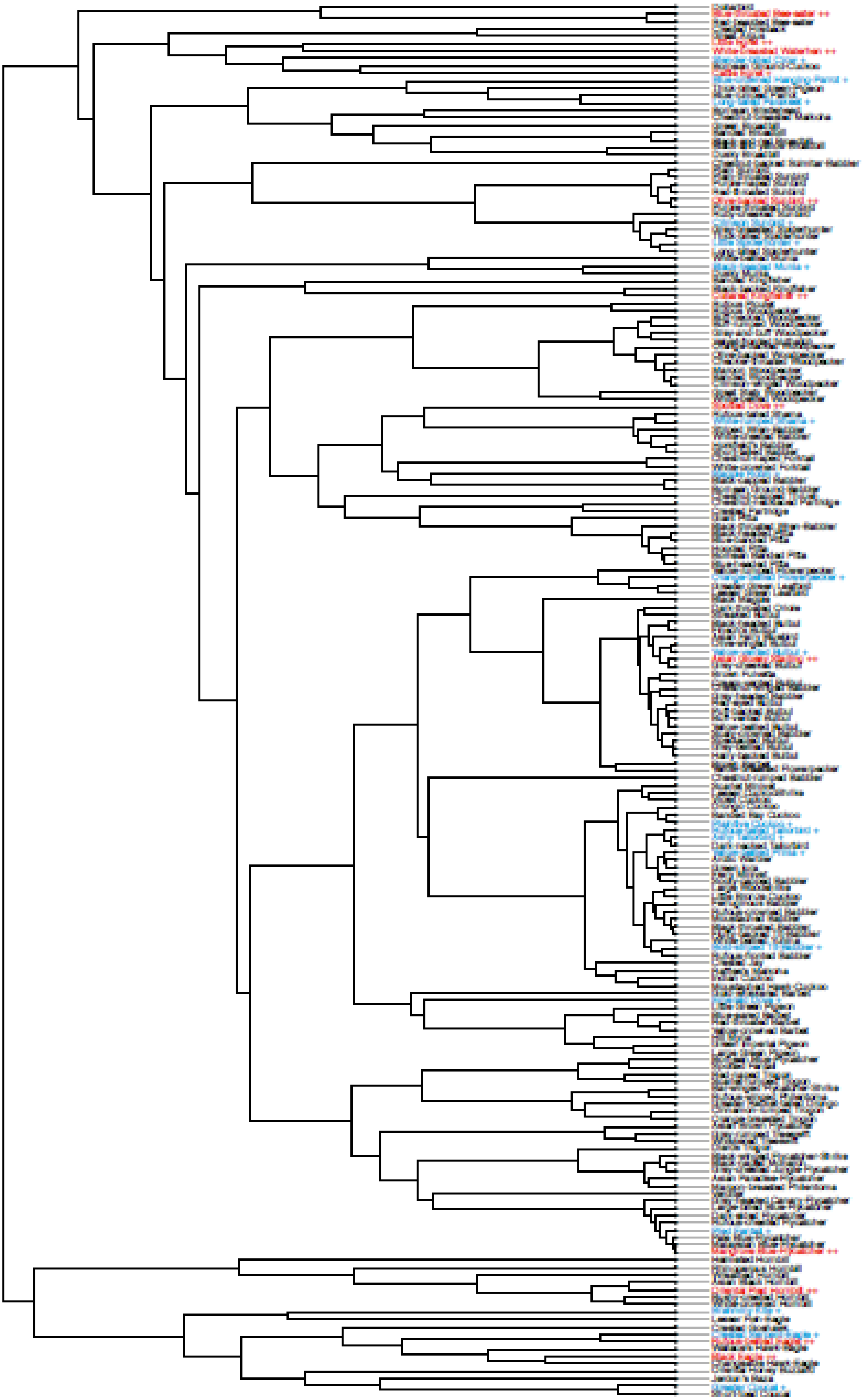

Figure 2.1: Functional dendrogram of the 188 study species: name in **black** = recorded in forest only; in **blue** = recorded in oil palm and one or more forest type; in **red** = recorded in oil palm only.

Functional diversity (FD) at the habitat-level was not affected by increasing intensities of logging, but declined sharply from twice-logged forest to oil palm (Table 2.2). The removal of rarely recorded species (1 and 1+2 abundances) from each habitat pool did not impact the overall pattern of habitat-level FD. Although there was a marginal increase in FD within oil palm, oil palm continued to have far lower FD than forest habitats. Similarly, there was no difference in FDiv across the four habitats. However, a second rotation of logging and conversion of forest to oil palm considerably lowered FEve compared to primary and once-logged forests (Table 2.2).

Analysis of FD at the smaller scales of individual transects ($F_{3,12} = 59.74$, $P < 0.01$; Table 2.2) and individual sampling points ($F_{3,12} = 39.92$, $P < 0.01$; Table 2.1) revealed broadly similar variation among habitats as the larger-scale, habitat-level analysis. Unlogged, once-logged, and twice-logged forests all had significantly higher FD than oil palm plantations at both spatial scales (all $P < 0.01$). There was no difference in FD between the two logging intensities ($P > 0.41$ at both scales), or between the logged forests and unlogged forest at the scale of transects (both $P > 0.48$). However, logging negatively affected FD at the scale of sampling points (both $P < 0.008$). There was no spatial autocorrelation of FD model residuals found across transects (Moran's I test: $P > 0.46$).

Table 2.2: Species richness (S), functional diversity (FD), functional evenness (FEve) and functional divergence (FDiv) across a land-use gradient of logging and agriculture. S and FD at transect- and sample-scales are means ± 1SE, with superscripts representing pairwise differences at $P \leq 0.05$. FD habitat scale (1) and (1+2) show the impact of removing rare species on FD. FD, FEve, and FDiv are scaled to 0 to 1, with FD standardised in comparison to a theoretical community of FD=188 species; FD(1)=165 species; and FD(1+2)=154 species.

	Unlogged	Once Logged	Twice Logged	Oil Palm
S				
Habitat scale	139	131	139	32
Transect scale	93 ± 3 ^{a}	87 ± 5 ^{a}	94 ± 5 ^{a}	18 ± 1 ^{b}
Sample scale	28 ± 1 ^{a}	26 ± 1 ^{a}	27 ± 1 ^{a}	11 ± 0 ^{b}
FD				
Habitat scale	0.87	0.84	0.85	0.25
Habitat scale (1)	0.90	0.87	0.85	0.32
Habitat scale (1+2)	0.84	0.82	0.82	0.32
Transect scale	0.61 ± 0.01 ^{a}	0.58 ± 0.02 ^{a}	0.60 ± 0.03 ^{a}	0.24 ± 0.02 ^{b}
Sample scale	0.29 ± 0.01 ^{a}	0.24 ± 0.01 ^{a}	0.25 ± 0.01 ^{a}	0.13 ± 0.004 ^{b}
FEve				
Habitat scale	0.43	0.42	0.33	0.34
FDiv				
Habitat scale	0.74	0.70	0.71	0.68

Observed and expected functional diversity within habitats

Observed FD of the avian communities was on average lower than expected by chance (with a negative model intercept = -0.29) but showed variation between habitats (lme: $F_{3,12} = 5.68$, $P = 0.01$). Unlogged forest showed significantly higher observed FD than expected (Figure 2.2; one-sample t-test: $t_{47} = 3.51$, $p < 0.01$), whereas, logged forests were less functionally diverse than expected from the regional pool of species (Figure 2.2; once-logged, $t_{47} = -3.48$, $P < 0.01$; twice-logged, $t_{47} = -3.45$, $P < 0.01$). Oil palm showed no significance ($t_{47} = 1.22$, $P = 0.23$; Fig. 2.3), which is comparable to a random community assembly.

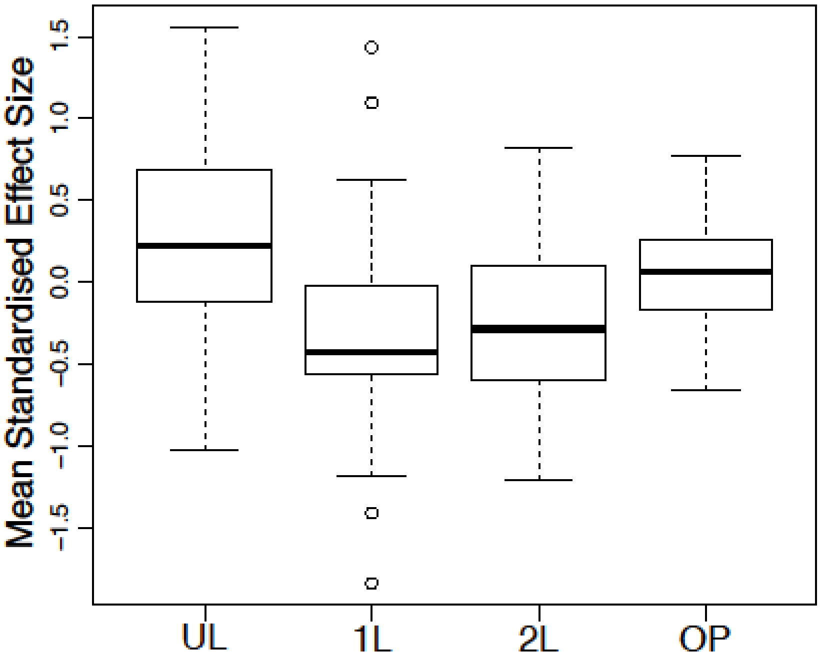

Figure 2.2: The mean standardised effect size (SES) of functional diversity (FD) in each habitat. SES=(Observed FD - mean Expected FD)/SD Expected FD. SES is calculated from 1000 randomisations of the regional pool of species, where species frequency occurrence and species richness are maintained. Values of SES above zero indicate that the species pool of a habitat is more functionally diverse than the regional species pool. UL = Unlogged, 1L = Once-logged, 2L = Twice-logged, and OP = Oil Palm.

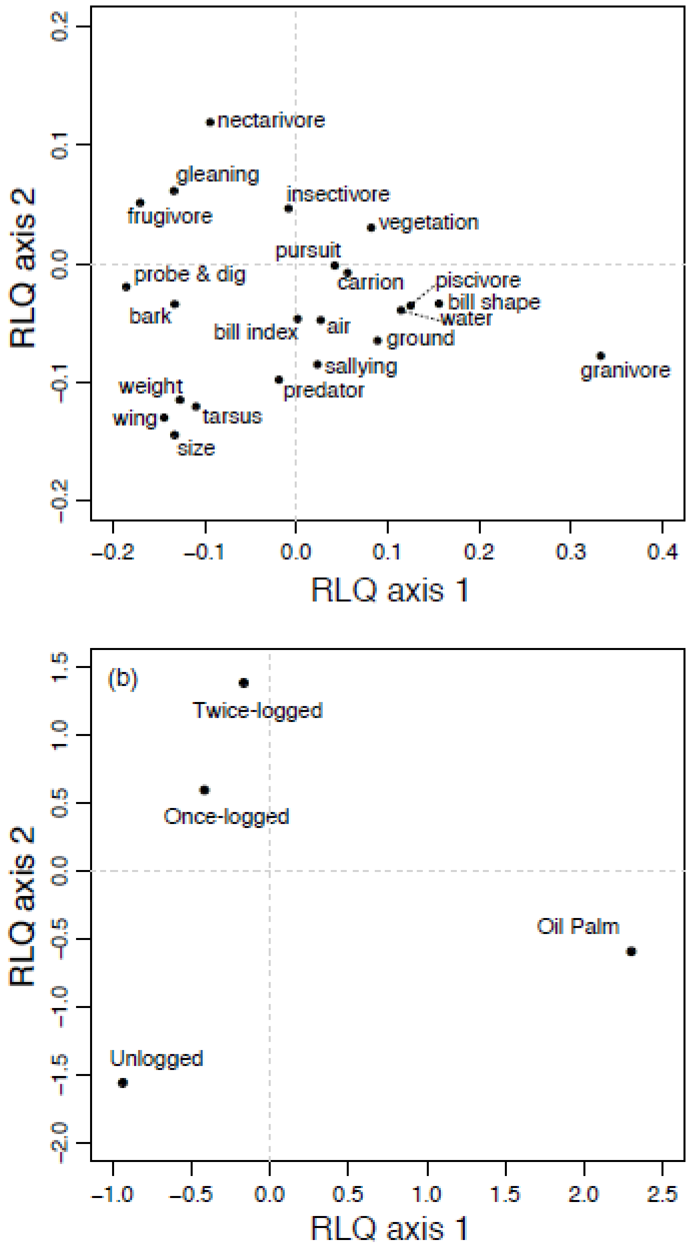

Figure 2.3: The RLQ scores showing the relationship between **(a)** functional traits and **(b)** land-use change (habitat types). Axes 1 and 2 explain 72% and 25% of the total variation in habitat type and in species functional traits. Note the different axes scales on **(a)** and **(b)**.

Species composition and variation in functional traits

Changes in species composition between forest and oil palm altered the functional traits exhibited by the community, with the RLQ analysis revealing a significant relationship between habitat type and species traits ($P < 0.01$, permutation test). Furthermore, the first two RLQ axes accounted for 97% (Axis 1 = 72% and Axis 2 = 25%) of the total variance from the data matrix that crosses the habitat types (R) and the species functional traits (Q). Granivorous species were positively related to RLQ Axis 1, and were found more commonly in oil palm. In particular, Black-headed Munia *Lonchura atricapilla* and Spotted Dove *Spilopelia chinensis* were highly abundant in oil palm but largely absent from forest (Figure 2.3). RLQ Axis 2 was explained by (i) smaller species with shorter wing and tarsus lengths, which were indicative of unlogged forest, and (ii) nectar feeding species, which was indicative of logged forest (Figure 2.3). An additional seven species of the Nectariniidae family (e.g., Purple-throated Sunbird *Leptocoma sperata* and Red-throated Sunbird *Anthreptes rhodolaemus*) were present in logged forests, but not in unlogged forest or oil palm (Figure 2.1).

Plotting individual species present in a particular habitat against the first two RLQ axes revealed that there is a degree of functional overlap between species within primary and logged rainforests, but a lack of such functional overlap when comparing any of the forest habitats with oil palm (Figure 2.4). The extinction of species within oil palm resulted in the loss of several pairs of functionally similar species (e.g. Great Slaty Woodpecker *Mulleripicus pulverulentus* [81] and White-bellied Woodpecker *Dryocopus javensis* [175]) and of some functionally unique species (e.g. Helmeted Hornbill *Rhinoplax vigil* [97]) (Figure 2.4, Appendix 2). These losses were counterbalanced to some degree by the replacement of species lost from forest with species that occupied similar functional space (e.g. Black Eagle *Ictinaetus malayensis* [14] replacing Changeable Hawk Eagle *Nisaetus cirrhatus* [46]) and by the addition of new species that were functionally isolated (e.g. Little Egret *Egretta garzetta* [110] and White-breasted Waterhen *Amaurornis phoenicurus* [177]) (Figure 2.4, Appendix 2). In contrast, whilst species composition also changed between unlogged and logged forest, there was minimal impact on the combinations of functional traits exhibited within logged forest (Figure 2.4), suggesting that community functioning between primary and degraded forest is similar.

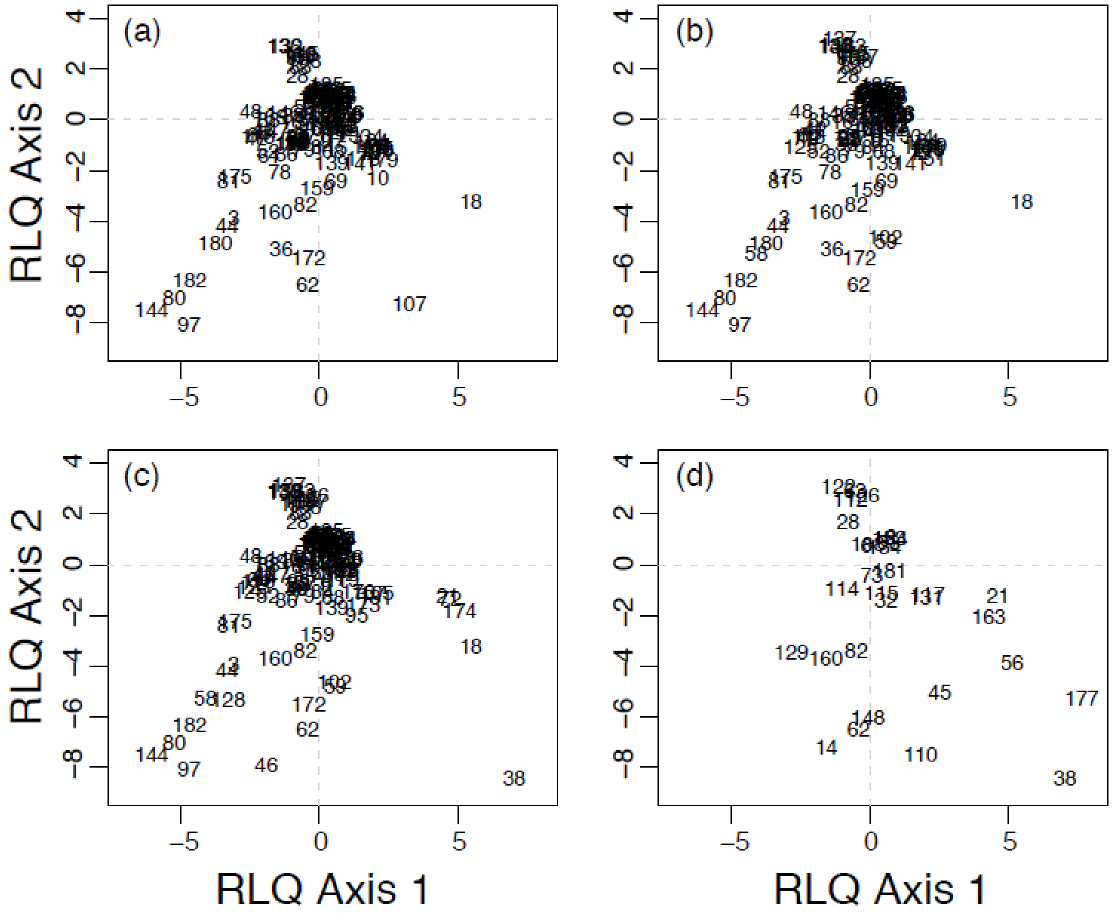

Figure 2.4: The impact of changes in species composition on the functional traits exhibited by the community within: **(a)** unlogged forest; **(b)** once-logged forest; **(c)** twice-logged forest; and **(d)** oil palm plantation. Species are plotted within functional trait space along RLQ coordinate Axes 1 and 2, which explain 72% and 25% of the total variation between habitat type and functional traits, respectively. See Appendix 1 for species names.

Discussion

Across our gradient of increasing habitat disturbance from unlogged (primary) rainforest through logged forest to oil palm there was a substantial reduction in avian functional diversity (Table 2.2). These negative impacts were, however, most severe following the conversion of logged forest to oil palm. Despite having experienced some of the highest rates of timber extraction globally, degraded rainforest retained similar levels of overall functional diversity of birds to primary rainforest, but were less functionally diverse than expected by chance (Figure 2.2). In contrast, conversion to oil palm monoculture led to a marked reduction in functional diversity (Table 2.2) and a decline in functional evenness.

The functional dendrogram for the entire species pool (Figure 2.1) revealed that there were both clusters of species and some isolated species with distinctive traits. Species clusters reveal high levels of functional overlap, with multiple species occupying similar resource-use roles within the community. The loss of some of these species following habitat disturbance would be unlikely to lead to a major loss of functional diversity (Duffy 2002; Bihn *et al.* 2010; Laliberte *et al.* 2010). In contrast, isolated species have a combination of resource-use traits that are rarely provided or are not provided by other species in the region, making these species more critical to the maintenance of functional diversity (Petchey *et al.* 2008). Interestingly, the most isolated species (for examples, Chestnut-backed Scimitar-Babbler *Pomatorhinus montanus* and Asian Green Broadbill *Calyptomena viridis*) are primarily forest specialists that were absent after conversion to oil palm (Fig. 2.1; Edwards *et al.* 2011b). Forest specialist species often have particular functional attributes that mean they play important roles in forest ecosystems. In the cases of Asian Green Broadbill and Chestnut-backed Scimitar-Babbler, both have distinctive bill morphologies that provide important ecosystem functions, via dispersal of large–seeded, understorey and midstorey plants (Lambert 1992), and the exploitation of invertebrates that reside in bark crevices, respectively.

The apparent lack of substantial change in functional diversity after logging (Table 2.2) indicates that the avian community of logged forests maintained a similar diversity of resource use traits as the community of unlogged forest. Previous studies have indicated that whilst on average there is a retention of species richness following logging (as also demonstrated here, Table 2.2), the composition of species changes following the first logging rotation (e.g., Berry *et al.* 2010) and those changes in composition are in turn magnified by a second logging rotation (Edwards *et al.* 2011b; Woodcock *et al.* 2011). The results suggest that those species that colonise or increase in abundance after logging provide a similar set of resource-use traits to those of the primary forest specialists that they replace (Figures 2.3 and 2.4) and thus we might expect functional processes in logged forests to be similar to those in primary forest. This contrasts with conversion of forest to agroecosystems, where changes in species composition may be accompanied by concomitant changes in functional diversity (Tscharntke *et al.* 2008; Lewis 2009).

I show that logged forest communities harbour less FD than expected by chance (Figure 2.2) suggesting strong environmental filtering effects. The altered environmental conditions of these disturbed forests, including structural and micro-climatic changes (such as a lower canopy, dense understory, and increased temperatures; Berry *et al.* 2008; Ansell *et al.* 2011; Lucey & Hill 2012) could influence the nesting, foraging or physiology of certain species, which in turn could limit their ability to exploit logged forests. In contrast, I provide evidence that unlogged forest communities are driven by stronger niche partitioning (SES > zero,

Figure 2.2), where competition between species over time increases the dissimilarity between species (Petchey *et al.* 2007). However, this pattern could also be partially an effect of weak environmental filtering where the unlogged forest conditions are more benign.

The avifauna in oil palm had very low functional diversity (Table 2.2), indicating that conversion of forest represents a dramatic loss of functional strategies. This shift was apparently driven partly by the loss of particular functionally grouped species, especially arboreal bark foragers (which were lost completely), and probing and digging foragers (e.g., woodpeckers Picidae, pheasants Phasianidae and pittas Pittidae; Figures 2.3 and 2.4). Losses in functional diversity were offset to a small extent by replacement with species of similar functional impacts (Figures 2.1 and 2.4; for example, Oriental pied Hornbill *Anthracoceros malayanus* replaced Asian black Hornbill *Anthracoceros albirostris* and Bushy-crested Hornbill *Anorrhinus galeritus*). However, I do not know whether the net loss of functional strategies resulted in under-utilisation of resources available within the oil palm (e.g., fruits or insects on bark). Alternatively, the resource base in oil palm may have contracted, such that those few resources available were being used just as effectively in oil palm as in forests. Under this second possibility, bark foragers do not persist in oil palm because the resource-base of bark-dwelling invertebrates has been lost. Determining to what extent the changes I recorded were due to under-utilisation of resources within oil palm or a reduction in the resources present is an important next step.

The functional evenness of the oil palm community was also lower compared to unlogged and once-logged forest communities (Table 2.2). The relative abundance of species with different functional traits is thus less even and the distances between these species is less regular within the functional space occupied by oil palm than forest communities (Villéger *et al.* 2008). For example, Black-headed Munia is functionally isolated (Figure 2.1), while Ashy Tailorbird *Orthotomus ruficeps*, Rufous-tailed Tailorbird *Orthotomus sericeus* and Yellow-bellied Prinia *Prinia flaviventris* are functionally very similar (Figure 2.1), yet they are all common species (total abundance > 74 individuals) within oil palm. There thus appears to be both some degree of functional redundancy in oil palm, with clusters of functionally similar species (Figure 2.1; for instances, clusters of raptors and small-bodied insectivores), but also a more general pattern of low functional overlap in other groups. In this latter case, any further extinctions from oil palm would reduce functional diversity even further, because lost species are likely to have a set of traits that are not offered by other species present. Such extinctions could impact negatively upon ecosystem functioning within oil palm, as well as food-web stability and resistance to invasions (Mason *et al.* 2005; Flynn *et al.* 2009).

Those functionally unique species that colonised the landscape after conversion to oil palm were typically generalists with very large geographical ranges and are of no conservation concern, whereas functionally unique species within forest were forest-interior specialists, often of global conservation concern (e.g., Asian Green Broadbill). The shifts in functional diversity seen across our disturbance gradient in Southeast Asia mirror findings from the Neotropics, where logging and fire caused no detectable loss of functional diversity in birds, mammals or plants, but conversion to agriculture resulted in significant declines (Flynn *et al.* 2009; Loiola *et al.* 2010; Hidasi-Neto *et al.* 2012). However, in contrast to these findings, logging did reduce the functional diversity of amphibians in both Africa and the Neotropics (Ernst *et al.* 2006), suggesting that certain taxa within Sundaland might also respond differently to these observed patterns for birds. Furthermore, although the results appear to be independent of spatial scale (Table 2.2; Edwards *et al.* 2011b; Woodcock *et al.* 2011) and of spatial autocorrelation (see **Results**) I cannot rule out the possibility that recently modified twice-logged forest may carry an extinction debt. Additionally, populations in modified habitats may be sustained to some extent by dispersal from areas of natural habitat (although Fisher *et al.* 2011b found no evidence to support the latter suggestion). Hence the functional diversity of the study system may change over time or if unlogged forests are removed from the landscape. Nevertheless, these results support previous data indicating that even heavily-logged rainforests can retain high conservation value (Meijaard & Sheil, 2007; Berry *et al.* 2010; Edwards *et al.* 2011b).

This study illustrates the potential of Sundaland's logged tropical forests to retain a similar level of bird functional traits as in primary forest, but vastly more functions than in oil palm. It suggests therefore that ecosystem functioning is relatively stable in these logged forests, adding weight to the argument that they are of critical importance to the conservation of Sundaland's avifauna and other biodiversity (Edwards *et al.* 2011b; Woodcock *et al.* 2011). However, degraded forests remain at serious risk of conversion to agriculture (Gibbs *et al.* 2010) and are in urgent need of funding for protection. In this context, I urge for an increased role of Reducing Emissions from Deforestation and Forest Degradation (REDD+) and other Payments for Ecosystem Service (PES) schemes in funding the protection of logged rainforests. The net present value of logged forest timber is so reduced compared to a primary forest (\$2000 versus \$12750 ha^{-1}) that such schemes might be able to compete with further destruction (Edwards *et al.* 2011a; Fisher *et al.* 2011a, b). These could do so with direct payments for carbon and biodiversity conservation, as well as payments for active management—such as Reduced-Impact Logging (Pinard & Putz 1996) and carbon sequestration via forest restoration (Edwards *et al.* 2010a)—that maintain (but seem not to enhance) the value of logged forests for birds (Edwards *et al.* 2009, 2012b; Ansell *et al.* 2011). This study suggests that these managements will also likely retain bird functional traits and thus ecosystem functions. If this is true, then this will be a major benefit for the conservation of Sundaland's threatened and functionally rich avifauna.

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Chapter 3: Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot?

The following paper, *F. A. Edwards, D. P. Edwards, T. H. Larsen, W. W. Hsu, S. Benedick, A. Chung, V.K. Chey, D. S. Wilcove & K. C. Hamer (2014). Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? Animal Conservation, 17:163-173,* is a modified version of this chapter.

FAE designed the study with advice from KCH and was solely responsible for statistical analysis and interpretation of the data, and for writing and structuring the paper. Data and field samples (dung beetles) were collected and identified to species by FAE and WWH with assistance from THL. KCH and DPE provided comments on draft manuscripts. Other co-authors provided logistical support.

Abstract

Forests in Southeast Asia are rapidly being logged and converted to oil palm. These changes in land-use are known to affect species diversity but consequences for the functional diversity of species assemblages are poorly understood. Environmental filtering of species with similar traits could lead to disproportionate reductions in trait diversity in degraded habitats. Here, I focus on dung beetles, which play a key role in ecosystem processes such as nutrient recycling and seed dispersal. I use morphological and behavioural traits to calculate a variety of functional diversity measures across a gradient of disturbance from primary forest through intensively logged forest to oil palm. Logging caused significant shifts in community composition but had very little effect on functional diversity, even after a repeated timber harvest. These data provide evidence for functional redundancy of dung beetles within primary forest and emphasise the high value of logged forests as refugia for biodiversity. In contrast, conversion of forest to oil palm greatly reduced taxonomic and functional diversity, with a marked decrease in the abundance of nocturnal foragers, a higher proportion of species with small body sizes and the complete loss of telecoprid species (dung-rollers) all indicating a decrease in the functional capacity of dung beetles within plantations. These changes also highlight the vulnerability of community functioning within logged forests in the event of further environmental degradation.

Introduction

Land-use change is the major driver of ecosystem degradation and biodiversity loss globally (Nepstad *et al*., 1999; Brooks *et al*., 2002; Nelson *et al*., 2006; Laurance, 2007), with an ever-growing proportion of the world's natural habitats being altered by anthropogenic activities (Morris, 2010). Roughly 13 million hectares of forest were converted annually between 2000 and 2010, concentrated within the tropics and principally for agricultural expansion (Hansen *et al*., 2008; FAO, 2010). In addition, 403 million hectares of tropical forest are designated for logging (Blaser *et al*., 2011), with the rate of logging about 20 times that of forest clearance (Asner *et al*., 2009).

The impacts of land use change on biodiversity are often examined , particularly in tropical ecosystems, using measures of diversity (e.g. species richness and Simpson or Shannon diversity indices) that take no account of differences in species' life-history traits and ecological niches. Yet changes in environmental conditions following disturbance may well act as a filter, allowing only a narrow spectrum of traits to persist (Hamer *et al.*, 2003; Gray *et al.*, 2007; Cardinale, *et al.*, 2012; Fauset *et al.*, 2012). As a consequence, such traditional diversity measures may be inappropriate indicators of changes in community structure, underestimating the true extent of biodiversity loss following disturbance (Cardinale *et al.*, 2012; Mouillot *et al.*, 2013). One solution is to use measures of functional diversity, which seek to quantify the range of functional (i.e. trait) differences among species in a community (Tilman, 2001; Petchey & Gaston, 2006), thus bridging the gap between species diversity and species composition, and giving insight into potential resilience and recovery of species in response to land-use change (Koh, Sodhi & Brook, 2004; Hillebrand,Bennett & Cadotte, 2008; Ockinger *et al.*, 2010; Mouillot *et al.*, 2013).

Despite the value of functional diversity metrics in inferring ecosystem processes (de Bello *et al.*, 2010; Naeem, Duffy & Zavaleta, 2012; Mouillot *et al.*, 2013), the impacts of tropical land-use change on functional diversity are poorly understood. Examination of the literature identified just 12 studies that quantified the functional diversity of tropical communities across a terrestrial disturbance gradient (Table 3.1). Of these studies, only three compared the functional diversity of communities in logged forest with those in primary forest. They found that amphibian functional diversity was higher in primary forest (Ernst, Linsenmair & Rödel, 2006), but that arboreal and avian functional diversity were not different (Baraloto *et al*., 2012; Edwards *et al.*, 2013).

In addition, only one previous study has investigated the impacts of oil palm agriculture on functional diversity (Table 3.1; Edwards *et al*., 2013), yet this is a widespread and rapidly expanding crop globally (Fitzherbert *et al*., 2008; Gibbs *et al*., 2010). In Southeast Asia, the conversion of forest (both primary and logged) to oil palm agriculture has been rampant, with several million hectares of oil palm plantation replacing forest over the last two decades (Koh & Wilcove, 2008; Gibbs *et al*., 2010; Reynolds *et al*., 2011). Dung beetles provide key ecosystem functions and services, including nutrient recycling, soil aeration, secondary seed dispersal, and parasite suppression (Nichols *et al*., 2008), as their habit of breaking apart dung piles and distributing the material away from the source. However, only one previous study has examined impacts of land-use change on the functional diversity of dung beetles (in Mexico; Barragán *et al*., 2011), yet these are globally widespread, highly abundant (Hanski & Cambefort, 1991), sensitive to environmental changes (Larsen, Williams & Kremen, 2005; Nichols *et al.*, 2007) and key indicators for other taxonomic groups, especially mammals (Nichols *et al.*, 2009).

Table 3.1: Studies investigating functional diversity in the tropics across a land-use gradient. Functional metric abbreviations; functional dendrogram (FD), functional attribute diversity (FAD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional specialisation (FSpe), functional dispersion (FDis). Superscript (*) represents a meta-analysis.

Taxa	Geographic Region	Land-use Change	Functional Metric(s)	Study
Amphibians	**Ivory Coast and Central Guyana**	Primary and selectively logged forest	FD	Ernst et al., 2006
Ants	**Brazilian Atlantic forest**	Forest fragmentation (size)	FEve	Leal et al., 2012
Ants	**Brazilian Atlantic forest**	Secondary forest (age)	FD, FAD	Bihn, Gebauer & Brandl, 2010
Birds	**Malaysian Borneo**	Primary and selectively logged forest, and oil palm	FD, FEve, FDiv	Edwards et al., 2013
Birds	**Brazilian Amazon**	Unburned and burned (frequency) forest	MPD, MNTD	Hidasi-Neto, Barlow & Cianciaruso, 2012
Birds, Plants, Mammals	**Costa Rica to USA**	Temperate and tropical, natural, semi-natural and agricultural habitats	FD	Flynn et al., 2009 *
Dung Beetles	**Mexico**	Forest fragmentation (size)	FRic, FEve, FDiv	Barragán et al., 2011
Dung Beetles	**Mexico**	Continuous forest, forest fragmentation and pasture	FRic, FEve, FDiv	Barragán et al., 2011.
Trees	**French Guiana**	Primary and selectively logged forest gaps	FRic, FEve, FDiv	Baraloto et al., 2012
Trees	**Mexico**	Secondary forest (age)	FD	Lohbeck et al., 2012
Understory plants	**Solomon Islands**	Primary forest, secondary forest, plantations and pastures	FRic, FEve, FDis	Katovai, Burley & Mayfield, 2012
Utilitarian plants	**Madagascar**	Continuous and fragmented forest (varying degradation), and agricultural habitats	FD	Brown et al., 2013
Woody plants	**Brazilian Cerrado**	Fire (frequency)	FD	Cianciaruso et al., 2012

In this study, I address these key knowledge gaps by investigating the impacts of land-use change on the taxonomic and functional diversity of dung beetles in the global biodiversity hotspot of Sundaland, Southeast Asia (Myers *et al*., 2000). I examine a gradient of increasing habitat disturbance from primary forest through once-logged and twice-logged forest to oil palm. I test the hypothesis that disturbance acts as an environmental filter, selecting species more functionally similar than expected by chance and hence leading to lowered functional diversity in disturbed habitats.

Materials and Methods

Study location

Our study is based within the Yayasan Sabah (YS) logging concession and adjacent oil palm plantations, in eastern Sabah, Malaysian Borneo (4^{o} 58′ N, 117^{o} 48′ E). Within the YS concession is 45,200 ha of primary forest in the Danum Valley Conservation Area and Palum Tambun Watershed Reserve, which is dominated numerically by valuable timber species of the family Dipterocarpaceae (Fisher *et al*., 2011). Adjacent to this primary forest is the 238,000 ha Ulu Segama-Malua Forest Reserve (US-MFR) containing selectively logged forest, of which 97,000 ha (41%) has undergone a single rotation of timber extraction (once-logged forest) and the remaining area has undergone two rotations of logging (twice-logged forest). The first rotation of timber extraction took place between 1987 and 1991, with commercial stems >0.6 m diameter removed to yield ≈115 m^3 of timber per ha (Fisher *et al*., 2011). Twice-logged locations were re-logged between 2001 and 2007 with the minimum harvested tree diameter reduced to >0.4 m, yielding an additional 15 – 72

m^3 of timber per ha (Edwards *et al*., 2011; Fisher *et al*., 2011). Surrounding the US-MFR are oil palm plantations, with sampling locations restricted to mature plantations (10-15 years old), with a density of ≈100 palms ha^{-1} (Edwards *et al*., 2010).

Dung beetle sampling

Fieldwork was conducted between August and October 2009, and between February and September 2011. In each of our four habitats, four sampling sites were created, widely spaced across the landscape. Sites within a habitat were separated by ≥ 2 km, and distances between sites in different habitats ranged from 1 - 92 km. I used standardised baited pitfall traps to sample dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) across the four habitat types. Within each site two transects were created (separated by 500 - 900 m), and along each transect five pitfall traps were positioned, baited with human dung, at 100 m intervals (total traps = 160; see Edwards *et al*. 2011 for further details), which was sufficient to ensure independence (Larsen & Forsyth, 2005). I left traps for four days and re-baited after 48 hrs, with beetles collected every 24 hrs (Edwards *et al*., 2011). I used reference collections (T. Larsen) housed at the Forest Research Centre, Sandakan, Malaysia and Smithsonian Museum, Washington DC, USA for species determinations.

Data Analysis

Species richness, diversity, evenness and composition

I compared dung-beetle species richness between forested habitats and oil palm using sample-based rarefaction curves with 95% confidence intervals and standardised by the total abundance of individuals in a particular habitat (Gotelli &

Colwell, 2001). To assess the accuracy of the sampling I calculated the average of four commonly used abundance based estimators of species richness (ACE, CHAO1, JACK1 and Bootstrap) using ESTIMATES v. 8.2 (University of Connecticut, Storrs, CT). I measured species diversity using the Shannon-Wiener index and calculated species evenness using Pielou's evenness index in Vegan package (Oksanen *et al*., 2011).

To investigate the change in species composition between habitats, I used a non-metric multidimensional scaling ordination (MDS; Clarke & Warwick, 2001), using the isoMDS function with Bray-Curtis dissimilarity measure within the MASS package (Magurran, 2004). Communities were standardised as a proportion of the total number of individuals on each transect. To test for significant differences in composition, I used a permutational multivariate analysis of variance (ADONIS function in Vegan; Oksanen *et al*., 2011) with 1000 permutations.

Measuring functional diversity

I examined five traits: behavioural guild, diel activity, body size, diet breath and diet preference (Table 3.2). Behavioural guilds were categorised into three main groups: rollers (telecoprid), tunnellers (paracoprid), and dwellers (endocoprid) (for descriptions see Hanski & Cambefort, 1991). Information on species behavioural guilds and diel activity (diurnal or nocturnal foragers) was obtained from the literature (Davis, 1999; Krikken & Huijbregts, 2007; Slade *et al*., 2007; Qie *et al*., 2011; Slade, Mann & Lewis, 2011) and personal observations. I used a dial caliper to measure body length (pygidium to anterior margin of pronotum) and elytra width to the nearest 0.01 mm (n=1 - 27 individuals per species). Body size was then calculated as the product of these two variables (Larsen, Lopera & Forsyth, 2008). I investigated diet breadth with alternative baited traps: rotting vertebrate carrion (n = 19 trap days), rotting fruit (n = 18 trap days) or rotting fungus (n = 16 trap days). Trap design was identical as for traps baited with dung, beetles were collected every 24 hrs but traps were left for 48 hrs. Following Larsen *et al*. (2008) I used the number of different baits a species was attracted to (range = 1 - 4) as a measure of dietary breadth, and the bait a species was most frequently recorded on as a measure of dietary preference, standardised by the number of trap days (abundance/number trap days). Functional traits were not highly correlated (Kendall correlation: $\tau < 0.54$).

Table 3.2: Broad trait categories. Scale indicates the type of trait, Functional Trait shows how the trait is measured, and Functional Importance suggests the impacts of the trait for ecosystem functioning.

Trait category	Scale	Functional Trait	Functional Importance
Behavioural Guild	Categorical	Dweller; Roller; Tunneller	Resource re-location
Activity	Categorical	Diurnal; Nocturnal	Resource opportunity
Body size	Continuous	Length x width	Potential volume of dung buried Burial depth
Diet Breadth	Nominal	Number of bait choices	Type of resource/s used
Diet Preference	Categorical	Most frequented bait type	Resource use and dietary preference

Having obtained trait data I used the formulae of Villéger *et al.* (2008, 2010, 2011) to calculate five complementary measures of functional diversity: (1) functional richness (FRic), which quantifies the volume of functional space that a set of species occupies; (2) functional evenness (FEve), which describes how species' abundances are distributed throughout the occupied functional space; (3) functional divergence (FDiv), which summarises the variation in species abundances with respect to the centre of functional space; (4) functional specialization (FSpe), which describes how functionally unique a community is relative to the regional pool of species, and; (5) functional dissimilarity (FDis), which indicates the overlap of functional space between two or more communities. In these methods, traits act as coordinates in functional space, thus identifying a species' functional niche (Villéger *et al.*, 2008). Traits were given equal weighting and species were weighted by their relative abundance. Because the functional traits were a mixture of variable types, I calculated a distance matrix using the Gower distance measure, before running a principal coordinates analysis (PCoA) to calculate a new trait matrix of transformed coordinates (Villéger *et al*., 2008). Four PCoA axes were used to calculate the functional measures using a multidimensional convex hull to position species in functional trait space.

Functional specialization was measured as the average distance of a set of species from the centre of functional space, relative to the regional pool of all species (Villéger *et al*., 2010). Functional dissimilarity (FDis) was measured as the volume of functional space that two communities share (Villéger *et al*., 2011). When two communities overlap completely, functional dissimilarity is equal to zero, and as the overlap in functional space is reduced so dissimilarity increases towards one.

Observed and expected functional diversity

To assess whether disturbance leads to the selection of more functionally similar species than expected by chance, I compared the standardized effect size (SES) of the four functional diversity metrics (FRic, FEve, FDiv and FSpe) across habitats. I defined SES as (*[observed – mean expected]/standard deviation of expected)*. Expected functional diversity metrics were calculated from 1000 random communities generated from the overall regional species pool. An independent swap algorithm was used to maintain species richness and species frequency occurrence in the random communities (picante package of R) (Gotelli 2000; Kembel *et al*., 2010). I then used one-sample t-tests with $\mu = 0$ to determine whether the SES of each functional diversity metric was significantly different from zero.

Comparing among habitats

To check that the results were independent of spatial scale (Hamer & Hill 2000), each of the species and functional diversity measures were calculated and compared at a large scale (the overall habitat) and a small scale (individual transects). For the latter, I used linear mixed-effect models (lme), including site as a random effect to account for repeated measures. Species abundance was square-root transformed prior to analysis. I also used a Monte-Carlo permutation test for Moran's I statistic (moran.mc within the spdep package), using the model residuals with 1000 repetitions, to test whether or not our transect level results were influenced by spatial autocorrelation. All analyses were run in R v.2.13.2 (R Development Core Team, 2011).

Results

Species richness, diversity and composition

Across the four habitats, 26,285 individual dung beetles were recorded of 65 species. The four common estimators of species richness suggest that I sampled ≥ 89% of species in each of the four habitats (Table 3.3). There was a decrease in the overall species richness, diversity, evenness, and abundance of individuals in oil palm compared to forest, both at the habitat scale (Figure 3.1; Table 3.3) and on individual transects (Table 3.3; lme: species richness, $F_{3,12} = 18.39$, $P < 0.001$; abundance $F_{3,12} = 12.51$, $P < 0.001$; species diversity $F_{3,12} = 16.14$, $P < 0.001$; evenness $F_{3,12} = 5.99$, $P = 0.01$). In contrast, logged forest communities did not differ significantly from those in primary forest with respect to species richness, diversity, evenness or abundance (all $P \geq 0.1$) (Table 3.3).

Table 3.3: Summary of taxonomic species metrics in primary forest, once-logged forest, twice-logged forest and oil palm plantations. Means (+1SE) are at the transect level. Superscripts ($^{a,\,b}$) represent pairwise differences tested at $P \leq 0.05$.

Measure	Primary	Once-logged	Twice-logged	Oil palm
Habitat level:				
Abundance	7885	7386	9231	1783
Sobs ^{c}	52	43	45	25
Sest ^{d}	58	45	48	27
Sobs/Sest ^{e}	0.89	0.96	0.93	0.93
Species diversity^{f}	2.75	2.67	2.50	1.85
Species evenness^{g}	0.69	0.71	0.66	0.58
Transect level:				
Sobs	32 ± 1.10 ^{a}	27 ± 2.50 ^{a}	29 ± 1.00 ^{a}	12 ± 1.30 ^{b}
Species diversity	2.62 ± 0.08 ^{a}	2.39 ± 0.13 ^{a}	2.37 ± 0.05 ^{a}	1.36 ± 0.13 ^{b}
Species evenness	0.76 ± 0.02 ^{a}	0.73 ± 0.26 ^{a}	0.71 ± 0.25 ^{a}	0.57 ± 0.20 ^{b}

^{c} Observed species richness, ^{d} Estimated species richness, ^{e} Proportion of species recorded, ^{f} Measured using Shannon diversity index, ^{g} Measured using Pielou's index

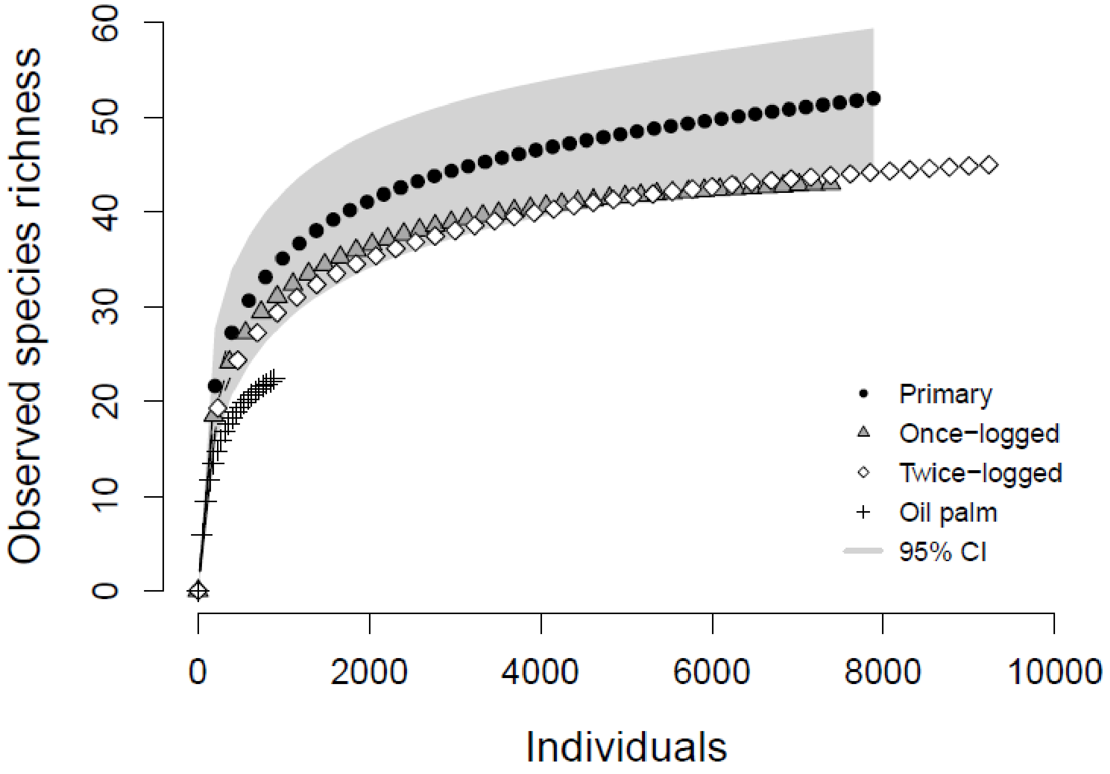

Figure 3.1: Observed species richness, calculated from sample-based rarefaction curves and scaled to show the number of individuals on the x-axis for dung beetles across a disturbance gradient. Grey shading represents 95% CI of primary forest.

Species composition differed significantly between forest and oil palm (Figure 3.2; ADONIS: $r^2 = 0.54$, df = 3, $P = 0.0001$), with the three most abundant species in each forest habitat (*Paragymnopleurus sparsus*, *Sisyphus thoracicus*, and *Onthophagus cervicapra*) replaced in oil palm by three congeneric species (*Onthophagus* sp. *B, O. obscurior, O. rugicollis)*. Additionally, 37 of 52 species recorded in primary forest (71%) did not occur in samples from oil palm, whilst a further nine species occurred in oil palm but not in forest. The species assemblage of primary forest was significantly different from that of both once-logged (r^2 = 0.20, df = 1, *P* = 0.001) and twice-logged forest (r^2 = 0.20, df = 1, *P* = 0.02), but the assemblages in the two logged forest treatments did not differ (r^2 = 0.08, df = 1, *P* = 0.29).

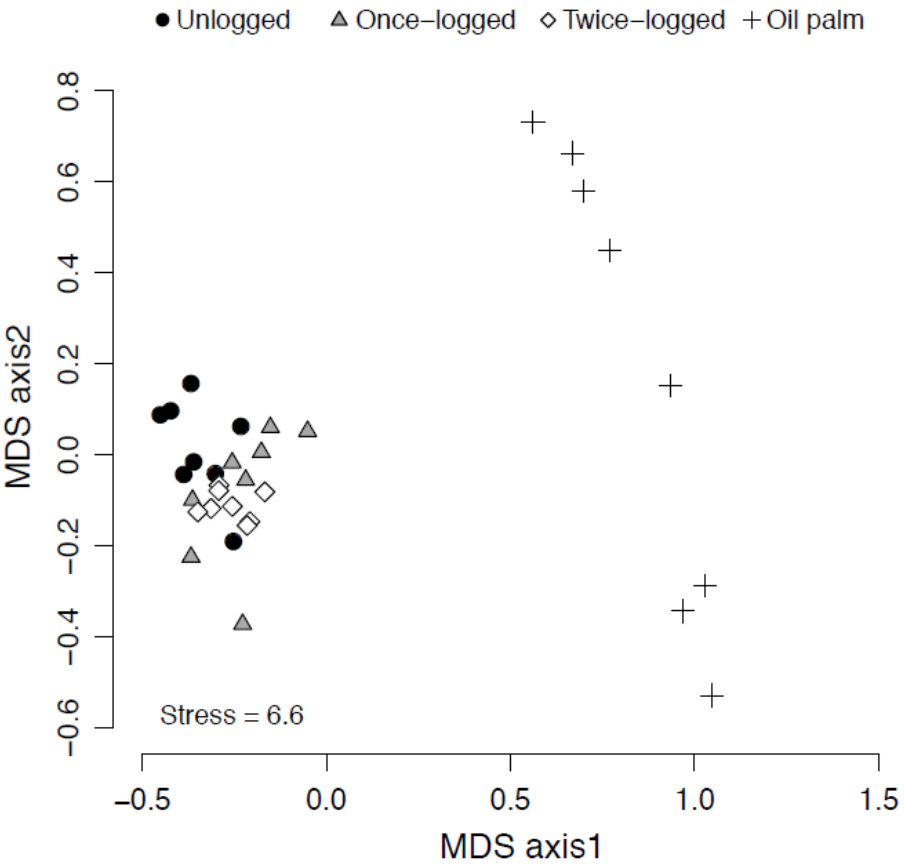

Figure 3.2: Non-metric multidimensional scaling (MDS) ordination of community assemblages between primary forest, once-logged forest, twice-logged forest and oil palm at the transect scale.

Functional diversity

Functional richness, divergence and evenness did not differ among the three forest treatments (Table 3.4; all $P > 0.16$). Functional specialization was significantly higher in primary forest than in once-logged forest (lme [value±SE]: 0.31 ± 0.12, df = 12, $P = 0.03$; overall model $F_{3,12} = 50.11$, $P < 0.001$) but not in twice-logged forest (Table 3.4). However, all forest treatments were more functionally specialised than expected from random community assemblages (Figure 3.3: all $P < 0.01$). Functional dissimilarity was high between forest and oil palm (> 98% non-overlap), but was low among all three of the forest treatments (< 13% non-overlap) (Appendix 3).

Table 3.4: Habitat and transect (mean ± 1SE) scale functional diversity indices in primary forest, once-logged forest, twice-logged forest and oil palm plantations. FRic, FEve and FDiv are bounded between 0-1, and FRic was standardised by a theoretical community of all 65 species in the regional pool. Superscripts ($^{a,\ b,\ c}$) represent pairwise differences at $P \leq 0.05$.

Functional measure	**Primary**	**Once-logged**	**Twice-logged**	**Oil palm**
Habitat level:				
FRic [d]	1.00	0.87	0.99	0.01
FEve [e]	0.28	0.31	0.29	0.45
FDiv [f]	0.74	0.68	0.72	0.54
FSpe [g]	2.17	1.85	2.06	0.87
Transect level:				
FRic	0.58 ± 0.07^{a}	0.42 ± 0.07^{a}	0.48 ± 0.09^{a}	0.35 ± 0.09^{b}
FEve	0.42 ± 0.03	0.39 ± 0.02	0.39 ± 0.02	0.37 ± 0.04
FDiv	0.76 ± 0.03^{a}	0.69 ± 0.03^{ab}	0.73 ± 0.02^{a}	0.58 ± 0.05^{b}
FSpe	2.21 ± 0.08^{a}	1.90 ± 0.10^{b}	2.07 ± 0.04^{ab}	0.87 ± 0.01^{c}

[d] Functional richness, [e] Functional evenness, [f] Functional divergence, [g] Functional specialisation

Functional richness, divergence and specialization were all much lower in oil palm than in any of the three forest habitats, at both spatial scales (Table 3.4; lme; Fric, $F_{3,12} = 11.52$, $P < 0.001$; Fdiv, $F_{3,12} = 3.68$, $P = 0.004$; Fspe, $F_{3,12} = 50.11$, $P < 0.001$). Observed functional richness (one-sample t-test: $t_7 = -7.90$, $P < 0.01$) and functional specialisation ($t_7 = -11.85$, $P < 0.01$) were also significantly lower than expected from the regional species pool in oil palm (Figure 3.3: a, d). Functional evenness, however, was not significantly different in oil palm than elsewhere (Table 3.4; $F_{3,12} = 0.37$, $P = 0.8$). The functional space occupied by dung beetles in oil palm showed major constrictions (Figure 3.4), indicating a marked reduction or complete loss of some functional traits. In particular, telecoprid species (dung-rollers) were abundant in forest but absent from oil palm, the proportion of nocturnal species was lower in oil palm (8%) than in forest (primary = 25%, once-logged = 30%, twice-logged = 22%), and the three most abundant species were smaller in oil palm (body size, mean ± SE: 20.83 ± 3.98 mm) than elsewhere (44.97 ± 26.02 mm). There was no spatial autocorrelation across transects for model residuals of any of the functional diversity metrics (Moran's I test: $P \geq 0.2$ in each case).

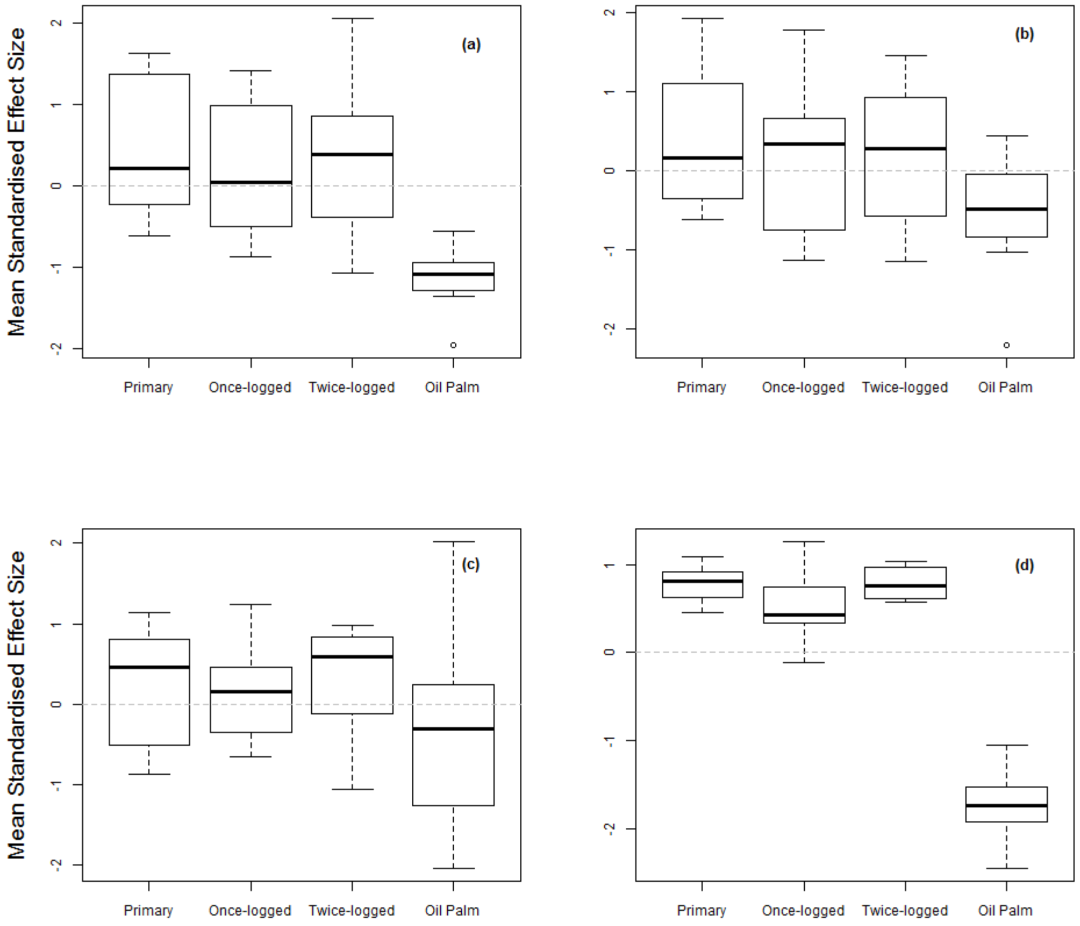

Figure 3.3: The mean standardized effect size (SES) of functional diversity metrics: **(a)** functional richness; **(b)** functional evenness; **(c)** functional divergence; **(d)** functional specialisation in each habitat. *SES = ([Observed – mean Expected]/SD Expected)*. Expected functional metrics are calculated from 1000 randomisations of the regional pool of species in which species frequency occurrence and species richness are maintained. SES > zero indicates greater functional diversity than the regional species pool.

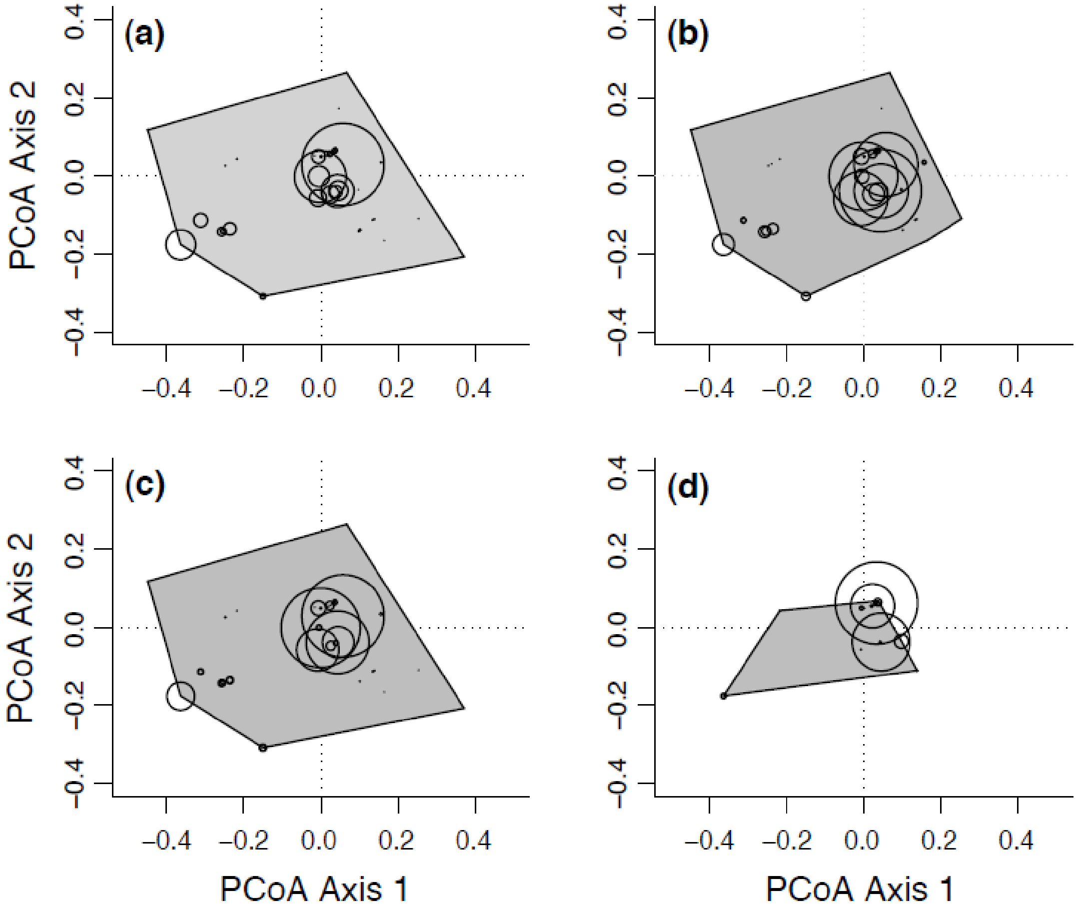

Figure 3.4: Functional richness of dung beetle communities, described as the minimum convex hull enclosing all species of a community and represented as the volume of functional space filled (denoted here by the area of the grey polygon), in (a) primary forest, (b) once-logged forest, (c) twice-logged forest and (d) oil palm. The black circles are proportional to the relative abundance of species in an individual habitat. Functional richness was much lower in oil palm than elsewhere.

Discussion

Primary rainforests in Southeast Asia are highly threatened by rampant logging and the expansion of large-scale oil palm agriculture (Sodhi *et al.* 2010; Wilcove *et al.* 2013), yet this study is among the first assessments of how land-use change affects functional diversity in the region. I found marked reductions in the taxonomic and functional diversity of dung beetles following the conversion of forest to oil palm. In contrast, however, there was very little evidence of any such loss within logged forests, despite significant changes in species composition in comparison to primary forest and even after repeated rotations of logging. These data provide evidence for functional redundancy of dung beetles within primary forest, as was also suggested for birds in Amazonian forests (Hidasi-Neto, Barlow & Cianciaruso, 2012). The results also emphasize the importance of degraded forests as refugia for biodiversity (Edwards *et al*., 2011; Woodcock *et al.*, 2011), and highlight the potential consequences of biodiversity losses for the support of ecosystem processes within agricultural systems.

Dung beetle communities in oil palm are compositionally distinct from those of primary and logged forest (Table 3.3), with a shift of numerically dominant species, a loss of numerous forest specialists and the addition of a much smaller number of new, presumably disturbance-tolerant species (Figures 3.2 and 3.4). These findings support previous work from western Africa that recorded lower species richness and diversity of dung beetles in oil palm plantations compared to logged and primary forests (Davis & Philips, 2005). However, I found significantly lower abundance of dung beetles in oil palm than in forest, whereas the opposite was found in Africa (Davis & Philips, 2005). This variability highlights the need for a more geographically complete understanding of the impacts of oil palm as it expands across tropical regions and replaces both forest and natural grasslands (Koh *et al*., 2011; Garcia-Ulloa *et al*., 2012). Assessing the ability of species to persist within remnant forest patches and disperse across the wider land-use matrix will also be critical to evaluating strategies to enhance biodiversity within agricultural landscapes (Edwards *et al*., 2010).

The dramatic decline that we observed in functional richness following conversion of forest to oil palm indicates that the loss of forest species (Figure 3.4) was not counterbalanced by the addition of new, disturbance-tolerant species that could either fill vacant functional niches or occupy different functional roles (Table 3.4; Figures 3.3: a,d; Figures 3.4; Appendix 3). The community changes in oil palm show strong evidence for environmental filtering (SES < 0, Fig. 3.3: a, d). In particular, the absence of rollers within oil palm may have been due to altered micro-climatic conditions including increased soil temperatures (Lucey & Hill, 2012) decreasing the survival of roller larvae, which typically occur at shallower depths within the soil (Sowig, 1995; Larsen, 2012). I also found a higher proportion of small-bodied species in oil palm, possibly because maximum temperatures in this habitat come closer to exceeding the thermoregulatory tolerance of larger-bodied species, again leading to reduced survival (Nichols *et al*., 2013). In addition, many dietary generalists (feeding on ≥3 bait types) and species feeding on dung plus carrion were absent from oil palm, in contrast to previous work indicating that species with broader diets were less vulnerable to local extinctions (Qie *et al*., 2011).

These results suggest that the transition from primary or logged forest to oil palm results in such environmental stresses, particularly due to micro-climatic changes, that large subsets of forest species are driven to local extinction irrespective of their dietary breadth or specialisation. The absence of rollers within oil palm is particularly important in functional terms, given that they are highly abundant in forests and are behaviorally distinct from tunnelers and dwellers, moving nutrients and seeds away from concentrated dung piles and burying dung balls at shallower depths. In addition, dung removal rate, tunnel depth and volume of dung buried are all positively related to body size, and so the smaller species occurring within oil palm are likely to bury less dung and at lower depths (Slade *et al.*, 2007; Nichols *et al.*, 2008). Changes in the diversity and abundance of nocturnal versus diurnal species may also lead to longer exposure of dung at the surface, resulting in higher gaseous losses of nitrogen (Yamada *et al.*, 2007). Consequently, these results suggest that the functional ability of dung beetles in oil palm is likely to be compromised.

The much lower taxonomic and functional diversity of dung beetles in oil palm also highlights the potential losses that could arise from further degradation of logged forests, for instance through wildfires, which can also act as strong environmental filters and alter microclimatic conditions within the forest (Peres, Barlow & Haugaasen, 2003; Silk and Van Balen, 2006; Lindenmayer *et al.*, 2009; Brodie, Post & Laurance, 2012). Measuring additional functional traits could help in predicting the longer-term impacts of logging and forest conversion. For instance, measures of endothermy and fecundity could aid our understanding of the impacts of microclimatic changes and the likelihood of extinction lags caused by disturbance.

In conclusion, this study provides new data on the impacts of land-use change on tropical dung beetles. Contrary to our expectations, even repeated timber harvests did not simplify the functional structure of dung beetle assemblages in Bornean rainforests, despite significant changes in species composition, highlighting the importance of protecting these degraded, logged-over forests. However, conversion of forests to oil palm greatly reduced both species and functional diversity. I suggest ecosystem functioning will be negatively impacted in oil palm, but quantifying the precise consequences across all habitats remains a major knowledge gap. For instance, the retention of forest patches and riparian strips within oil palm estates could support ecosystem services such as nutrient recycling within plantations, but data are needed to address this issue. These results support previous findings that traditional metrics such as species richness and composition can hide important information about the impacts of land-use change on species traits and functional ecology. The two approaches provide different but complementary mechanisms for understanding human impacts on biodiversity, which can contribute to future conservation and agricultural management decisions (Loyola *et al*., 2008; Vandewalle *et al*., 2010; Hidasi-Neto *et al*., 2012).

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Chapter 4: Species co-occurrence with tropical land-use change

Abstract

Species co-occurrence is a complex and debatable area of ecology, various assembly filters can be thought of to drive the structure of communities based on random (random dispersal) or non-random (niche-based) processes. Species possess a unique set of functional traits which allow them to (or not to) tolerate and be competitively successful in relation to certain abiotic and biotic influences. The way in which hundreds of species co-exist in the tropics is of particular interest, and with increasing pressure for land and resources, rainforest disturbance and conversion creates further complexity to how species react, adapt and thus co-exist in these new environments.

Here I apply complementary methods to understand and infer the dominant processes and mechanisms behind the co-occurrence of tropical species. I investigate three taxonomic groups – dung beetles, birds and ants, across a disturbance gradient of primary rainforest, selectively logged rainforest and oil palm plantations with consideration of two spatial scales (point and transect) in order to - 1) attribute co-occurrence patterns to random or non-random processes by assessing the C-score index, 2) assess pairwise species associations across communities using a probabilistic model to suggest dominant assembly processes, and 3) to infer the relative contribution of habitat filtering, dispersal abilities and limiting similarity towards species co-occurrence by considering species functional traits using a STEPCAM model.

Species co-occurred mostly by random processes, however those communities that indicated non-random processes, primary forest birds and dung beetles, as well as birds in oil palm, co-occurred less than expected (segregated). Dominant processes varied across taxonomic groups, habitats and at the observed scale. Dung beetle co-

occurrence patterns were principally explained by dispersal assembly, and we found limited evidence of habitat filtering, supporting a non-niche based filter hypothesis of community assembly. Changes in assembly patterns after selective logging were in absence of minimal shifts in community metrics indicating the potential hidden effects of forest disturbance when species interactions are not considered.

Introduction

Species' co-occurrences are influenced by a number of factors which can be considered as biotic (i.e. species interactions) or abiotic (i.e. climate, resource availability or landscape configuration) filters to community assembly (Diamond 1975). Additionally, species possess a particular set of functional traits which allow them to tolerate, or not, specific abiotic filters and ensures they are, or not, competitively successful in relation to other species (Petchey *et al.* 2007; Van der Plas, Anderson & Olff 2012). Consequently, trait distributions and patterns of co-occurrence are inherently linked, for example abiotic filters are suggested to restrict the range of traits while biotic filters can lead to more distinct trait ranges (Van der Plas, Anderson & Olff 2012). Indeed, in an environment dominant by fire those species with adaptable traits will successfully survive, thus narrowing the range of traits, while species with similar body sizes are thought to co-occur less because they would utilise similar resources, thus leading to a broad range of body sizes in a particular community (Dayan & Simberloff 2005; Fayle, Turner & Foster 2013; Smith *et al.* 2013).

Broadly assembly filters can be grouped as non-random or random mechanisms, which form the framework of four hypotheses for explaining species co-occurrences and distributions (Mattsson *et al.* 2013; van der Plas *et al.* 2014; Royan *et al.* 2016). Non-random community assembly is driven by niche-based processes, where communities can exhibit significant patterns of species segregation (less co-occurrence than expected) or aggregation (more co-occurrence than expected), typically driven by a species' competitive ability or environmental preferences, respectively (Gravel *et al.* 2006; Leibold & McPeek 2006; Kraft *et al.* 2015) leading to a non-random distribution of functional traits. Species co-occurrences could therefore be seen to be driven by i) environmental filtering, where the heterogeneity of the landscape predominately influences the assembly of species; ii) interspecific interactions, where species are influenced predominately by heterospecifics; or iii) the combined effect of environmental variation and the interaction with heterospecifices. Alternatively, species co-occurrences are, iv) randomly assembled, based upon neutral theory (random demographic processes), such that competition is assumed strong but uniform (i.e. intraspecific equals interspecific), species have no environmental preferences (Hubbell 2005) and functional traits are randomly distributed. Determining the dominant processes driving community assembly, specifically the relative importance of non-random versus random mechanisms (Gotelli 2000), and how trait and environmental variation influence assembly processes (Pollock, Morris & Vesk 2012; Van der Plas, Anderson & Olff 2012; van der Plas *et al.* 2014) are important unresolved questions in ecology.

Anthropogenic land-use change continues to occur at an alarming rate (Gibbs *et al.* 2010; FAO 2011; Hansen *et al.* 2013; Newbold *et al.* 2015), and such disturbances to natural ecosystems have a relatively unknown effect on community assembly. Disturbance introduces further complexity to community structure because an individual species' presence, absence or relative abundance could shift with changing resources and habitat modifications, and in turn the interaction with other species could be altered, via species colonisation (including invasive species) or shifts in dominance (Sanders *et al.* 2003; Morris 2010; Blois *et al.* 2013; Bar-Massada 2015), and consequently a change in the distribution of functional traits (Edwards *et al.* 2013b; Edwards *et al.* 2014b; Senior *et al.* 2013). Evidence suggests that disturbance can alter assembly mechanisms (Sara, Bellia & Milazzo 2006; Fayle, Turner & Foster 2013; Larsen & Ormerod 2014). For example, in less disturbed habitats, bird (mature woodland) and leaf litter ant (primary rainforest) communities indicate patterns of species segregation compared to a random community assembly in more disturbed habitats (Sara, Bellia & Milazzo 2006; Fayle, Turner & Foster 2013), however canopy ants showed opposing patterns of community assembly across the same habitat disturbance gradient (Fayle, Turner & Foster 2013). Furthermore, interaction networks, which underpin the assembly and structure of ecological communities, with critical links to the stability and function of functional processes and thus ecosystem services can also be affected by disturbance (Tylianakis *et al.* 2008; Morris 2010; Schleuning *et al.* 2011; Edwards *et al.* 2013a; Woodcock *et al.* 2013; Weiner *et al.* 2014). For examples, liana-tree interactions in selectively logged forest had heavier liana loads, which combined with a preference for slower growing tree species as hosts, likely impacts future forest structure and timber yields (Magrach *et al.* 2016), while hymenoptera-parasitoid food webs in intensive agriculture had increased parasitoid diversity and higher parasitism rates, with potential negative consequences for pollination and biological control (Tylianakis, Tscharntke & Lewis 2007).

Habitat modification via selective logging and forest conversion to agriculture is extensive across the tropics (Asner *et al.* 2009; Gibbs *et al.* 2010; Hansen *et al.* 2013). Research on the impacts of tropical land-use change on biodiversity has focused extensively on how communities alter in terms of species richness, composition, and functioning (e.g., Barlow *et al.* 2007; Gibson *et al.* 2011; Edwards *et al.* 2014b; Edwards *et al.* 2014a), revealing much retention of conservation values within logged forest and much losses following forest conversion. To date, however, few studies have explored patterns of co-occurrence and community assembly with tropical land-use change. As with assessments of taxonomic diversity (Hill & Hamer

2004; Berry *et al.* 2008; Socolar *et al.* 2016), the spatial scale at which the impacts of land-use change are assessed is essential when considering co-occurrence patterns (Weiher *et al.* 2011; Kissling *et al.* 2012), with recent studies revealing that assembly processes can alter with the observed scale (Sanders *et al.* 2007; Ellwood, Manica & Foster 2009; Olivier & van Aarde 2014; Ulrich *et al.* 2016; though see Larsen & Ormerod 2014).

Here, I present the first study to compare co-occurrence patterns across multiple taxa at two spatial scales using the same land-use gradient. I believe this to be critical in identifying the likely dominant processes determining community assembly across a gradient of land-use change, providing important understanding of how communities behave under disturbance scenarios. I do so using field data of dung beetle, bird and ant communities from Sabah, Malaysian Borneo across an anthropogenic disturbance gradient of primary forest, selectively logged forest and oil palm plantations. I use these data to answer three key questions: 1) Are species co-occurrences attributed to random or non-random (aggregation/segregation) processes, and how does this vary across habitats and with scale?; 2) Considering pairwise species associations, how are species composition structured between habitats?; and 3) what is the relative contribution of habitat filtering, dispersal abilities and limiting similarity to community structure by considering species functional traits?

Methods

Study location

This study was conducted within the one million ha Yayasan Sabah (YS) logging concession in eastern Sabah, Malaysian Borneo (4^{o} 58′ N, 117 ^{o} 48′ E). The majority of the concession (~90%) has been selectively logged, which took place primarily between 1970's-2008 across two rotations of logging (for further details see Fisher *et al.* 2011; Reynolds *et al.* 2011). Within the YS concession are ~130,000 ha of primary forest (Danum Valley Conservation Area, Palum Tambun Watershed Reserve, Maliau Basin, Imbak canyon and adjacent Virgin Jungle Reserves), and adjacent are vast oil palm plantations, over 15,000 km^2 land coverage in Sabah (Reynolds *et al.* 2011).

Sampling

Fieldwork took place from July to October 2007, May to August 2008, May to October 2009 and February to September 2011 corresponding with the drier season each year. Across the study area, 17 sites were created spanning primary forest, once-logged forest, twice-logged forest and oil palm (Figure 4.1), which were then sampled for dung beetles, birds, and ants (data from Edwards *et al.* 2011, Edwards *et al.* 2014a; Woodcock *et al.* 2011). Sampling took place across a subset of these sites for different taxa ($n_{\text{Dung beetles}}$=16, n_{Birds}=16, n_{Ants}=11), with sampling effort equalised across habitat types for dung beetles and birds but not for ants (sampled at three sites in each forest habitat and at two sites in oil palm). Sampling within oil palm was restricted to mature plantations (10-15 years old) (Edwards *et al.* 2010; Edwards *et al.* 2014b). The environmental conditions across sampling years remained similar (i.e. no mast-fruiting, droughts or floods).

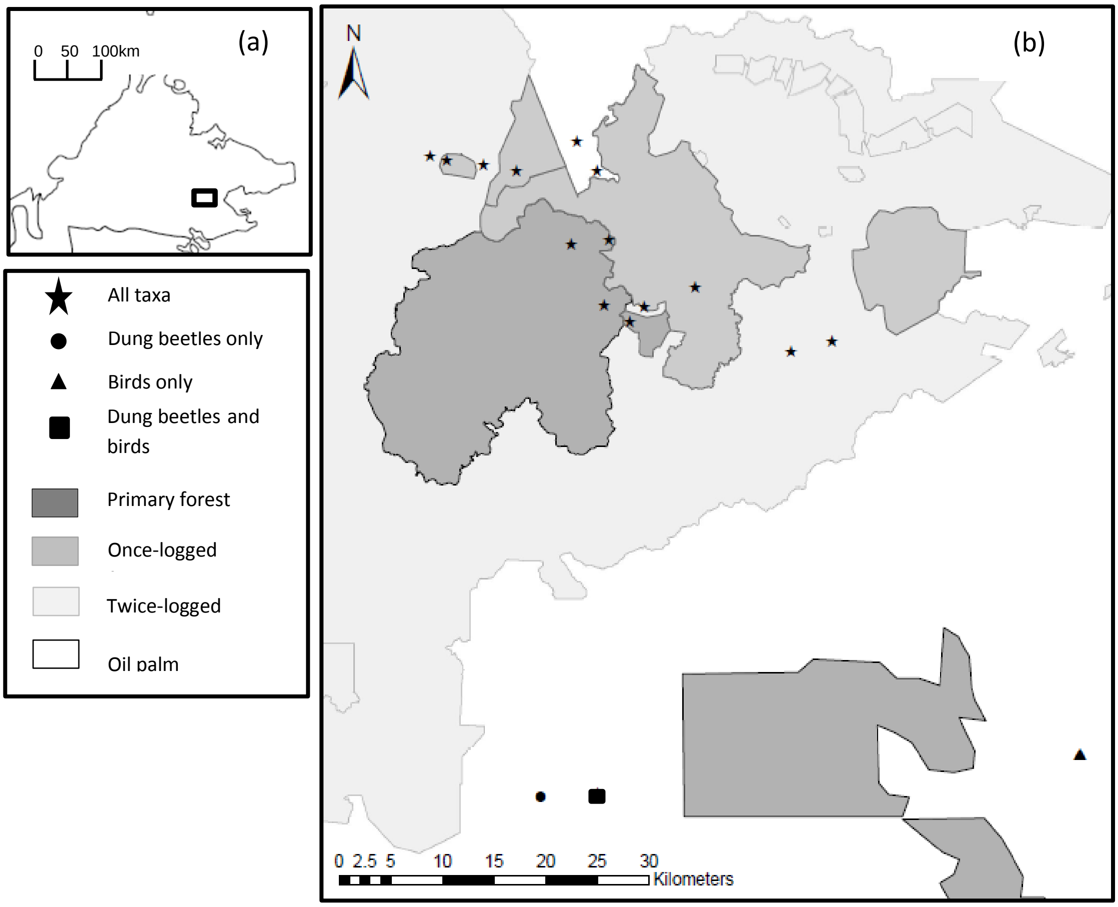

Figure 4.1: (a) A map of Sabah, Malaysian Borneo. The box outlines the study area. (b) A map of the study area. The dark grey solid area represents primary rainforest, mid-grey solid area represents once-logged forest, light-grey solid area represents twice-logged forest, and the adjacent white area represents oil palm plantations. The symbols on the map identify the 17 sampling sites; solid stars represent sites where dung beetles, birds and ants were sampled (n=15); solid circles are where dung beetles were sampled only (n=1); and solid triangles are where birds were sampled only (n=1). In all cases, the mid-point of the two transects, at a given site, is represented on the map.

Dung beetle sampling

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) were sampled using standardised baited pitfall traps across all habitats (n=160; following Edwards *et al.* 2011; Edwards *et al.* 2014b). Each site consisted of two transects (minimum of 500 m apart), with five pitfall traps each spaced 100 m apart set on each transect. A single trap, baited with human dung, was used in each location, set for four days and re-baited after 48 hrs, with dung beetles collected every 24 hrs. Individuals were identified to species level using reference collections (T. Larsen) housed at the Forest Research Centre, Sandakan, Malaysia and Smithsonian Museum, Washington DC, USA.

Avifaunal sampling

Unlimited-radius point counts were used to sample birds across all habitats (n=192; following Edwards *et al.* 2011). At each site, 12 point count stations each 250 m apart were located along a line transect, with each station visited for 15 min on three consecutive days. All birds which were heard or seen were recorded.

Ant sampling

Ants were sampled using a Winkler trap methodology (following Woodcock *et al.* 2011). At each site, two 150 m line transects were established, a minimum of 500 m apart, along which seven census points separated by 25 m were sampled on alternate sides of the transect (n=154). Leaf litter and loose top soil was collected from four 0.25 m^2 quadrats at each census point; these materials were then sieved, placed in mesh bags within the Winkler traps, and left for four days. Ants were then identified to genus, and sorted to morphospecies using online keys (Fayle 2011) and reference collections at the Natural History Museum (London) and Universiti Malaysia Sabah (Kota Kinabalu). Abundance estimates are not reliable due to the possible presence of a nest, therefore species were scored as present or absent for each census point.

Data Analysis

Community co-occurrence

To test for the dominant process in community assembly, I used the C-score index (*CS*), defined as the average number of checkerboards between all possible species pairs in a community (Stone & Roberts 1990). To assess variation in co-occurrence patterns with spatial scale, analyses were conducted at the transect and point (i.e., individual pitfall trap, point station or quadrat) scales across all habitats for each taxonomic group. Null models were run with a fixed-fixed algorithm (SIM9, (Gotelli 2000), which has low Type I and II errors, is not prone to false positive results when calculating the C-score, and is appropriate in the study sites where habitat quality is highly heterogeneous (Gotelli 2000). I used 125,000 randomisations, with an independent swap method, to minimise Type I errors, which increase with the number of sites and species (Fayle & Manica 2010). The number of randomisations was determined by repeat analysis of the largest matrix until the p-value was maintained. To allow comparisons across habitats, *CS* results were standardised using the standard effect size (SES) =$(\frac{Observed\ CS - mean\ simulated\ CS}{SD\ simulated\ CS})$. A SES value ≥ 1.98 indicates segregation within a community (i.e. fewer pairwise co-occurrences than expected), while a value ≤ -1.98 indicates aggregation within a community (i.e. more pairwise co-occurrences than expected) and a value between 1.98 and -1.98 suggests a random community assembly (Gotelli 2000; Sanders *et al.* 2003).

Species pairwise associations

Pairwise species associations were evaluated at two scales, transect and point, using a probabilistic model to calculate the observed and expected co-occurrence between species pairs within a habitat type (Veech 2013; Griffith, Veech & Marsh 2016). The number of species pairs that are positive, negative or random (non-significant) are calculated, along with associated probabilities that a given species pair will co-occur more (positive) or less (negative) than is observed indicating significant positive or negative community assembly patterns ($P < 0.05$) (Griffith, Veech & Marsh 2016). All species were included in the initial analysis, however those species pairs with expected low detection power (see Appendix 4 for methodological details) were removed before the false discovery rate (FDR) was used to correct for false positives as a result of the multiple tests for each individual species (using p.adjust).

Functional trait relations

I assess the effect of functional traits on co-occurrence patterns using an approximate Bayesian computation (STEPCAM) model which infers the relative contribution of habitat filtering, dispersal abilities and limiting similarity (Luskin & Van der Plas 2016). The STEPCAM model uses a stepwise removal procedure, where by at each step a species is removed from the regional pool of species until the species richness of the 'site' is reached, I also used a final acceptance rate of 0.0001 for each of the models. Species are removed based on 1) habitat filtering to indicate niche-based filters, 2) dispersal abilities to indicate non-niche based filters and 3) limiting similarity to indicate species with shared resources (van der Plas *et al.* 2014). A filtering step is organised by the removal of species which have the greatest Euclidean trait distance from the trait centre (optima). Under a dispersal event the likelihood of a species deletion is inversely proportional to the relative frequency of that species in the regional pool of species (greater frequency in the regional pool means a species is less likely to be removed). During a limiting similarity step the distances between species pairs in multidimensional space are identified, and species most similar to its neighbour are removed (see van der Plas *et al.* 2014 for further details).

Functional traits were only assessed for dung beetles across a subset of transects (primary=8, once-logged=7, twice-logged=8, oil palm = 5) due to statistical programming issues; I assessed the mean body size, guild, and diel activity (Table 4.1). Analyses were performed in R v.3.1.1 (R Development Core Team, 2014) using EcoSimR (Gotelli, Hart & Ellison 2015), cooccur (Griffith, Veech & Marsh 2016) and STEPCAM (Janzen & Van der Plas 2016).

Table 4.1: Description of dung beetle functional traits used in the STEPCAM analyses.

Taxa	Trait	Measure	Description
Dung beetles	Body size	Continuous	-
	Guild	Factor	Roller, Tunneller, Dweller
	Diel activity	Factor	Diurnal, Nocturnal

Results

Community co-occurrence

Overall patterns of community-wide C-scores indicated random community assembly in most incidences across taxonomic groups and habitats, with those significant non-random associations all indicating species segregation (fewer pairwise species co-occurrences than expected by chance; SES >2) irrespective of spatial scale (Figure 4.2).

Dung beetle and ant communities exhibited random assembly structure in primary forest at both scales, while bird communities indicated random patterns at the transect scale but showed significant species segregation at the point scale ($P < 0.01$; Figure 4.2). Logging primarily resulted in random community assembly across all taxonomic groups (Figure 4.2), but notably occurred in bird communities that had indicated significant non-random assembly in primary forest (Figure 4.2b). Contrastingly, ant communities showed a significant shift to species segregation at the transect scale ($P = 0.009$; Figure 4.2c). The overall co-occurrence structure remained the most stable within twice logged forest (Figure 4.2). Dung beetle and bird community structure was significantly segregated following forest conversion to oil palm ($P < 0.004$ and $P < 0.01$ respectively; Figure 4.2a,b). However, ant communities remained randomly structured with little change from twice-logged forest (Figure 4.2c).

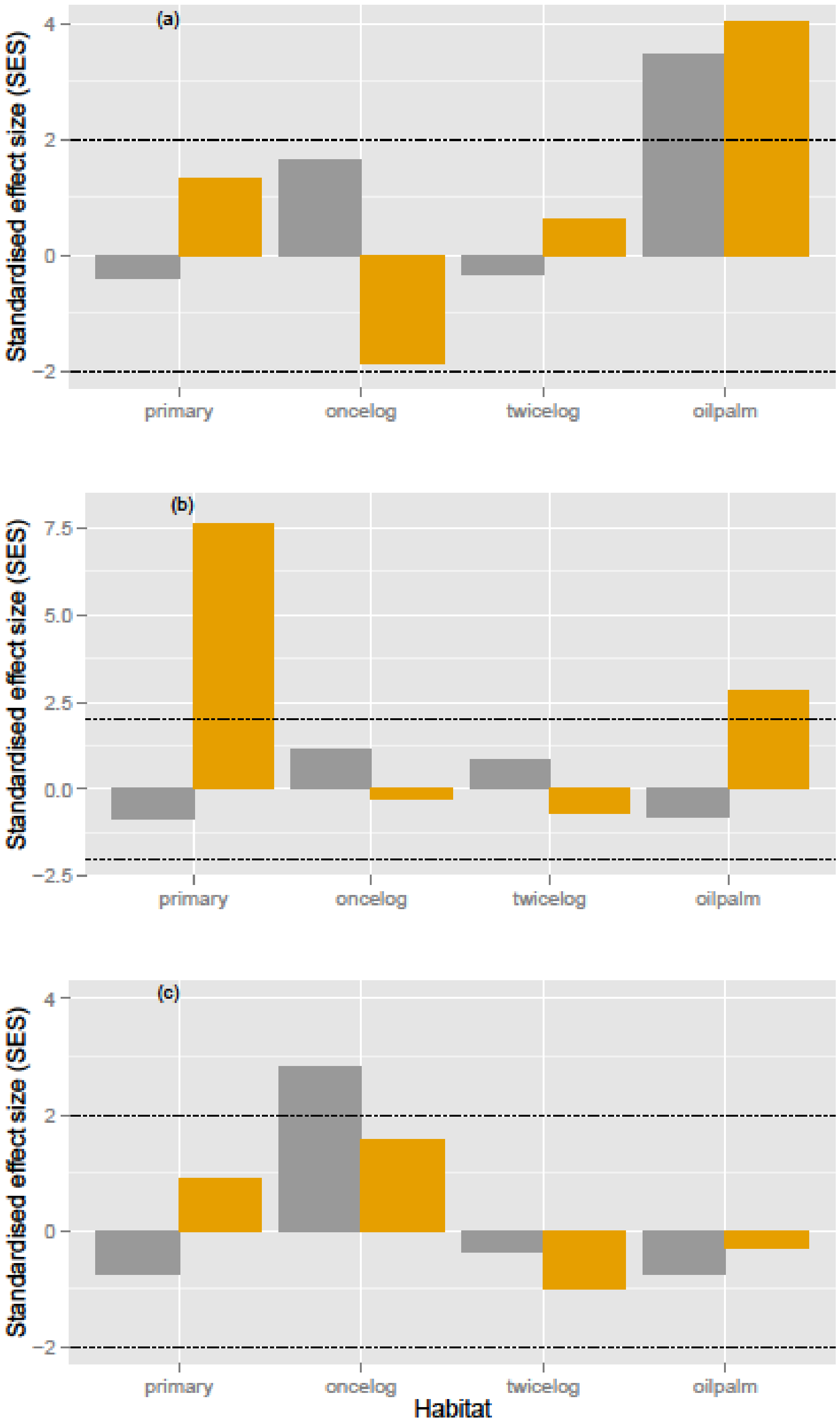

Figure 4.2: Variations in community co-occurrence using the standard effect size (SES) of C-scores across four habitat types and two sampling scales in Malaysian Borneo for, (a) dung beetles, (b) birds and (c) ants. Sampling scales are represented by grey columns for transect level analyses and orange columns for point level analyses. Dashed lines represent the significant distinction between random (>-1.98 SES <1.98) and non-random community assembly (segregation SES ≥1.98, aggregation SES ≤-1.98).

The scale at which overall community co-occurrences were investigated indicated variation in the SES, in some incidences resulting in a shift from non-random to random community co-occurrence, or vice versa. Although dung beetle communities were observed to be randomly structured in once-logged forest at the point and transect scale, there was opposing trends towards segregation and aggregation respectively (Figure 4.2a). At the point scale, the significant species segregation in primary forest and oil palm for birds was not translated at the transect scale (Figure 4.2b). Ant communities remained the most stable across sampling scales (Figure 4.2c).

Species pairwise associations

Analysis of species pairs revealed that species composition at the point scale, across all three taxonomic groups, followed random patterns of community assembly (90-99 % pairs), while 1-10% had positive associations (aggregated), and 0-3% had negative associations (segregation) (Figure 4.3). The proportion of aggregated and segregated dung beetle and bird species pairs remained constant across primary forest, while ant communities had a higher proportion of aggregated pairs. Similarly, in disturbed habitats (logged forests and oil palm) dung beetle, bird and ant communities showed an increase in aggregated species pairs. These species pairs however, were not significant once a false discovery rate was applied. The transect scale mirrored similar results with the exception of bird communities which had no non-random pairs.

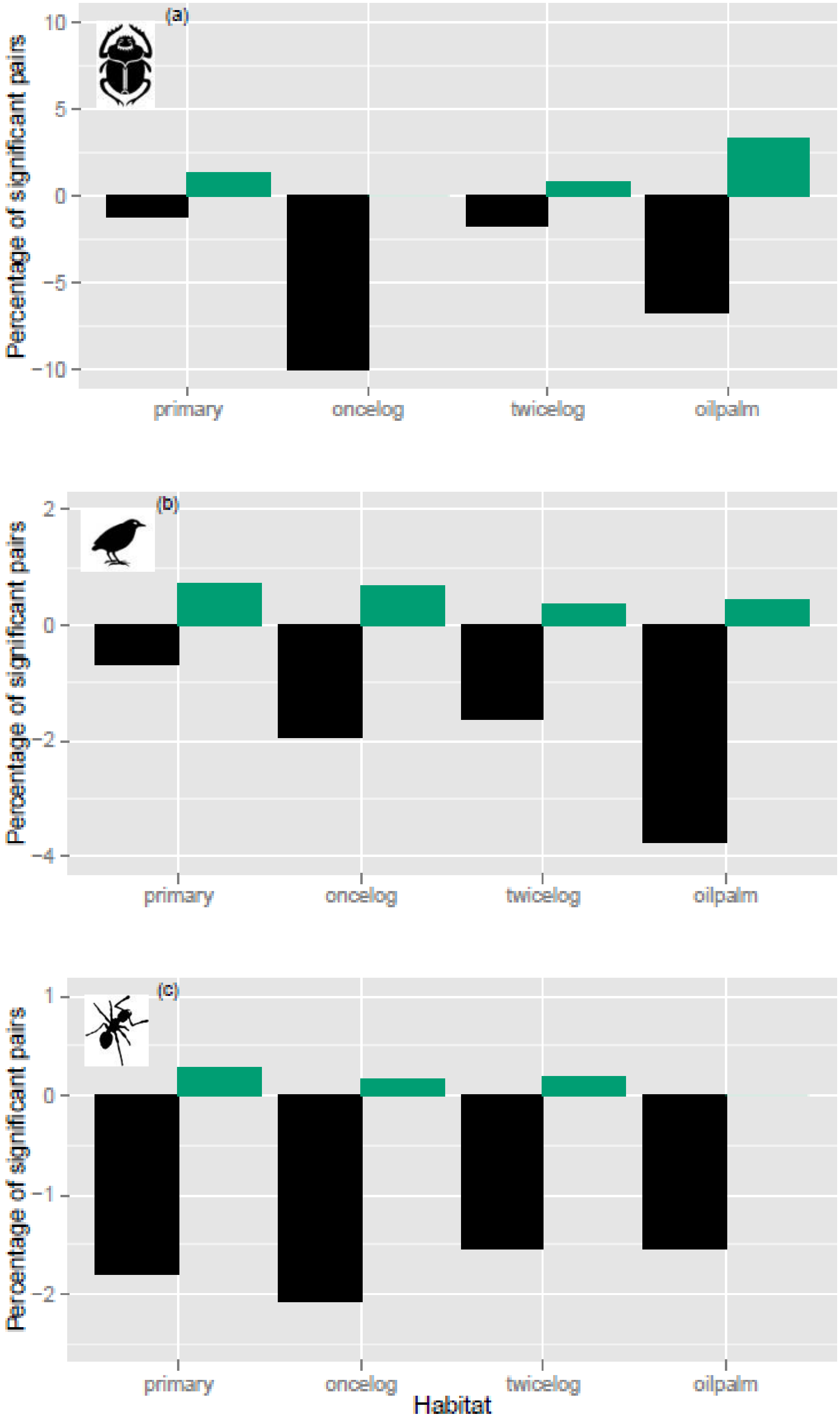

Figure 4.3: Pairwise species associations across three taxonomic groups, a) dung beetles, b) birds, and c) ants, and four habitats in Malaysian Borneo at the point scale, showing the percentage of species pairs classified as exhibiting positive or negative patterns of association. Green bars indicate positive associations suggesting segregation, and black bars indicate negative associations suggesting aggregation. Classifications are based on a probabilistic model of species co-occurrences.

Functional trait relations

Using the STEPCAM approach I accessed the relative contribution of community assembly processes in shaping forest and oil palm dung beetle communities. When averaging the distributions over transects, for each habitat, all communities were shown to have a high relative importance of dispersal assembly (means 41 - 49%), followed by limiting similarity (39 – 22%), and habitat filtering (20 – 29%) (Figure 4.4). Variation across transects was apparent (Figure 4.4). Primary and logged forests had a similar average contribution of assembly processes across transects, dispersal assembly had a strong influence in over half of transects, often combined with limiting similarity, while habitat filtering had minimal contribution in these forest habitats (Figures 4.5a-c). Habitat filtering became more important in oil palm communities, though communities were still primarily influenced by dispersal assembly (Figures 4.5d).

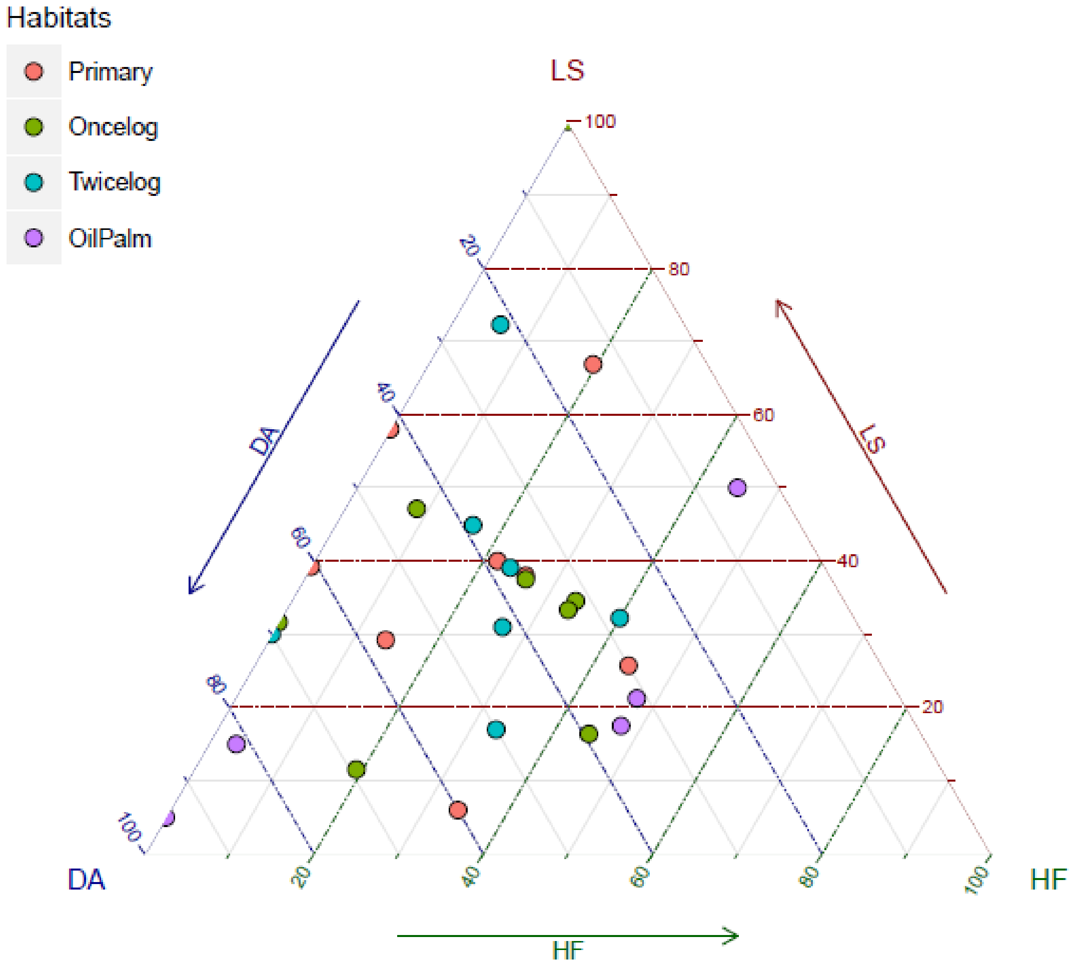

Figure 4.4: Ternary plot of the average STEPCAM models describing community assembly as the sum of dispersal assembly (DA), habitat filtering (HF), and limiting similarity (LS) in dung beetle communities, in Sabah, Malaysian Borneo. The dots represent individual transects grouped by habitat type; red represents primary forest, green represents once-logged forest, blue represents twice-logged forest and purple represents oil palm. Axis numbers are percentages, measuring the extent community assembly is driven by each processes.

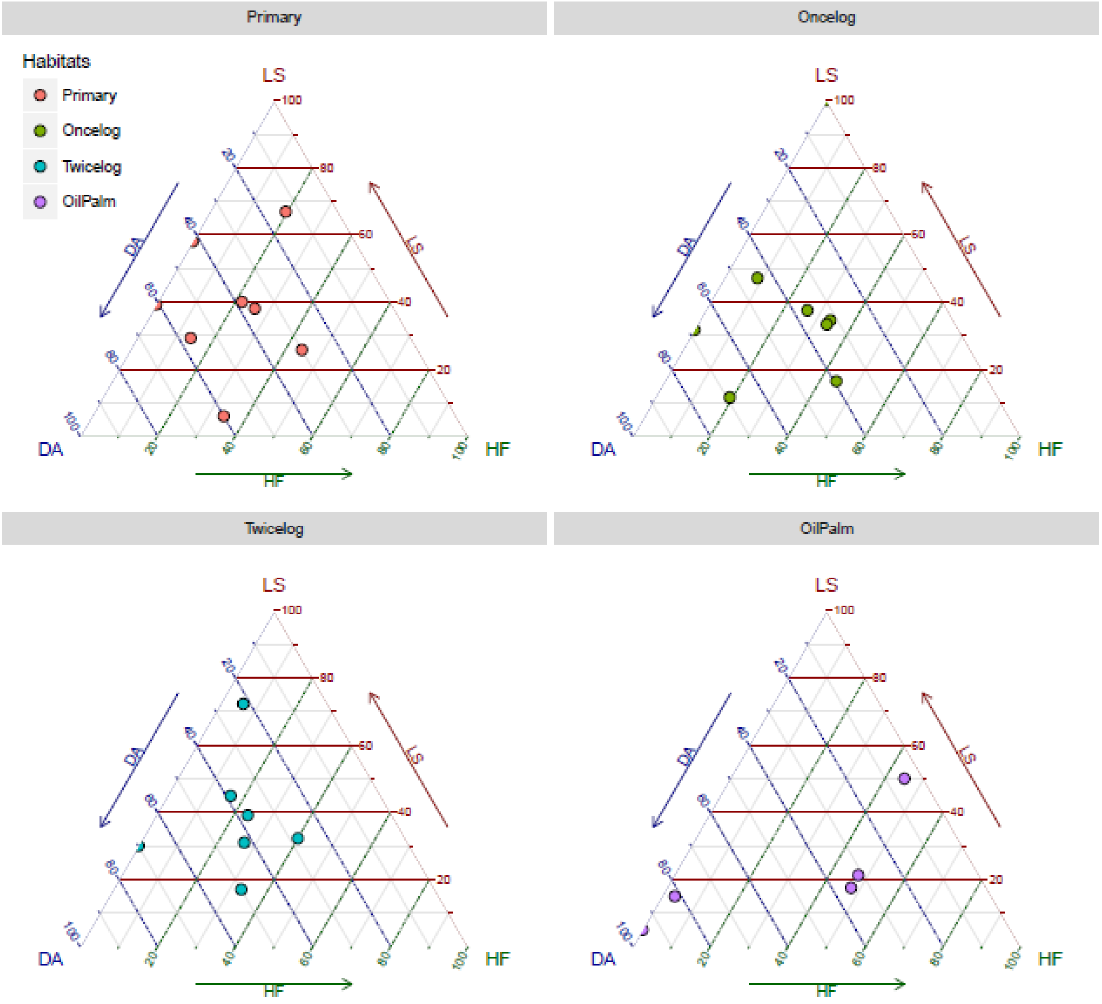

Figure 4.5: Ternary plot of the average STEPCAM models describing community assembly as the sum of dispersal assembly (DA), habitat filtering (HF), and limiting similarity (LS) in dung beetle communities, in Sabah, Malaysian Borneo. The dots represent individual transects, across habitats: primary forest, once-logged forest, twice-logged forest and oil palm. Axis numbers are percentages, measuring the extent community assembly is driven by each processes.

Discussion

I present the first study to compare species co-occurrence patterns across a tropical land-use gradient using multiple taxa (three key taxonomic indicator groups) and spatial scales. Overall community co-occurrences were mostly driven by random assembly processes across the four habitat types and three taxonomic groups (Figure 4.2). Those communities that indicated non-random patterns were more segregated than expected by chance, supporting previous work showing significant segregation in most plant and animal communities (Gotelli & McCabe 2002), but co-occurrence patterns did not remain stable with spatial scale (Figure 4.2). Similarly investigating pairwise species co-occurrence indicated primarily random associations with only a very small percentage of species pairs indicating positive or negative associations (Figure 4.3), thus suggesting species interactions are of primary importance relative to habitat variation (Royan *et al.* 2016). Likewise, dispersal assembly processes were the major relative contributor to dung beetle community assembly supporting a non-niche based filter hypothesis, however limiting similarity was influential across forest habitats, while habitat filtering became more important in oil palm communities (Figure 4.5). Patterns across the land-use gradient clearly indicate that anthropogenic disturbance disrupts assembly processes, principally in dung beetle and bird communities, and our study thus suggests that the assembly structure of tropical communities is highly variable, and requires greater investigation to gain a complete understanding.

Primary forest communities showed patterns of random assembly with the exception of primary forest bird communities (Figure 4.2b), which showed significant species segregation at the point scale. This mirrors previous work of bird communities in mature European woodlands which indicated significant species segregation compared to communities in more disturbed areas (Sara, Bellia & Milazzo 2006). Although segregation is principally associated with increased competition, these patterns could also be the result of environmental variation or phylogenetic processes (Cardillo & Meijaard 2010). The variation in the C-score between spatial scales (Figure 4.2), most notably for primary forest birds, could partially be the result of sampling effort. At the point scale, there are many more ‘micro communities’ sampled compared to the overall transect scale and thus segregation (fewer co-occurrences than expected) might be observed more frequently as fewer ‘point communities’ share species A and B, yet these are still common species, which at the transect level would be seen to co-occur. However, the shift seen in once-logged forest for dung beetles (towards aggregation) indicates this is not necessarily the case and perhaps instead is the result of the attractant trapping methods used, which could have overestimated the community due to an unknown lack of resources at the specific time of sampling in that area. Patterns across scales were not consistently higher or lower between scales, and were inconsistent across taxonomic groups and habitats suggesting there were other influential predictors.

The random assembly of forest dung beetles and ants does partly mirror previous findings of invertebrate co-occurrence (Gotelli & McCabe 2002; Sanders *et al.* 2007) and supports the idea of neutral theory in tropical forests (Hubbell 2005). Furthermore, co-occurrence patterns in diverse ant communities have been suggested to be influenced by non-niche based processes which affect the competitive abilities and dominance of species, such as a strong founder effect which relates to which ant species arrives at a resource first, or an evolutionary trade-off between efficiency in defences rather than resource acquisition (or vice versa) (Andersen 2008). Dung beetles and ants have strong overlaps in resource use, dung beetles predominately utilise dung (60% species solely utilise dung, Edwards *et al.* 2014b) by two key processes (rollers and tunnellers) (Hanski & Cambefort 1991) while ants are principally generalist predators and scavengers (Andersen 2008), thus it can be considered that there is a limit to how niche differentiation can explain high levels of species co-occurrence (Andersen 2008). The dominance of dispersal assembly processes for dung beetle communities (Figures 4.4 and 4.5) supports this idea, where dung is more plentiful competition can be expected to be minimal, and thus co-occurrence is more likely due to random demographic processes such as dispersal abilities. Indeed, forest habitats support large mammal populations which are minimally affected by selective logging (Berry *et al.* 2010) and dung availability is maintained. Limiting similarity however had a strong influence in forest dung beetle communities indicating niche based processes centred on shared resources (van der Plas *et al.* 2014).

Selective logging was predominately associated with random patterns of species co-occurrences, but dung beetle and ant communities in once-logged forest showed variability (Figures 4.2a,c), however this was not supported by the STEPCAM functional trait approach for dung beetles (Figure 4.5b). Dung beetle communities had strong patterns towards non-random assembly at both scales (Figure 4.2a), while at the transect level, ant communities exhibited significant species segregation (Figure 4.2c). Given findings in other habitats it is unclear why dung beetles and ants exhibited different species assembly structure in once-logged forest, and a more targeted investigation would be needed to understand this. The strong pattern of species segregation seen in primary forest bird communities was not observed in logged forests (Figure 4.2b), possibly driven by changes in habitat structure and community composition. Critically, these co-occurrence changes between primary and logged forests were observed independently of dramatic changes in species richness, diversity or abundance (Edwards *et al.* 2011; Woodcock *et al.* 2011; Edwards *et al.* 2014a), which highlights the potential for underestimation of the impact of anthropogenic disturbance on community dynamics and associated ecosystem processes by solely considering changes in taxonomic richness (Cardinale, Palmer & Collins 2002).

In oil palm the shift to significant species segregation and the increasing contribution of habitat filtering in community assembly suggests competitive, niche-based processes are dominating in dung beetle and bird communities (Figures 4.2a,b; 4.4). Oil palm plantations are monotypic and there is a clear homogenisation of the environment and the resources available following forest conversion to oil palm (Fitzherbert *et al.* 2008; Foster *et al.* 2011). Many species are lost from the regional (forest and oil palm combined) species pool and additional non-forest species are added (Edwards *et al.* 2013b; Edwards *et al.* 2014b), and those remaining/present tend to persist across the whole landscape. These characteristics correspond to suggestions of non-random assembly processes in harsher environments (Chase 2007), for example habitat filtering has been found to be more influential in stressed environments with high fire frequency (van der Plas *et al.* 2014). Ant communities have been observed to shift assembly structure with the presence of an invasive ant (Sanders *et al.* 2003) similarly, shifts in the species pool in oil palm could significantly alter the community organisation and thus the assembly structure of dung beetle and bird communities. Interestingly, leaf litter ant communities predominately maintained a random community assembly across habitats, mirroring findings from previous works (Fayle, Turner & Foster 2013).

In conclusion this study gives a first insight into the processes that structure the high biodiversity of tropical forest habitats and the impacts on community assembly following habitat disturbance (selective logging) and conversion (to oil palm plantations). I provide evidence of random community assembly, but with influences of niche based (non-random) processes, indicating a balance of assembly filters (Chave 2004; Adler, HilleRisLambers & Levine 2007; Vergnon, Dulvy & Freckleton 2009), though the driving mechanisms behind such filters are not fully understood. Therefore, an important next step is to examine the relative contribution of assembly processes for additional taxonomic groups and assess more precisely the underlying mechanisms of non-random processes, specifically the influence of micro-habitat variables (Boulangeat, Gravel & Thuiller 2012; Pollock, Morris & Vesk 2012; van der Plas *et al.* 2014). Critically, I highlight the potential hidden effects of land-use change beyond taxonomic evaluations (Royan *et al.* 2016), and the variation that sampling scale can create and thus the likelihood for assembly rules to be spatially dependent (Sanders *et al.* 2007). The variations seen across transect and point scale analyses, particularly in the case of bird communities (Figure 4.2b), stresses the need for a detailed consideration of scale relative to the question in mind to precisely inform ecological understanding and conservation. Furthermore, I suggest focusing on specific species interactions is of key importance for our ecological understanding of tropical ecosystems.

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Chapter 5: The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve

The following paper, *F. A. Edwards, J. Finan, L.K. Graham, T. H. Larsen, D. S. Wilcove, W. W. Hsu, V.K. Chey, & K. C. Hamer. (2017)* The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. *Biological Conservation, 205: 85-92,* is a modified version of this chapter.

FAE designed the study with advice from co-authors, and was solely responsible for statistical analysis and interpretation of the data and for writing and structuring the paper. Data were collected by FAE; JF; LKG; WHS; THL. Other co-authors provided logistical support and comments on draft manuscripts.

Abstract

The demand for timber products is facilitating the degradation and opening up of large areas of intact habitats rich in biodiversity. Logging creates an extensive network of access roads within the forest, yet these are commonly ignored or excluded when assessing impacts of logging on forest biodiversity. Here I determine the impact of these roads on the overall condition of selectively logged forests in Borneo, Southeast Asia. Focusing on dung beetles along >40km logging roads we determine: (i) the magnitude and extent of edge effects alongside logging roads; (ii) whether vegetation characteristics can explain patterns in dung beetle communities, and; (iii) how the inclusion of road edge forest impacts dung beetle assemblages within the overall logged landscape. I found that while vegetation structure was significantly affected up to 34m from the road edge, impacts on dung beetle communities penetrated much further and were discernible up to 170m into the forest interior. I found larger species and particularly tunnelling species responded more than other functional groups which were also influenced by micro-habitat variation. I provide important new insights into the long-term ecological impacts of tropical logging. I also support calls for improved logging road design both during and after timber extraction to conserve more effectively biodiversity in production forests, for instance, by considering the minimum volume of timber, per unit length of logging road needed to justify road construction. In particular, we suggest that governments and certification bodies need to highlight more clearly the biodiversity and environmental impacts of logging roads.

Introduction

Large areas of intact habitats rich in biodiversity are being opened up through extractive industries, including selective logging. Logging concessions account for ≈ 50% of the total area of tropical forests (Blaser et al. 2011), yet a largely overlooked impact of timber extraction is the creation of logging roads. Roads are an integral part of extractive industries, which require not only large transportation routes, but also secondary haulage trails and smaller access pathways, creating a sprawling ‘fishbone’ pattern of compressed barren surfaces mostly unpaved. For instance, in Borneo alone it is estimated there are over 270,000 km of such logging roads (Gaveau et al. 2014).

Roads can have negative ecological consequences by removing and degrading adjacent habitat, acting as barriers to dispersal, creating edge effects, and increasing the risk of road kill, fire, hunting and the colonisation by invasive species (Laurance et al. 2009; Benitez-Lopez et al. 2010; Rytwinski & Fahrig 2013; Clements et al. 2014; Padmanaba & Sheil 2014; Dar et al. 2015). The construction of roads across the tropics is therefore an urgent concern for conservation (Laurance & Balmford 2013; Bicknell et al. 2015; Barber et al. 2014; Laurance et al. 2014), but further attention is needed to evaluate the long-term impacts of logging roads, which remain in the landscape long after logging has been completed (Gullison & Hardner 1993; Ernst et al. 2016). Few studies, however have focused on the impacts of roads in tropical forests, let alone specific logging roads. Understorey bird communities and amphibian populations were observed to decline, while termite community composition differed with proximity to unpaved road clearings in Amazonia (Laurance 2004; Dambros et al. 2013; Whitworth et al. 2015). Dung beetle communities were negatively affected by logging dumps, skid trails and access roads shortly after logging in Malaysia (Hosaka et al. 2014a), and small mammal community composition differed between logging road types (variations in size, use and time since adandonment) in Central Africa (Malcolm & Ray 2000). However, most studies of the impacts of logging on biodiversity have either explicitly or implicitly avoided roads in their sampling protocols, leading to calls for further studies of their impacts on biodiversity and ecosystem functioning (Hamer et al. 2003; Broadbent et al. 2008; Laufer et al. 2013).

This study is based within a 1Mil ha logging concession in Sabah, Malaysian Borneo. Selective logging has been widespread in this region with extraction levels some of the highest globally (Cleary et al. 2007). In Sabah alone the total length of logging roads is estimated at >37,000km, with a density of 0.65 km per km^2 (Gaveau et al. 2014). Timber extraction in the immediate area of our study site was completed 23 years ago, which provides an ideal opportunity to examine the long-term impacts of logging roads across a large scale and through continuous forest. I use dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae) as our model taxon, as they are a key indicator group that contributes to diverse ecosystem processes (Gardner et al. 2008; Nichols et al. 2008) and is sensitive to environmental changes (Nichols et al. 2007).

The question of how far edge effects alongside roads penetrate into the forest is vital for understanding the overall impacts of logging on biodiversity. I address this key question by investigating the magnitude and extent of edge effects along logging roads (Haper et al. 2005; Harper & Macdonald 2013), focusing on key vegetation and soil characteristics, and the species richness, community composition and abundance of different dung beetle functional groups. I then assess whether changes in vegetation characteristics can explain the observed changes in dung beetle community structure from the road edge to the logged forest interior. Finally, I compare logged forest with nearby primary forest to assess the additional impact of roads on dung beetle biodiversity, beyond that directly attributable to harvesting of timber.

Material and methods

Study location

The study site was the Yayasan Sabah (YS) logging concession in eastern Sabah (4° 58′ N, 117 ° 48′ E). Most of this concession (95%) has been selectively logged, including the 238,000 ha Ulu Segama-Malua Forest Reserve (US-MFR) of which 97 000 ha (41%) has undergone a single rotation of timber extraction (once-logged forest). Harvesting took place between 1987 and 1991, with a yield ≈115 m^3 of timber per ha (Fisher et al. 2011), and 17% of the land area was marked by roads and skid trails (Pinard & Cropper 2000). All roads used in this study are un-paved and are still in use and maintained, though not for logging activities. Vegetation along the road edge varies in height and complexity due to initial logging activities and more recent maintenance (e.g. repairing of collapsed bridges).

Dung beetle sampling

Fieldwork was conducted between August and October 2009, February and September 2011, and June and August 2014. To quantify changes in dung beetle assemblages in proximity to roads, I created 24 sampling plots which were widely spaced across the landscape with a minimum distance of 650m (mean ± SE: 5.9 km ± 0.2) between plots. Each plot contained six traps at distances of 0 m, 6 m, 12 m, 25 m, 50 m and 100 m from the road edge (144 traps in total). To ensure independence of samples, traps were a minimum of 50 m apart (Larsen & Forsyth 2005) in a staggered design following Barnes et al. (2014) (see Appendix 5). I considered that edge effects were unlikely to extend beyond 100 m (Benedick et al. 2006; Broadbent et al. 2008; Lucey & Hill 2011; Gray et al. 2016) but to check whether or not this was the case and to determine how dung beetle assemblages differed between road edges and the interior of logged forest, I also placed traps (n = 58) 100 m apart along 14 transects at distances of 110m to 550m from the nearest road edge, with 4-5 traps per transect and a minimum distance of 500 m (mean ± SE: 11.9 km ± 0.9) between transects. I also sampled in primary forest, using 60 traps placed a minimum of 100 m apart along 12 transects of five traps each (mean distance between transects ± SE: 4.5 km ± 0.4)(see figure 5.1). I used standardised baited pitfall traps for all sampling. In each case a single trap, baited with human dung, was placed for four days and re-baited after 48 hrs, with beetles collected every 24 hrs (Edwards et al. 2011). I used reference collections (T. Larsen) housed at the Forest Research Centre, Sandakan, Malaysia and Smithsonian Museum, Washington DC, USA to assist identification

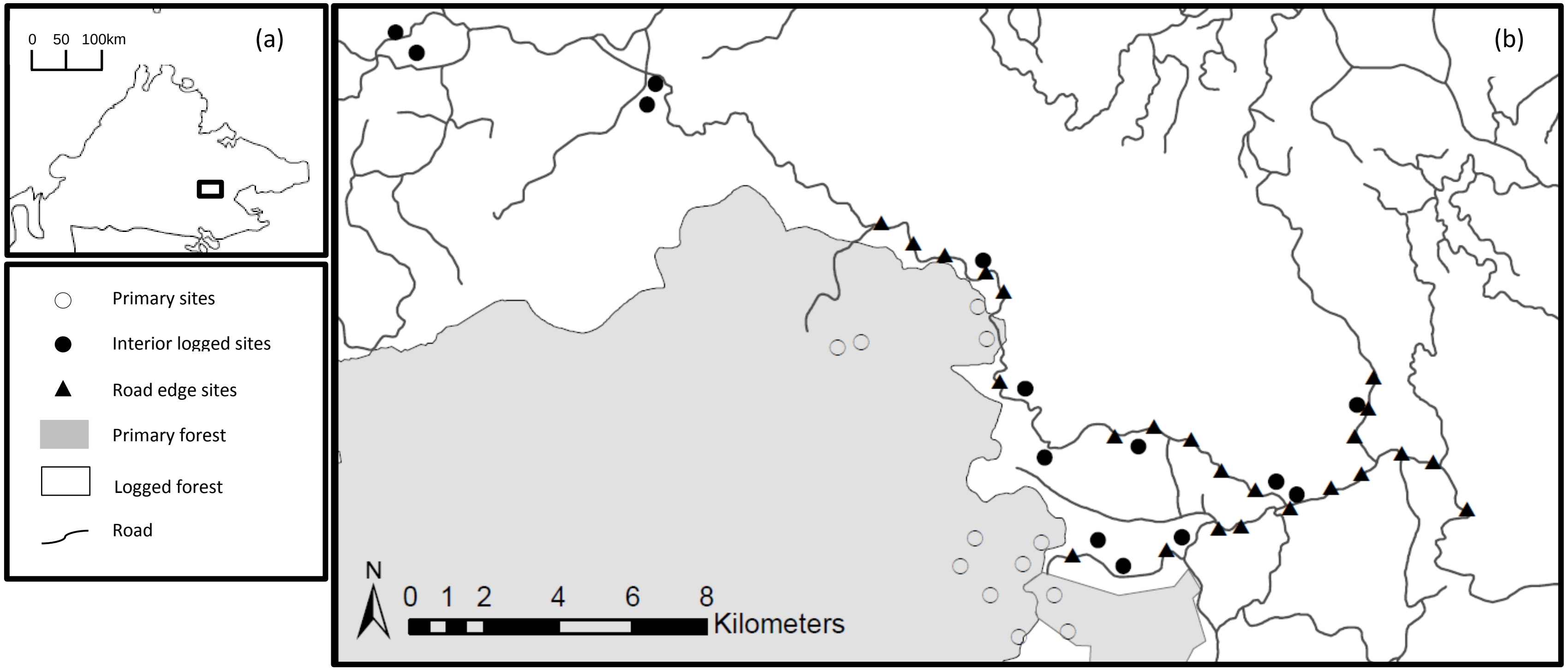

Figure 5.1: (a) A map of Sabah, Malaysian Borneo. The box outlines our study area. (b) A map of the study area. The grey solid area represents primary rainforest with the adjacent white area representing selectively logged rainforest. The symbols on the map identify sampling sites; open circles are within primary for est, solid black circles are within logged forest more than 100m from the road edge (interior logged forest), and solid black triangles are within logged forest up to 100m from the road edge (road edge forest). In all cases, the mid-point of the sampling traps, at a given site, is represented on the map.

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Species vary greatly in their contributions to community biomass, which in turn can affect ecosystem functioning (Slade et al. 2007). To determine biomass per trap, I calculated the average mass (g) of each dung beetle species, multiplied this by the number of individuals in a trap, and summed across species. To determine body masses, individuals (up to a maximum of 15 per species) were dried for four days at 60°C and weighed to the nearest 0.001 g using a precision balance (SBC 31; Scaltec Instruments GmbH, Germany). I also measured body length (base of head to tip of elytra) and width (distance between outer margins of elytra), to the nearest 0.1 mm using dial callipers and calculated body size (length * width) to allow extrapolation of body mass for species that could not be weighed. Biomass was calculated using a regression of body size (mm) against dry mass (g) based on 23 dung beetle species of 181 individuals (regression adj-R^2 = 0.96, Appendix 6), excluding the three largest species because these skewed the data for smaller species. The biomass of these larger species was calculated separately.

Additionally, 13 micro-habitat variables were measured at each sampling location within 100 m of the road edge (n = 144) and a subset of interior forest locations (n = 24) to determine how soil characteristics, leaf litter depth and vegetation structure, including tree characteristics, varied with distance from the road edge. *Soil bulk density (*dry soil weight (g)/soil volume (cm^3)) was measured as the mean from three soil cores randomly taken within 0.5m of the trap at a depth of 0-10cm. The wet weight, measure to the nearest 0.1g, and length of soil cores was taken before cores were dried for four days in an oven at 60°C, before being weighed again. L*eaf litter depth* was measured at ten random points, five within 1m and five within 2m of the trap and the average taken. The *percentage ground cover* was estimated within $2m^2$

around the trap and included all vegetation up to 0.5m above the ground. *Canopy openness* was measured using a spherical densitometer above the trap. The vegetation stand was measured by the *girth* at breast height and estimated *height* of the eight nearest small (≤60cm GBH) and large (>60cm GBH) trees to the trap. *Small tree density* was measured as the number of small trees within $10m^2$ of the trap and *large tree density* was measured as the number of large trees within $30m^2$ of the trap. *Vine density* was estimated for large (> 5cm diameter) and small (≤ 5cm diameter) vines, and *successional vegetation density* was estimated for bamboo, climbers, grass, ginger, ferns and rattan. Both vine density and successional vegetation were estimated using a categorical scale; 0 – none present, 1 – one or two plants/clumps, 2 – less than 25% cover, 3 – 26-50% cover, 4 – 51-75% cover, 5 – 76-100% cover, and the sum taken per trap.

Data Analysis

Edge effects

To examine how species richness, abundance and biomass of dung beetles, the abundance of different functional groups, vegetation structure and soil characteristics varied with distance from the road edge, I firstly used a piecewise regression to determine if a breakpoint (an abrupt change in a relationship) in the data was present. I ran a GLM with negative binomial error distribution (or in the case of certain vegetation variables a LM) with *distance* as a continuous variable and then using this model I ran a piecewise regression (using the *segmented* package in R). To determine if the piecewise regression was the best model I compared AIC values (following Ochoa-Quintero et al. 2015; Magnago et al. 2015). The piecewise regression allowed me to determine whether there was a significant influence of distance and to identify any discrete breakpoint in a particular variable ($P < 0.05$).

Secondly, I assessed the magnitude of edge influence (MEI: Harper et al. 2011; Dodonov et al. 2013), described as the amount a particular variable differs at the 'edge' compared to the 'interior', and is calculated as $MEI = \frac{(e-i)}{(e+i)}$

where *e* represents the average of a given variable at a *particular distance* from the edge, and *i* represents the average of a given variable within the *interior* habitat away from the edge. If a given distance from the edge (e) is equal to the interior (i) then MEI = 0, MEI is bounded by 1 and -1 allowing for ease of comparison between variables. To calculate the extent of edge influence (DEI: Harper et al. 2011; Dodonov et al. 2013), described as the range of distances away from the edge (towards the interior) where there is a significant edge influence (Harper et al. 2005), I used a randomised method of edge influence (RTEI: Harper & MacDonald 2011). This method follows three steps; i) observed MEI is calculated, ii) then randomised values of MEI are calculated from a complete variable pool (edge plus interior values) where the number of edge and interior sites are kept constant, and iii) then randomised values of MEI are compared to observed values to determine the significance of observed MEI (see Harper & MacDonald 2011 for further details). The analyses were run separately for each distance (e) away from the road edge. This randomisation technique reduces type 1 errors by accounting for variation between sampling sites at a specific distance from the edge. I used 10,000 randomisations with a significance level of 0.05 for determining p-values. I also used this technique to assess the change in soil characteristics, leaf litter depth and vegetation structure away from the road edge.

Functional groups were determined using categories described by Slade et al. (2007), which represent the main behavioural guilds, diel activities and size categories of dung beetles, which have been found to relate to dung beetle functional activity within the study area (Slade et al. 2007; Slade et al. 2011).

Community composition

To investigate how species composition changed with increasing distance from road edges, I used a non-metric multidimensional scaling ordination (Clarke & Warwick, 2001), using the Bray-Curtis dissimilarity measure (metaMDS function in *Vegan*; Oksanen et al. 2011). Communities were standardized as a proportion of the total number of individuals on each transect. To test for significant changes in community composition with distance from the road edge, I used a multivariate generalised linear model (GLM) framework, which allowed more accurate modelling of mean–variance relationships compared to pairwise matrix techniques (e.g. Bray–Curtis index), reducing type II errors (Warton et al. 2012). I used a negative binomial GLM, where multivariate p-values were calculated using PIT-trap bootstrapping with 1000 permutations, and were adjusted for multiple testing (anova.manyglm in Mvabund; Wang et al. 2014).

Relationship of dung beetles to vegetation

To test whether there was a relationship between the changes in dung beetle community metrics and the observed vegetation changes, I ran generalised linear mixed effects models (GLMM) for each community metric (i.e. abundance, biomass) with a negative binomial error distribution. Each model included eight vegetation measures as predictors (successional vegetation, ground cover, canopy cover, the number of large and small trees, the height of large and small trees, and the girth of large trees) and ‘plot’ as a random factor to account for repeated measures. Those vegetation measures that showed no variation in the MEI analysis (see ‘edge effects’ above) were not included. I used a subset of the overall data where both vegetation and community data were available (n=144 road edge plots with 24 plots per distance class plus 24 plots in the interior of logged forest, all surveyed in 2014). The vegetation variables were standardised to allow for analysis across different scales using the formula (x-mean(x))/SD(x) where x is the vegetation variable to be standardised. To test whether or not our results were influenced by spatial autocorrelation I used a Monte-Carlo permutation test for Moran’s I statistic (moran.mc function in *spdep*: Bivand et al. 2013), using the model residuals with 1000 repetitions. There was no evidence of spatial auto-correlation for any of the models (Moran’s I: $P \geq 0.3$).

Spatial extent of logging roads and edges

Using the calculated DEI values I determined an overall distance edge influence. I then used a GIS layer of major and minor hard roads (excluding skid trails) across the YS logging concession to determine the area comprising logging roads and edges. This layer covers the majority of the YS concession and was the most detailed layer available to me. The area (km^2) comprising logging roads and edges, beyond the linear feature of the road surface itself, was estimated as:

$$(Total\ road\ length \times [limit\ of\ edge\ effects \times 2])$$

(Equation 1)

All statistical analyses were run in R v.3.1.1 (R Development Core Team, 2014), and all spatial analyses were run in ArcGIS 10.1 (ESRI 2011).

Results

I sampled 23 570 individual dung beetles of 74 species. Those species recorded in the interior of logged forest were a subset of primary forest species, but I recorded an additional eight species at road edges, which were not found elsewhere in the study (or from previous studies in the same study area, Edwards et al. 2014b).

Magnitude and extent of edge effects

Successional vegetation declined significantly with increasing distance from the road (piecewise regression: t= -4.28, $p < 0.001$) while the number of small and large trees (t =2.82, p = 0.005 and t = 2.78, p = 0.006 respectively), and the height and girth of large trees (t = 4.0, $p < 0.001$ and t = 2.86, p = 0.005 respectively) increased along the same gradient (Appendix 7, 8 & 9). A randomization test of edge influence (RTEI) supported these models but with the addition of canopy cover, ground cover and small tree height showing a significant decrease compared to interior logged forest (Appendix 8). There was, however, no effect of distance from edge on soil characteristics or leaf litter depth (Appendix 7, 8 & 10).

Abundance and biomass of dung beetles per trap both increased with increasing distance from the road (t = 3.73, $P < 0.001$ and t = 4.26, $P < 0.001$, respectively), with the greatest increase occurring around 130m (Fig. 5.2). RTEI confirmed that the magnitude of the difference in each of these two response variables was significant up to 100m from the road edge (Appendix 11 & 12).

In terms of functional groups, large nocturnal tunnellers, large diurnal rollers and both large and small diurnal tunnellers all increased significantly in abundance with increasing distance from the road edge (t = 5.32, $P < 0.001$, t = 4.86, $P < 0.001$, t = 4.82, $P < 0.001$, and t = 4.30, $p < 0.001$ respectively) up to a distance 130 m (Fig.

5.3). Large nocturnal rollers and small nocturnal tunnellers ($t = 2.78$, $p = 0.006$ and $t = 3.10$, $p < 0.002$, respectively) changed in abundance much closer to the road edge (<50 m, Fig.5.3d,g), whereas small diurnal rollers were unaffected ($P = 0.19$, Fig. 5.3f). The magnitude of edge effects and the RTEI confirmed similar patterns, highlighting significantly different abundances up to 100m from the road edge compared to interior logged forest for the majority of functional groups, with the exception of small nocturnal tunnellers (DEI of 25m) and small diurnal rollers which were found not to differ (Appendix 11 & 12). Finally, community composition indicated that beetle assemblages within 100 m of the road were significantly different from those at greater distances (Fig. 5.4; manyglm: Wald statistic = 26.25, $P = 0.001$). There was no evidence of spatial auto-correlation for any of the above models (Moran's I: $P \geq 0.1$).

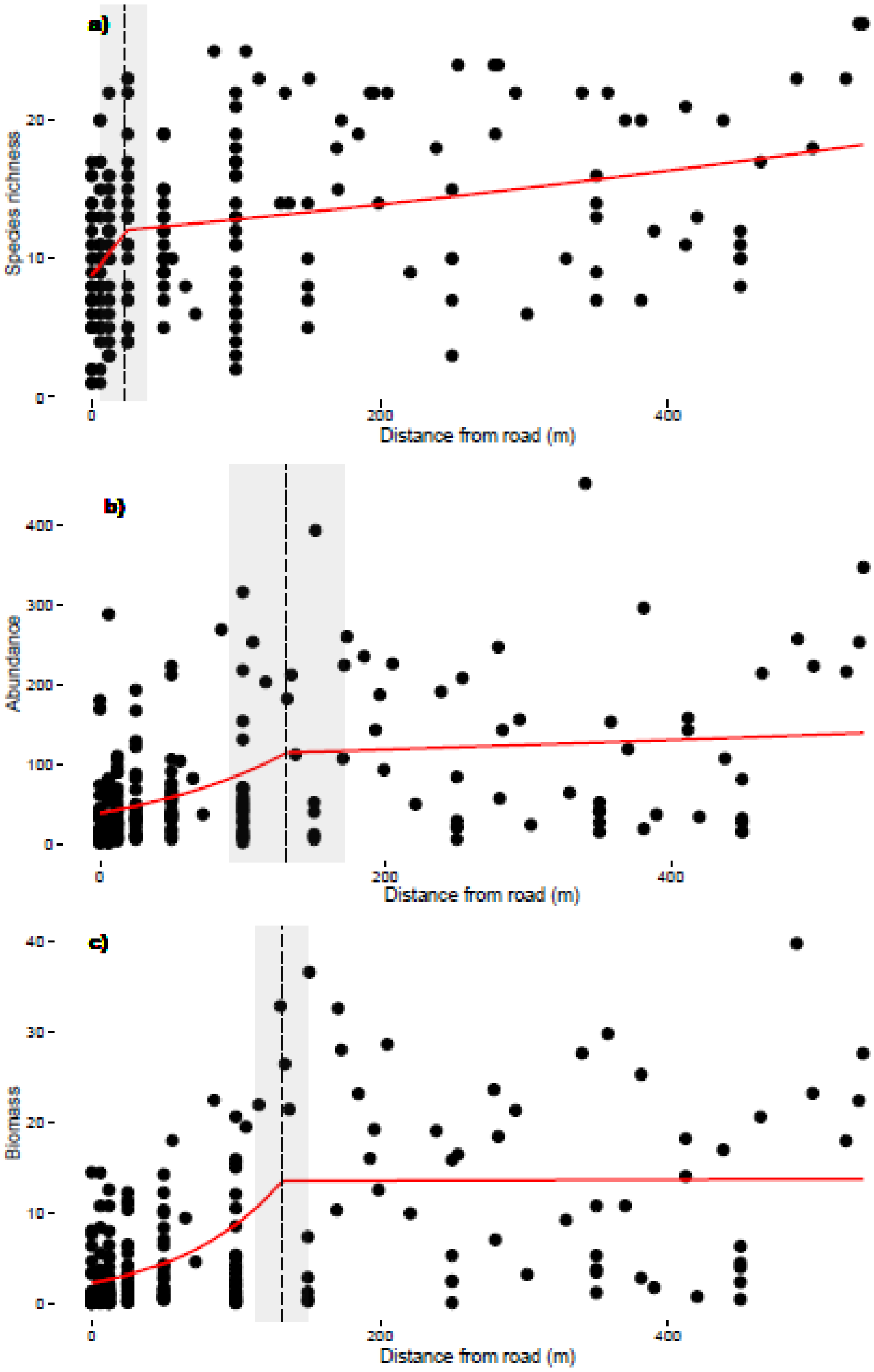

Figure 5.2: The effect of distance from the road edge (m) on the a) abundance, b) species richness, and c) biomass of dung beetles communities. Solid red lines are based on piecewise regression, dashed vertical lines represent significant breakpoints ($P < 0.05$), and grey shaded areas represent SE around breakpoint distance.

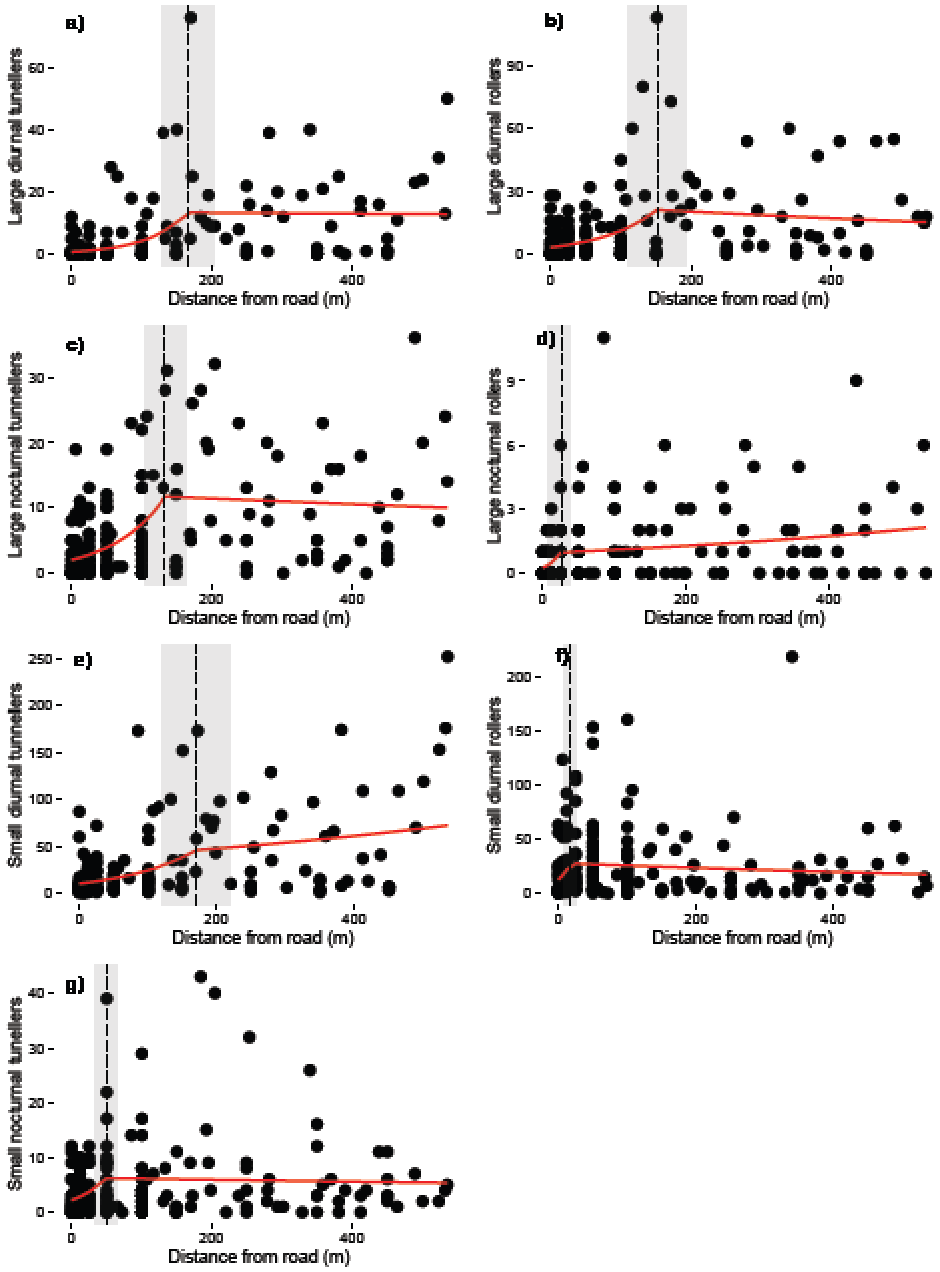

Figure 5.3: The effect of distance from the road edge (m) on the abundance of seven key dung beetles functional groups; a) large diurnal tunneller, b) large diurnal roller, c) large nocturnal tunneller, d) large nocturnal roller, e) small diurnal tunneller, f) small diurnal roller, g) small nocturnal tunneller. Solid red lines are based on piecewise regression, dashed vertical lines represent significant breakpoints ($P < 0.05$), and grey shaded areas represent SE around breakpoint distance.

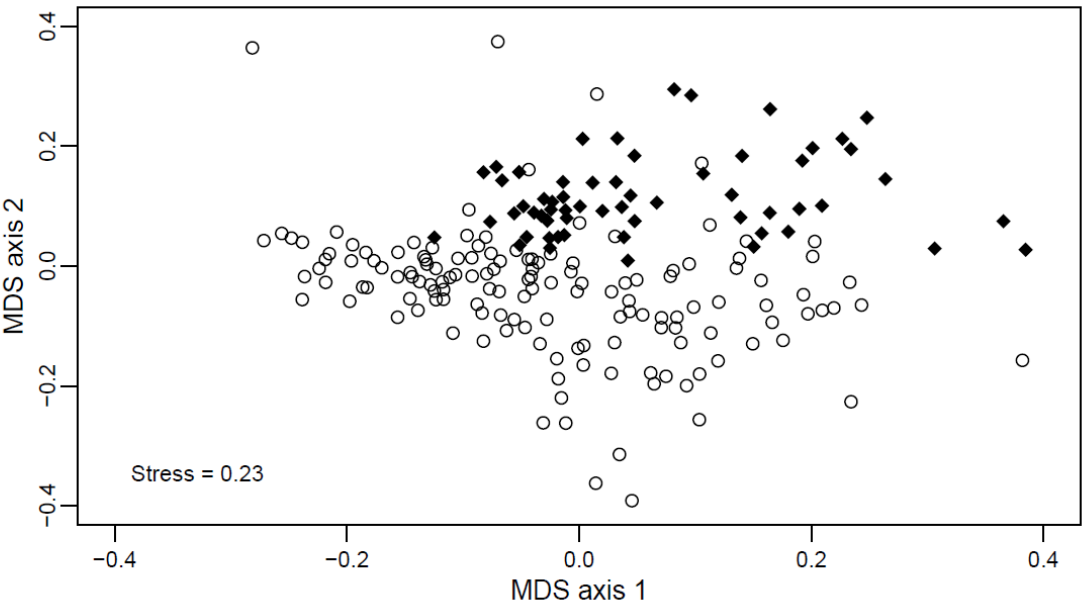

Figure 5.5: The relationship between non-metric multidimensional scaling (NMDS) ordination axis 1 and axis 2. Open circles represent traps between 0-100m from the road edge, and solid diamonds represent traps in the interior logged forest, more than 170m from the road edge.

Relationship of dung beetles to vegetation

The overall biomass of dung beetles and the abundance of large diurnal and nocturnal tunnellers were all significantly positively related to ground cover, while the abundance of large and small nocturnal tunnellers were significantly negatively related to the density of early successional vegetation (Appendix 15). Some additional variables also increased significantly with increasing densities or sizes of tress but there was no relationship between the abundance or biomass of rollers and any of the measured vegetation characteristics (Appendix 15).

Spatial extent of logging roads and edges

I estimated that the area affected by logging roads within the YS concession (i.e. including edge effects) was 817 km^2, which is 9.0% of the total area of logged forest within the concession. Accounting for this area of road edge forest resulted in an additional decline of 3-8% in overall community metrics and in the abundance of different functional groups in the logged landscape compared to the effect of timber removal only (Table 5.1).

Table 5.1: Biodiversity metrics (mean [SE]) for dung beetles sampled within primary forest, >100m from the nearest road within logged forest (interior), within 100m of logging roads (road edge) and the combined logged landscape* in Sabah, Malaysian Borneo.

		Logged forest		
Metric	**Primary forest**	**Interior**	**Road-edge**	**Combined**
Overall community				
Species richness	18.5 (0.7)	15.8 (0.8)	10.7 (0.4)	13.9 (0.4)
Abundance	147.7 (14.3)	129.3 (14.0)	48.6 (4.5)	122.0 (7.4)
Biomass (g)	24.7 (2.3)	14.1 (1.4)	3.4 (0.3)	14.7 (0.8)
Functional group abundances				
Large diurnal tunnelers	9.6 (1.1)	13.0 (1.9)	0.9 (0.2)	6.2 (1.0)
Large nocturnal tunnelers	8.5 (1.0)	11.3 (1.2)	3.1 (0.3)	11.9 (0.7)
Small diurnal tunnelers	43.5 (5.0)	55.6 (7.4)	12.7 (1.3)	51.7 (3.8)
Small nocturnal tunnelers	17.5 (1.6)	6.4 (1.2)	4.4 (1.0)	10.6 (0.8)
Large diurnal rollers	26.8 (3.3)	20.4 (3.1)	4.3 (0.6)	19.0 (1.6)
Large nocturnal rollers	5.4 (0.9)	1.5 (0.3)	0.6 (0.1)	1.4 (0.2)
Small diurnal rollers	33.7 (5.8)	21.0 (4.3)	22.6 (2.5)	21.1 (2.3)

Discussion

Edge effects

This study provides one of the first examples of how tropical biodiversity responds to logging roads per se (Laurance 2004; Hosaka et al. 2014a), and also assesses what the broader impact of timber extraction is by accounting for the hidden additional effects of logging roads. These results show clear evidence that while vegetation structure and composition were significantly affected up to 34m from the road edge, impacts on dung beetle communities penetrated much further and were discernible up to 130 m into the forest interior (Figs. 5.2, 5.3, Appendix 12). Moreover, these changes were observed more than 20 years after timber extraction ended, supporting previous findings of the long term impacts of roads in Central Africa and Amazonia (Malcolm & Ray 2000; Laurance et al. 2004) and highlighting a need for longstanding conservation efforts.

These results for dung beetles accord with the median extent of edge effects within forest fragments in the Brazilian Amazon (100 m; Broadbent et al. 2008), suggesting that transection of forest by logging roads could be considered akin to fragmentation in terms of edge effects. We also found that the distances of edge influence extended much further than previously recorded in Southeast Asian forests that had been selectively logged less than 18 months previously (<10 m; Hosaka et al. 2014b), possibly indicating a time lag in species' responses. More broadly, the declines we recorded in dung beetle community and functional metrics between road edges and elsewhere within logged forest exceeded the difference between primary forest and the interior of logged forest, highlighting the stark decline in biodiversity in proximity to roads (Table 5.1).

Impact of roads on logged forest biodiversity

The changes I recorded in community composition indicate potential changes in the ecosystem functions provided by dung beetles within logged forest. The magnitude of edge influence was greater for diurnal tunnellers and larger species compared to rollers and smaller species (Fig. 5.2, Appendix 11&12). Notably the decline of large tunnellers, which have been shown to remove more dung than the other functional groups (Slade et al. 2007), could have important implications for the overall rate of dung removal. Furthermore the decline in larger species may contribute to changes in local-scale species interactions including the greater numerical dominance of smaller species, particularly diurnal rollers, in road edge forest (Table 5.1). Tunnelling species, including larger species, were shown to associate with greater tree density and structure but with ground cover present. Micro-habitat and micro-climatic changes, have been highlighted as a key determinant in changes in small mammal and dung beetle populations, specifically a loss of canopy cover, following road creation (Malcolm & Ray 2000; Hosaka et al. 2014b) but also in other extreme environments (oil palm plantations and logging yards) which represent similar extreme changes in habitat structure as with roads and logged forest edge (Edwards et al. 2014b; Hosaka et al. 2014a). These findings highlight the unknown interactions between functional traits and community assembly, and the need for a greater understanding of assembly filters in varied disturbed habitats (Pollock et al. 2012; Van der Plas et al. 2012).

Management implications

Roads are an essential but financially costly element of logging activities (Putz et al. 2008; Medjibe & Putz 2012), and this study highlights the long-lasting ecological consequences of road creation during selective logging, above and beyond the direct effects of the removal of trees. Consequently, there are incentives and benefits to both concession holders and biodiversity conservation to improve the design and implementation of logging roads.

The logging concession I studied is a relatively closed area with tightly controlled access, low traffic volumes and minimal human settlements (principally three well-contained forest research stations and a tourist lodge), and thus further degradation has been minimal while promoting forest recovery. These results show that even under this ‘best-case scenario’ there are significant impacts of logging roads. Furthermore, where logging roads facilitate uncontrolled access to the forest long after logging has ceased, edge effects could be greatly exacerbated and penetrate further into the logged forest interior. Thus I support suggestions for the closure (permanent or temporarily) of logging roads, where appropriate, once timber extraction has been completed, to facilitate forest recovery and discourage encroachment (Bicknell et al. 2015; Klienschroth et al. 2016).

In conclusion I suggest that governments and certification bodies (e.g. the Forest Stewardship Council - FSC) need to highlight more clearly the biodiversity and environmental impacts of logging roads. I also encourage the increased use of reduced impact logging techniques (RIL; Edwards et al. 2012; Putz et al. 2012; Bicknell et al. 2014) and suggest that the planning of roads within logging concessions needs to take further steps to preserve forest, for instance by considering the minimum volume of timber that would need to be extracted per unit length of logging road in order to justify road construction. This is a timely and important discussion as large logging concessions open up across South-east Asia, South America and tropical Africa, and there is a need and desire to encourage more sustainable and conservation-focused planning for logging activities.

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Chapter 6: Sustainable Management in Crop Monocultures: The Impact of Retaining Forest on Oil Palm Yield

The following paper, *F. A. Edwards, D. P. Edwards, S. Sloan & K. C. Hamer (2014). Sustainable Management in Crop Monocultures: The Impact of Retaining Forest on Oil Palm Yield. Plos One, Volume 9, Issue 3, e91695,* is a modified version of this chapter.

FAE designed the study with advice from DPE, and was solely responsible for statistical analysis and interpretation of the data and for writing and structuring the paper. Data were collected and collated mainly by FAE with assistance and advice from other co-authors, who also provided comments on draft manuscripts.

Abstract

Tropical agriculture is expanding rapidly at the expense of forest, driving a global extinction crisis. How to create agricultural landscapes that minimise the clearance of forest and maximise sustainability is thus a key issue. One possibility is protecting natural forest within or adjacent to crop monocultures to harness important ecosystem services provided by biodiversity spill-over that may facilitate production. Yet this contrasts with the conflicting potential that the retention of forest exports dis-services, such as agricultural pests. I focus on oil palm and obtained yields from 499 plantation parcels spanning a total of ≈23,000 ha of oil palm plantation in Sabah, Malaysian Borneo. I investigate the relationship between the extent and proximity of both contiguous and fragmented dipterocarp forest cover and oil palm yield, controlling for variation in oil palm age and for environmental heterogeneity by incorporating proximity to non-native forestry plantations, other oil palm plantations, and large rivers, elevation and soil type in our models. The extent of forest cover and proximity to dipterocarp forest were not significant predictors of oil palm yield. Similarly, proximity to large rivers and other oil palm plantations, as well as soil type had no significant effect. Instead, lower elevation and closer proximity to forestry plantations had significant positive impacts on oil palm yield. These findings suggest that if dipterocarp forests are exporting ecosystem service benefits or ecosystem dis-services, that the net effect on yield is neutral. There is thus no evidence to support arguments that forest should be retained within or adjacent to oil palm monocultures for the provision of ecosystem services that benefit yield. I urge for more nuanced assessments of the impacts of forest and biodiversity on yields in crop monocultures to better understand their role in sustainable agriculture.

Introduction

More than 50% of the global land area that is purportedly suitable for agriculture has already been converted to farmland (Green et al. 2005). Moreover, by 2050, projections suggest that an increase of one billion hectares in agricultural land is required to feed a growing population and to meet increasing consumption per capita (Tilman et al. 2001), much of which will come at the expense of natural habitat in the tropics (Gibbs et al. 2010). Following agricultural development, the landscape is often left with highly fragmented patches of natural habitat that create sharp habitat boundaries with agriculture, and with remaining patches of natural habitat showing varying degrees of degradation and isolation (Tscharntke et al. 2005; Ribeiro et al. 2009). The simplification of vegetation structure and altered environmental conditions within the agricultural matrix often prove too extreme for much native biodiversity to persist, and valuable ecosystem services may also be threatened by the loss of natural habitats (Benton etal. 2003; Hooper et al. 2005; Tscharntke et al. 2005; Karp et al. 2013). Consequently, agricultural expansion is one of the key threats to biodiversity (Tilman et al. 2001; Green et al. 2005), and there is an increasing strain between conserving biodiversity and maximising agricultural production (Ranganathan et al. 2010; Karp et al. 2013; Sayer et al. 2013).

Many crops are highly dependent on functional interactions provided by biodiversity, such as soil nutrient supply, pollination, and biological pest control (Thies & Tscharntke 1999; Kremen et al. 2002; Sande et al. 2009; Tscharntke et al. 2012). Integration of remnant natural habitat features such as forest fragments, riparian strips, and hedgerows within agricultural landscapes is advocated as a means to enhance ecosystem services and thus yield, in addition to providing conservation benefits to native biodiversity, within sustainable landscapes (Landis et al. 2000; Klein et al. 2003; Ricketts et al. 2004; Koh 2008; Tscharntke et al. 2008; Chaplin-Kramer et al. 2011; Woltz et al. 2012). While there is a large literature on how the retention of natural habitat can encourage biodiversity and ecosystem services, there is a lack of knowledge of the degree to which remnant habitat might negatively affect yield. The spill-over of biodiversity from natural habitats to agricultural land can negatively alter species diversity and food web interactions (Tscharntke & Brandl 2004; Zhang et al. 2007), with ecosystem dis-services potentially arising as a consequence of providing reservoir populations of insect or fungal pests, crop raiders, invasive weeds, or predators and parasites of beneficial species (Kremen et al. 2002; Zhang et al. 2007).

Retaining natural habitat remnants within agricultural landscapes also reduces the land available for growing crops, and so may constitute an opportunity cost to local production as well as potentially increasing the demand for converting land elsewhere to agriculture (Green et al. 2005). Landscape-scale planning for agricultural sustainability and conservation therefore hinges on whether or not remnant habitat features provide a net benefit for agricultural production, for conservation, or for both. This is a particularly important issue in the tropics, where conversion to agriculture consumed 1.4% of the tropical forest biome between 2000 and 2005 (Asner et al. 2009). To date, research on the relationship between natural vegetation cover and crop yield in the tropics had focused on two agro-forestry crops: coffee (Klein et al. 2003; Ricketts et al. 2004; Olschewski et al. 2006; Olschewski et al. 2010; Karp et al. 2013) and cocao (Clough et al. 2011; Bisseleua et al. 2013; Maas et al. 2013). Both coffee and cocao plantations consist of a mix of crop plants and (non)-native shade trees, which results in an agro-forestry matrix that is comparatively hospitable to forest species (e.g., Steffan-Dewenter et al. 2007), and can enhance spill-over from forest and resulting ecosystem services. Consequently, these studies found that close proximity to forest improved pollinator bee numbers (Ricketts 2004) and thus coffee yields by up to 20% (Ricketts et al. 2004) compared to locations 1,400-1,600 m from forest, and that distance to forest had a marginal positive effect on yield in cacao plantations (Clough et al. 2011), which have increasing numbers of predatory ant and spider species with higher densities of native shade trees (Bisseleua et al. 2013). Furthermore, exclusion experiments showed that bird and bat predation, and the extent of forest cover were important in controlling pest populations and thus positively impacting yield (Karp et al. 2013; Maas et al. 2013).

To my knowledge, the impact of forest on yield has not been assessed in the context of tropical crop monocultures, in which a single crop species is planted in stands that do not contain non-crop trees or other crop species, yet the majority of crop expansion within the tropics now creates monocultures of sugar cane, soya, oil palm, and even cocao. Oil palm *Elaeis guineensis* is one of the world’s highest yielding and most financially lucrative monoculture crops (Fisher et al. 2011). As such, it is expanding very rapidly, with production increasing by >5.5 million ha between 2001 and 2011 (FAOSTAT 2013) and with the majority of this expansion occurring at the expense of hyperdiverse tropical rainforest in Southeast Asia (Wilcove et al. 2013). Unlike coffee and cocao plantations, which can retain high levels of within-plantation biodiversity, whole-sale forest conversion to oil palm results in dramatic local extinctions of most forest-dwelling species (Fitzherbert et al. 2008; Edwards et al. 2010; Fayle et al. 2010). To reduce the environmental footprint of oil palm, The Roundtable for Sustainable Palm Oil (RSPO), via the high conservation value (HCV) forest protocol (Edwards et al. 2012; Edwards & Laurance 2012), and conservation scientists (e.g., Bhagwat & Willis 2008; Koh et al. 2009) have both highlighted the potential benefits of creating oil palm landscapes that retain forest remnants and riparian strips within plantations, but the net effect of such management on oil palm yield is not known (Foster et al 2011).

In this study, I explore the impacts of the local extent of forest cover and the proximity to forest on oil palm yields in Sabah, Malaysian Borneo, where palm oil production covers 19% of the state land area (Reynolds et al. 2011) and where there is increasing pressure for further expansion. I thus assess whether the retention of forest within and adjacent to oil palm plantations has a positive, negative or neutral impact on oil palm yield, with the aim of informing sustainable land-use planning.

Materials and Methods

Study Area

The study landscape spans 49.5 km x 29.8 km (total area=1474 km^2 or 147,400 ha) in Sabah, Malaysian Borneo (Figure 6.1). The landscape comprises >91,000 ha of contiguous oil palm plantations owned by multiple companies, plus a single >28,000 ha block of plantation forestry (*Eucalyptus* spp., Teak, *Acacia* spp.; Sabah Softwoods Bhd.) (Figure 6.1). All of the soils within our study oil palm plantations are Acrisols, as defined by the World Reference Base for Soil Resourses (FAO 2014). However, these soils also contain other main soil components (e.g., Luvisols, Cambisols, etc.) and they have a mixture of alluvium, mudstone, sandstone and igneous rock as parent material (Director of National Mapping 1974); these are combined into ten soil groups (Appendix 14 and 15). Study oil palm plantations also span an elevational range from 10 to 379 m a.s.l. (Appendix 16).

Surrounding these plantations are two areas of contiguous lowland dipterocarp forest >100,000 ha in size, which were not bounded by our study area: to the west and north is the Yayasan Sabah (YS) logging concession and to the east is the Ulu Kalumpang forest reserve (itself contiguous with Tawau Hills National Park). Surrounding contiguous forests have both undergone at least two rotations of selective logging (Edwards et al. 2011; Fisher et al. 2011). To the south of our study area is a coastline of tidal mangrove creeks, >2 km from the nearest oil palm coupe.

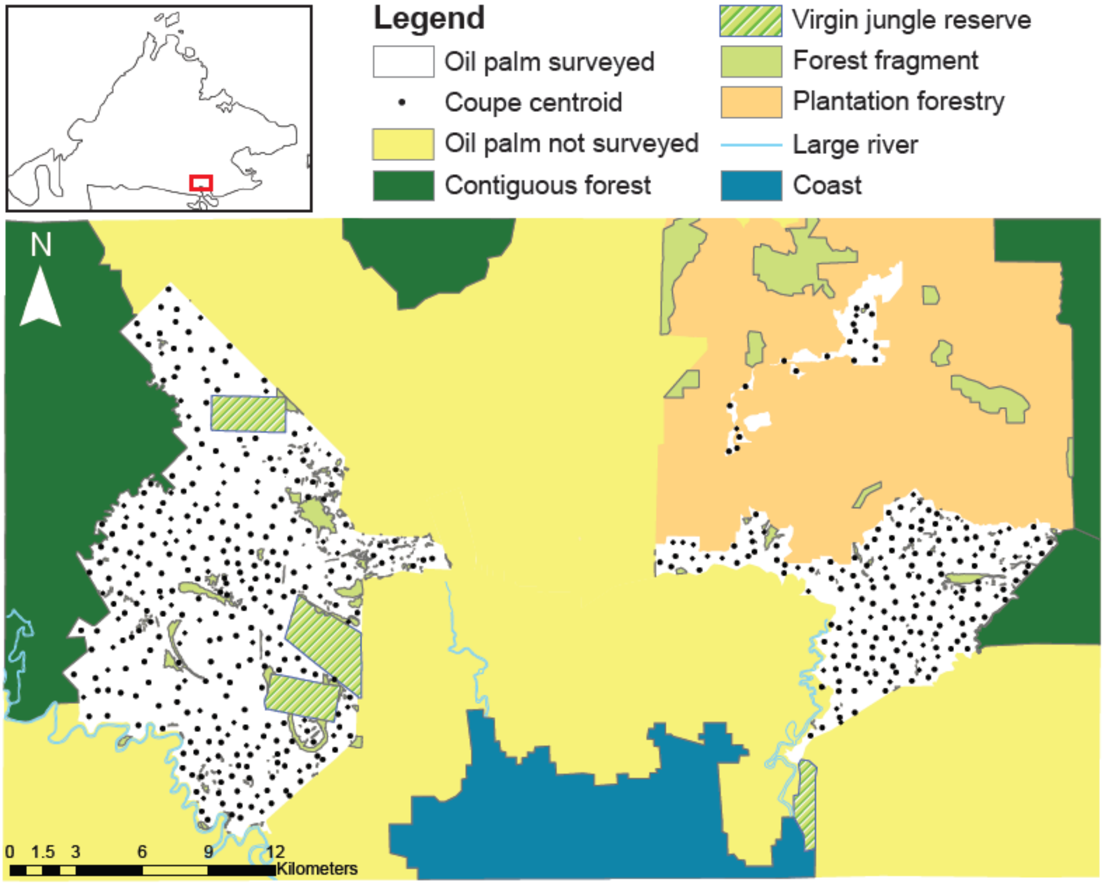

Figure 6.1: Different land-use types within the study area. The inset shows Sabah, Northeast Borneo, and the red box denotes the study area.

I focus on the oil palm of a single company—Sabah Softwoods Bhd. (I thank Sabah Softwoods Bhd. for providing data, logistical support and site access), a subsidiary of the state-owned Yayasan Sabah Group—with ≈23,000 ha of plantings (Figure 6.1, in white). Oil palm plantings are separated into three separate zones, which are 2.5 to 9.3 km apart, partitioned by other oil palm plantations between the western and eastern blocks and by plantation forestry between the two eastern blocks (Figure 6.1). Each zone is sub-divided into discrete parcels known as coupes (n_{total} = 499), which vary in size from 3 to 89 ha (mean±SE: 45±0.7 ha) and which are planted with a density of 100 palms per ha (Edwards et al. 2010).

The Sabah Softwoods oil palm plantations border both contiguous areas of forest, plus numerous isolated forest fragments, increasing in size from tiny patches to large fragments of dipterocarp forest. Forest fragments are divided into Virgin Jungle Reserves (VJRs), which are large (n=4; mean±SE: 813.95±197.6 ha), were gazetted prior to industrial-scale logging, and thus contain mostly primary forest; whereas privately owned patches (herein 'private fragments') tend to be smaller (n=307, 11.5±4.2ha, range=0.01 to 886 ha), to have been selectively logged at least once (the precise logging history of each fragment is unknown) and open to other disturbances (e.g., hunting). Forest fragments were typically retained within plantations due to their steepness and/or unfavourable underlying substrate.

Oil Palm Yields

Yield data were fresh fruit bunch (FFB) weights (metric tonnes) per hectare for individual coupes from 2008 to 2010. Sabah Softwoods employees visit each oil palm tree within a coupe to harvest ripe fruit bunches and cut decaying fronds twice per month. Bunches are collected into trailors and weighed at the depot. I was provided with the total weight of fruit bunches collected in each coupe on a yearly basis. Oil palm age varied across coupes, from 3 to 15 years old, and because yield varies with age of an oil palm (Butler et al. 2009) I used the *deviation from the mean expected yield by age* (i.e., observed yield - mean yield for the age of palm) as our indication of yield per coupe. A positive value indicates greater yield than expected, while a negative value indicates a lower yield than expected, given the age of the oil palm. Observed yield data were used from all 499 coupes in 2010. Expected yield was calculated from two yield-by-age curves: firstly, generated from the subset of coupes for which data were provided in 2008 (n=240 coupes) and 2009 (n=400; yldSS), and secondly from Butler *et al.* (2009) using their average FFB curve (yldB; Appendix 17).

Quantifying Extent of Forest Cover and Proximity to Forest

Forest coverage maps were supplied by Sabah Softwoods, and supplemented with additional maps obtained from the literature (Reynolds et al. 2011; Miettinen et al. 2012) and Google Earth images from 2009. The extent of dipterocarp forest cover surrounding and within each oil palm coupe was calculated within circles of radii 100 m, 250 m, 500 m and 1,000 m from the centroid of each coupe. Radii thus span a range of spatial scales relevant to different taxonomic groups, as determined by observations of species' movements between forest and oil palm (Lucey & Hill 2012). From these four radii, an inverse distance-weighted measure of forest-cover area as a proportion of the 1000-m radius circle areaF_{IDW} was calculated, giving greater weight to forest area closer to a coupe centroid than forest further away (Peterson et al. 2011; Rheinhardt et al. 2012), using the formula:

$$\mathrm{F}_{IDW} = \sum_{i=1}^{i=4} \frac{fi}{d+1}$$

where f*i* is the proportion of forest within a buffer ring (0-100 m, 100-250 m, 250-500 m, and 500-1,000 m) and d (m) is the mean distance of a buffer ring.

Dipterocarp forest included three qualitatively different classes that differed in size and/or logging history, and thus vegetation composition and species communities (e.g., Benedick et al. 2006; Edwards et al. 2011; Hill et al. 2011), namely (i) contiguous forest, (ii) Virgin Jungle Reserves, and (iii) private fragments. To account for this variation, I also assessed proximity to these dipterocarp forest classes by calculating, from each coupe centroid, the shortest distance to each class. I also calculated distance to plantation forestry, which directly borders some oil palm coupes and which in this study area has more bird biodiversity than local oil palm (Sheldon et al. 2010; Styring et al. 2011), largely due to the secondary forest understorey that develops under plantation trees. In addition, I included the distance to the nearest surrounding oil palm (i.e. not owned by Sabah Softwoods Bhd.) since a coupe located within a large expanse of oil palm monoculture could benefit if dis-services such as pest infestations originate from within forest or could be disadvantaged if they develop within oil palm. Finally, I evaluated the proximity of the nearest large river from each coupe centroid, the mean elevation across the coupe, and the dominant soil type by area (mean dominant soil coverage was 96.4% ± 0.01 SE of coupe area), because these environmental variables have the potential to influence oil palm growth and yield. Elevation (m a.s.l.) was calculated from a digital elevation model at 90 m resolution (Jarvis et al. 2008). Soil types were grouped into ten categories (see above; appendix 14) and were assessed using a regional soil survey map at 1:250000 scale (Director of National Mapping 1974).

Statistical Analysis

I used Generalised Least Square models (GLS) to firstly test whether the distance-weighted proportional area of forest affected oil palm yield at the coupe level. The distance-weighted measure of forest cover was square-root transformed to reduce the influence of two outliers. Secondly, I used a GLS to test whether proximity of a coupe centroid to the nearest dipterocarp forest class (contiguous forest; VJR; private fragment) affected oil palm yield. Distance to the nearest forest class was square-root transformed to account for the likely declining effect of forest and the associated reduction of biodiversity spill-over at increasing distances (Clough et al. 2011). Additionally, the area of the nearest private fragment was also included as a covariate in proximity models, because different sized fragments could export different levels of services or dis-services. In both cases, the minimum adequate model was achieved by a model selection process comparing nested models (Zuur et al. 2009). All models included proximity to tree plantation, proximity to large river, proximity to other oil palm plantation, mean elevation and dominant soil type as fixed effects. All models also included a correlation structure using the latitude and longitude of the coupe centroids to account for spatial autocorrelation (Dormann et al. 2007). Lastly, using the model residuals with 1000 repetitions, I performed a Monte-Carlo permutation test for Moran's I statistic (moran.mc within spdep package) to test whether the results were influenced by spatial autocorrelation (i.e., that the correlation structure had effectively accounted for impacts of space).

All spatial analyses were run in ArcGIS 10.0 (ESRI 2011) and all statistical analyses were run in R 2.15.2 (R Development Core Team 2011).

Results

Oil palm coupes within the landscape spanned a range of distances to forest and degrees of forest cover (Table 6.1), with the percentage of forest cover at 1000 m ranging from 0 to 79% and distances to forest classes from 30 m and 20.7 km (Table 6.1), indicating a perfect landscape within which to test the impacts of forest on oil palm yield. Across the study area, there was also a large variation in oil palm yield, spanning over an order of magnitude from 0.12 to 33.46 mt ha^{-1} (Table 6.1), with a strong correlation between yield and oil palm age ($r^2 = 0.88$). However, having accounted for the increase in yield with palm age (see **Materials and Methods**), the spatial distribution of oil palm yield in relation to forest cover showed no clear visual pattern, with a mix of high yield oil palm both close and far from major blocks of forest (Figure 6.2a, b), and with the same visual pattern for lower yields.

Table 6.1: The range and mean (±SE) of oil palm yield, elevation, and nearest distance to different forest classes, forestry plantations, large rivers and other (not within Sabah Softwoods Bhd.) oil palm plantations within 499 oil palm coupes in Sabah, Malaysian Borneo.

Measure	**Maximum**	**Minimum**	**Mean**	**SE**
2010 oil palm yield (mt ha^{-1})	33.46	0.12	16.82	0.39
Elevation (m.a.s.l.)	393.53	7.83	127.51	3.11
Forest cover (%) within radii:				
100m	36.00	0.00	0.18	0.08
250m	70.00	0.00	1.43	0.24
500m	83.00	0.00	3.74	0.38
1000m	79.00	0.00	6.43	0.51
Distance (km) to nearest:				
Contiguous forest	14.63	0.12	5.03	0.15
Virgin forest reserve (VJR)	20.71	0.05	5.93	0.19
Privately owned fragment	3.89	0.03	0.84	0.03
Plantation forestry	26.95	0.09	13.35	0.41
Large river	16.06	0.20	5.79	0.16
Other oil palm	8.66	0.04	2.96	0.10

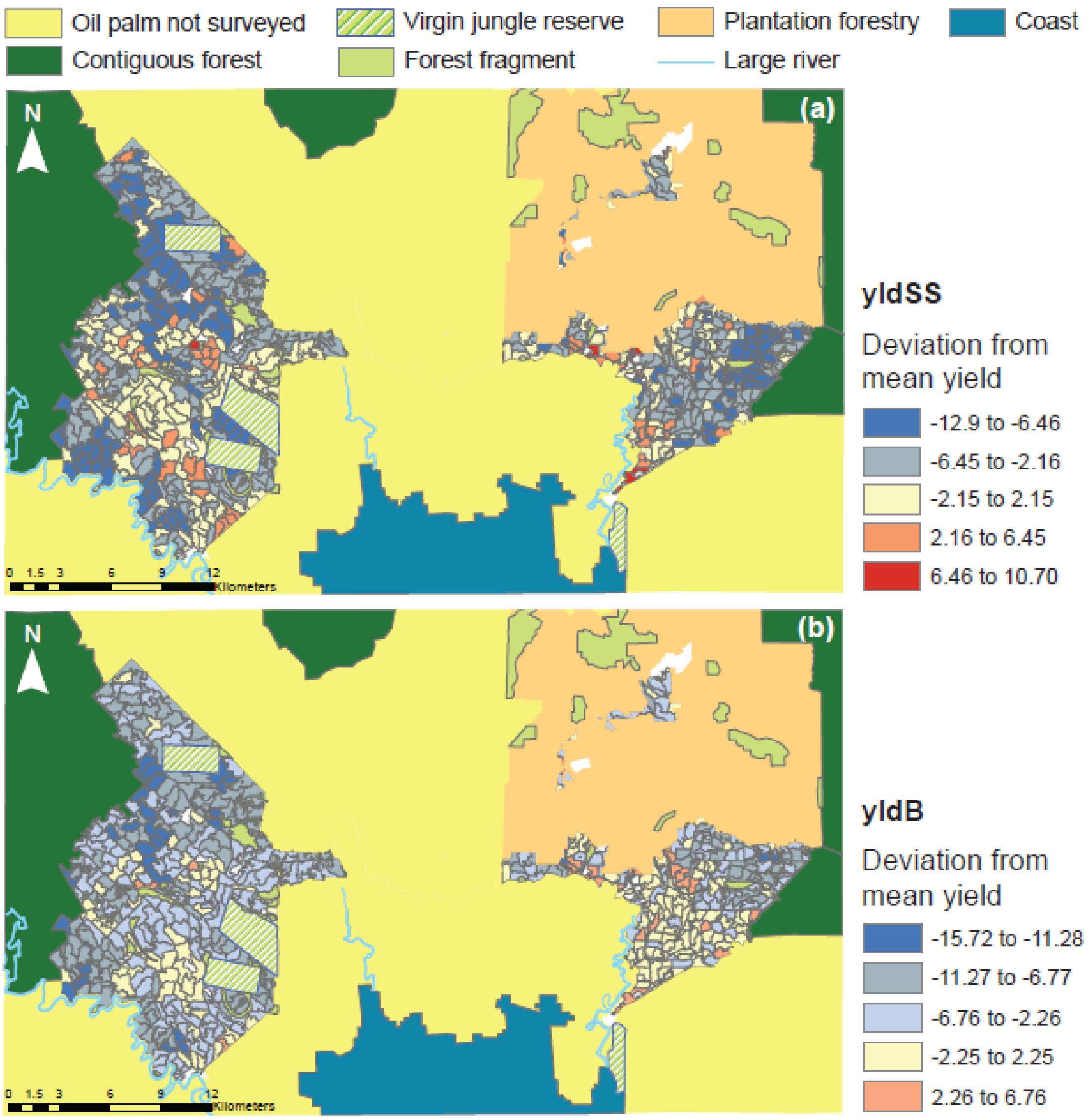

Figure 6.2: The variation in oil palm yield with adjacent land-uses across the study area. Oil palm yield is measured as the mean deviation from yield-by-age curves (a) generated from the study area data (yldSS), and (b) published by Butler et al. (2009) (yldB). Yield is quantified as the fresh fruit bunch weight per hectare (mt ha^{-1}).

Yield Response to Forest Cover

The distance-weighted area of forest cover was retained by the minimum adequate model (MAM), but it was not a significant predictor when yield was derived from either yield-by-age curves: i) the yield-by-age curve generated using Sabah Softwoods coupes (yldSS; GLS: $t_{499} = 1.52$, $P = 0.13$), and ii) Butler *et al.'s* (2009) average FFB yield-by-age curve (yldB; $t_{499} = 1.03$, $P = 0.30$) (Table 6.2). The environmental variables of elevation and distance to nearest forestry plantation were found to be significant predictors when yield was derived from Butler *et al.'s* (2009) average FFB yield-by-age curve (yldB; elevation: $t_{499} = -3.93$, $P < 0.01$, plantation: $t_{499} = -3.05$, $P < 0.01$) (Table 6.2). All model residuals had no spatial autocorrelation ($P \geq 0.39$).

Yield Response to Forest Proximity

Proximity to any of the three classes of dipterocarp forest (contiguous, VJR, or private fragment) did not have a significant effect on oil palm yield when considering yield derived from either yield-by-age curves (Table 6.2). Instead environmental variables were more important predictors when oil palm yield was derived from Butler *et al.'s* (2009) average FFB yield-by-age curve. Increasing elevation (Figure 6.3a; $t_{499} = -3.46$, $P < 0.01$) and increasing distance from tree plantation (Figure 6.3b; $t_{499} = -2.24$, $P = 0.03$) both had a significant negative effect on yield (Table 6.2). Proximity to large river or other oil palm plantation, size of private fragment, and soil type were not significant predictors of yield when using either yield-by-age curve. All model residuals had no spatial autocorrelation ($P \geq 0.06$).

Table 6.2: The estimates and parameter coefficients from the minimum adequate generalised least square models testing the effects of forest cover and forest proximity on oil palm yield across the study landscape in Sabah, Malaysian Borneo. Bold indicates significance at $P<0.001$.

Model	**Parameter**	**Estimate**	**SE**	**T**	***P***
Forest cover (yldSS*)					
	(Intercept)	-3.1284	0.6915	-4.5240	0.0000
	forest cover	20.2703	13.3163	1.5222	0.1286
Forest cover (yldB§)					
	(Intercept)	-0.6051	1.0429	-0.5802	0.5620
	forest cover	13.1835	12.7962	1.0303	0.3034
	elevation	**-0.0162**	**0.0041**	**-3.9334**	**0.0001**
	tree plantation	**-0.0002**	**0.0001**	**-3.0541**	**0.0024**
Forest proximity (yldSS)					
	(Intercept)	-1.2576	5.7548	-0.2185	0.8271
	contiguous forest	-0.0042	0.0423	-0.0985	0.9216
Forest proximity (yldB)					
	(Intercept)	-0.9506	1.2752	-0.7455	0.4563
	elevation	**-0.0143**	**0.0041**	**-3.4587**	**0.0006**
	tree plantation	**-0.0002**	**0.0001**	**-2.2356**	**0.0258**

* yldSS – yield estimate derived from the yield-by-age curve generated from Sabah Softwoods coupes.

§ yldB – yield estimate derived from the Butler et al.'s (2009) average FFB yield-by-age curve.

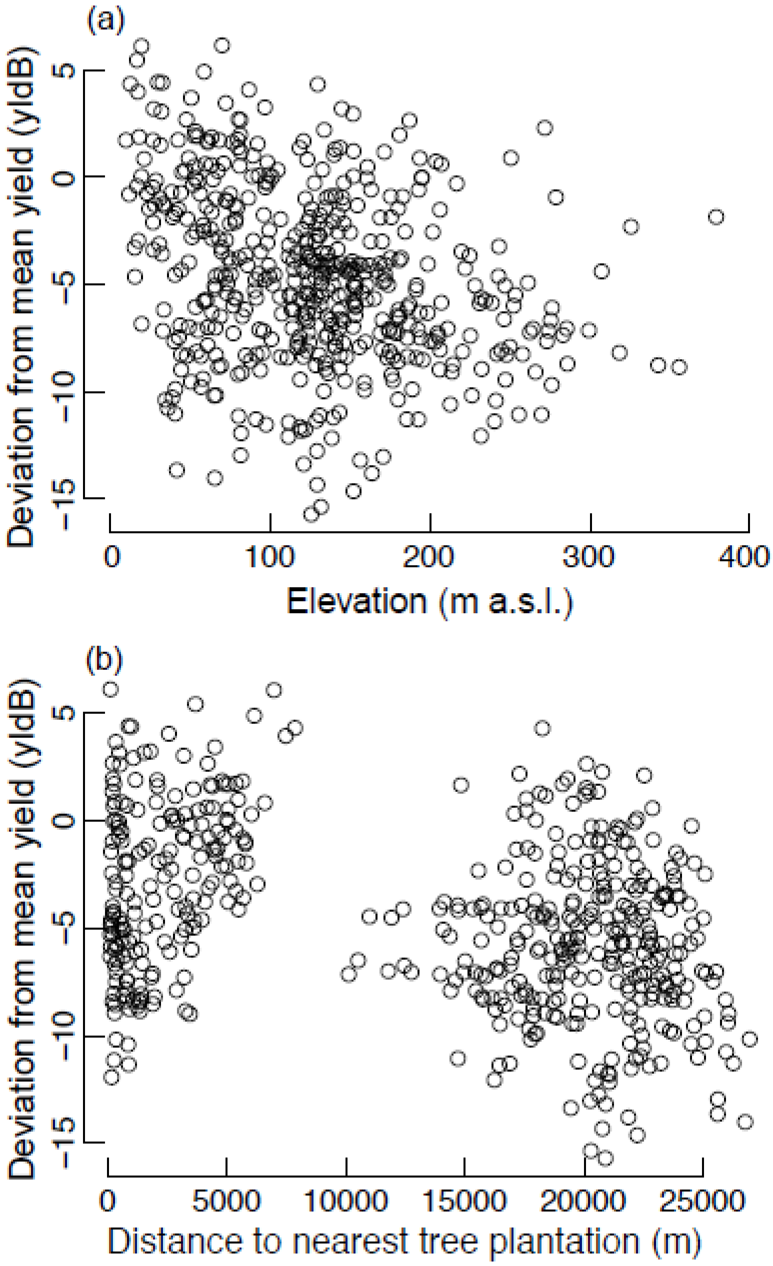

Figure 6.3: The relationship between oil palm yield and (a) elevation (m a.s.l.), and (b) distance to nearest non-native tree plantation. Oil palm yield was measured as the mean deviation from the yield-by-age curve generated from Butler et al. (2009) (yldB), and is quantified as the fresh fruit bunch weight per hectare (mt ha^{-1}).

Discussion

Agricultural expansion in the tropics is a key driver of the global biodiversity crisis. Pressure to mitigate threats from agriculture and improve sustainability has encouraged suggestions that the retention of natural habitat patches within and adjacent to tropical agriculture would result in the export of ecosystem services (Fischer et al. 2006; Koh 2008a; Perfecto & Vandermeer 2010; Foster et al. 2011; Tscharntke et al. 2012), including to oil palm (Bhagwat & Willis 2008; Koh et al. 2009). Yet the potential for spill-over of biodiversity from these features into the agricultural landscape Ricketts 2004; Lucey & Hill 2012), and in turn, whether this impacts upon crop yields positively or negatively has only received attention in the context of coffee and cocao agro-forestry plantations (Klein et al. 2003; Ricketts et al. 2004; Olschewski et al. 2006; Olschewski et al. 2010; Clough et al. 2011; Bisseleua et al. 2013). This study is thus the first to focus on the link between forest and crop yield in a tropical monoculture crop, focusing specifically on oil palm, which is rapidly expanding at the expense of forest and highly lucrative. Spill-over from forest is difficult to quantify (Kremen 2005), especially across large scales and when there are various taxa that may spill-over to different degrees and have contrasting impacts. In this study, I instead assess the impacts of the extent of local forest cover and of forest proximity on oil palm yield directly; I therefore did not focus on biodiversity *per se*, and a precise link between biodiversity and yield is absent.

Using both forest cover and proximity metrics, I found that the retention of dipterocarp forest had no significant effect on yield in oil palm monocultures, whereas the environmental variables of elevation and proximity to tree plantations did. These results provide a cautionary note for arguments that forest retention within monoculture landscapes can enhance ecosystem service provisioning and thus improve crop yields (Fischer et al. 2006; Koh 2008a; Perfecto & Vandermeer 2010; Foster et al. 2011; Tscharntke et al. 2012). They also do not support concerns that ecosystem dis-services, such as increased pest populations or mammal crop raiders, are a major issue resulting from the protection of HCV forests under the RSPO. Because I did not directly measure either ecosystem benefits or dis-services, I do not rule out that these are occurring. Rather, our results suggest that either there is an equal balance between ecosystem service benefits and dis-services, resulting in a net neutral impact on yield, or that there is no spill-over occurring. Across our monoculture landscape, it is likely to be a combination of these possibilities, with the former more likely close to forest where species are known to spill-over into oil palm, and the latter more likely far from forest.

These results suggest that there is no economic rationale for greater forest protection within and adjacent to oil palm monocultures. However, I acknowledge that riparian forest strips and larger fragments may have other important roles. They could provide hydrological and erosion prevention benefits, which might have longer-term benefits that cannot be quantified by focusing only on a single year of oil palm yield. These features could also provide biological benefits, harbouring some biodiversity (Benedick et al. 2006; Edwards et al. 2010; Hill et al. 2011) or by acting as stepping-stones and corridors for dispersal of species through the oil palm matrix (Koh 2008; Lucey & Hill 2012), which could be vital for retaining meta-population dynamics.

The optimum growing conditions of oil palm (*Elaeis sp.*) are in lowland wet tropics of <1000 m elevation (Corley & Tinker 2003): the negative effect of increasing elevation on yield is thus not surprising. This result highlights the limitation for future expansion of oil palm, especially in regions such as Southeast Asia where many of the prime locations have already been developed, and less optimum areas are already being considered and converted for oil palm development (Wicke et al. 2011). Proximity to tree plantations may provide some positive spillover, for example pest predation by birds, which are supported in greater numbers in tree plantations than oil palm (Sheldon et al. 2010; Styring et al. 2011). In other agricultural systems multi-cropping has been found to be beneficial (Perfecto et al. 2004; Tscharntke et al. 2012 and references there in), and this is an important future direction for optimal agricultural landscape design. However, these results should be interpreted with caution, because elevation and proximity to tree plantation are positively correlated (Pearson's correlation: $r = 0.12$, $p = 0.02$), with lower lying areas of higher oil palm yield also closer on average to tree plantations.

In this study, I did not consider the potential impacts of different management activities, such as the use of pesticides or permitting the growth of understory vegetation, or of palm condition (e.g. pest abundance, disease, or structural damage) on yield, which represent important next steps to disentangle drivers of yield change (Foster et al. 2011). With the exception of VJRs, which have only been lightly logged in patches, all of the forests in the study area have been selectively logged on an intensive, industrial scale. It is plausible that proximity to primary, unlogged forest could impact differently upon yield. However, this seems unlikely because previous work in the region has shown the retention of high levels of biodiversity, including most primary forest species (Berry et al. 2010; Edwards et al. 2011; Woodcock et al. 2011), and high functional diversity (Edwards et al. 2013; Senior et al. 2013) within contiguous blocks of logged forests. It is also possible that ecological services or dis-services from forest could affect palm oil quality, and hence price. Finally, I only focused on Southeast Asia and on one monoculture crop, and there could be different relationships between forest and yield in other tropical biomes, where oil palm is now expanding rapidly (Garcia-Ulloa et al. 2012), or with other crops such as soya and sugar cane.

Conclusion

These results show a neutral effect of forest on oil palm yield. Consequently, dipterocarp forests appear neither to export sufficient ecosystem service benefits to result in a net increase in yield nor to export sufficient ecosystem dis-services to result in a net reduction of yield within oil palm plantations. I therefore observed no evidence to support arguments for the retention of forest for the provision of ecosystem services explicitly for yield benefits within oil palm monocultures (Koh 2008a; Foster et al. 2011). Many arguments have been made for implementing an integrated framework of agricultural design, which considers biodiversity conservation, ecosystem services and agricultural output (Foster et al. 2011; Schroth & McNeely 2011; Phalan et al. 2013). These are to be warmly welcomed, but in light of this study the proposed benefits of such designer landscapes within monocultures should avoid couching arguments for forest retention in the context of yield benefits. I finish by urging for more empirical assessments of the impacts of forest and biodiversity on crop monoculture yields to better understand their potential role in sustainable agriculture: I fear that by resting arguments for the retention of forest on improved oil palm yield, there could be unintended consequences such as the clearance of retained forest patches and thus the removal of refugia for biodiversity if no such empirical support were to emerge.

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Chapter 7: General Discussion

Global conservation planning and policy with anthropogenic land-use change

Biodiversity, people and economics

Increase pressure for land-use change is among the biggest challenges that conservation faces (Laurance, Sayer & Cassman 2014; Newbold *et al.* 2016). Logging and the conversion of forest to agriculture have severe impacts on biodiversity and the functioning of communities (Flynn *et al.* 2009; Sodhi *et al.* 2010; Smith *et al.* 2010; Newbold *et al.* 2015; Chapter 2,3,4), and more widely the structure of the landscape (chapters 5,6). A better understanding of the micro-, meso- and landscape-scale impacts of land-use change is essential for conservation efforts aimed at finding an optimum balance between protecting biodiversity and meeting the demands of a global economic market (Sodhi *et al.* 2011).

We are now faced with a new age of conservation where economics, social development and human welfare are increasingly considered when addressing conservation concerns (DeFries, Foley & Asner 2004; Sayer *et al.* 2013; Laurance *et al.* 2014; Reed *et al.* 2016). Isolated untouched national parks are increasingly rare, existing reserves are increasingly being downgraded in their protection status, reduced in size or degazetted (no protection given) to allow the extraction of resources, hydropower, human settlement or the conversion to agriculture (PADDD - Laurance *et al.* 2012; Pack *et al.* 2016; Mascia *et al.* 2014). For conservation to be effective, we must apply research knowledge and evidence to different scenarios through engagement with practitioners, governmental and non-governmental organisations and other stakeholders. Integrated strategies for conservation that accept a degree of natural habitat loss or degradation but with specific biodiversity and environmental goals are the new reality, but for these to be robust they must consider characteristics of vulnerability for protected areas (Laurance *et al.* 2012; Symes *et al.* 2016).

Sampling limitations

Although all measures were taken to ensure that data collections were as thorough and accurate as possible there are specific limitations to rainforest sampling, principally the issue of detectability, which in a highly specious and vertically structured environment is particularly poignant. The avian data set was collected using point counts, which gave the most realistic estimation of communities (see methods of chapter 2). Most of the individuals recorded were heard not seen which is more reliable in a complex environment such as a rainforest, between forest habitats the overall structure did not differ such that the detection of acoustics would vary, indeed the only increase in detectability would have been in the more open oil palm plantations, yet community differences were still significantly reduced with this potential bias towards increasing the value of oil palm plantations (chapter 2). Furthermore, alternative methods have their own specific limitations; mist netting only samples understory species (though results using these techniques show comparative results across habitats – Edwards et al. 2011); while recording devices (acoustic recognition) would suffer complications with background interference from insects and the reduced detectability with increasing vertical stratification, as well as difficulties distinguishing song or call variations which in person potentially can be checked with visual sightings.

The dung beetle sampling technique I used is an attractant form of pitfall trapping, which creates potential bias for over sampling as individuals, from an unknown distance, fly to the trap. Alternative trapping techniques, such as flight intercept traps and non-attractant pitfall traps however, collect extremely few individuals from a small subset of the overall community (pers comm). Dung is used as the attractant as the majority of species feed upon this resource, and only a few specialist species (carrion, fruit or fungi feeders) will be missed from the community by using it. Maintaining standardised protocols and ensuring sampling effort was consistent was the best solution to the issue of detectability, with traps a minimum of 50m apart but often 100m apart to increase the likelihood of independence. I note however that primary rainforest is likely to be the most under sampled community, with single unique individuals still being samples after hundreds of sampling hours, though differences were still observed compared to other habitats (chapters 2, 3, 4, 5).

The value of a functional approach

Anthropogenic land-use change alters the provision of ecosystem functions and services provided by biological communities and habitats, such as water catchment protection, carbon storage or pollination (Lambin, Geist & Lepers 2003; Foley *et al.* 2005; Lewis, Edwards & Galbraith 2015). Changes to the way an ecosystem functions has important implications for how communities are structured, how ecological processes occur, and in turn how ecosystem services are provided. Therefore at a finer scale, taking a functional approach to assessing communities after disturbance allows for a more complete picture of community resilience, composition and assembly (chapters 2, 3, 4, 5). For example, forest conversion to agriculture had a more dramatic impact on the functional diversity of communities compared to forest degradation via selective logging, which retained similar levels of overall functional diversity to primary rainforest for birds and dung beetles (chapters 2, 3). Furthermore, the assembly structure of dung beetle communities remained similar between primary and logged forests, while the influence of habitat filtering increased in oil palm plantations (chapter 4).

Logged forests were, however, less functionally diverse than expected by chance for birds, suggesting strong environmental filtering effects (chapter 2). Logged forests have altered vegetation structure (Berry *et al.* 2008; Ansell, Edwards & Hamer 2011), and consequently likely changes to micro-habitat availability and micro-climates compared to primary forest, these shifts are influential for avian communities (e.g. relating to nesting, foraging or physiology of certain species) but not strongly for dung beetles (chapters 2 & 3). This may have been because mammalian populations responsible for providing dung are often maintained or increase in logged forests (Berry *et al.* 2008; Meijaard & Sheil 2008), therefore food resources which dung beetles are often suggested to be limited by are not a restricting factor. Although the interior of logged forests retained similar biodiversity and functional resilience to primary forest, specifically investigating road edges within logged forest highlighted the long-lasting functional and community impacts of logging infrastructure (chapter 5). Overall, changing patterns of species co-occurrence, across three taxonomic groups, was strongly influenced by random assembly filters (chapter 4). However, these changes in abundances and shifts in the numerical dominance of different species could lead to particular functions being lost (Kremen 2005). These results highlight the need for varying and broad-ranging investigations including functional elements, to more fully understand community dynamics.

Emerging topics in functional ecology look to examine the turnover of species in relation to ecosystem functioning, and further explore the intra-specific differences in functional traits, how specific environmental features influence functional processes and directly linking functional diversity with functional provisions (Weiher *et al.* 2011; Griffiths *et al.* 2016). Furthermore, understanding the spatial variation of functional traits and diversity (Craven *et al.* 2016), and the potential for trait evolution with disturbance is a virtually unexplored topic. This gives vital understanding of how communities are structured, how species react to land-use change, and how knowledge of ecosystem functions and services can be incorporated into decision making (DeFries, Foley & Asner 2004). Importantly, because ecosystem functions and services often occur at different spatiotemporal scales, this creates an inherent complexity of how communities interact with the environment and increasingly with anthropogenic land-use change (Kremen 2005; du Toit 2010; Cimon-Morin, Darveau & Poulin 2013), which poses difficulties incorporating ecosystem functions and services into policy (Perrings *et al.* 2010). However, without acknowledging finer scale ecology we cannot understand at a larger scale what we need to conserve and how best this is achieved (DeFries *et al.* 2010). Finding ways to bridge the gap between different scales of knowledge and understanding is essential for future conservation successes.

Using a functional approach to assessing communities, habitats or ecosystems is unquestionably a valuable exercise, and research outputs should be communicated more freely and accessibly to key practitioners. Knowledge of functional traits can be specified to specific questions, and from baseline biodiversity surveys numerous follow on questions can be investigated by considering species' functional traits. However, the availability of trait matrix information can be restrictive and assembling such data may be time-consuming for specific taxonomic groups and regions. Therefore the ability for practitioners to use these techniques in-situ has its limitations, however using knowledge from other studies (i.e. functional traits, ecosystem functioning and interaction networks) combined with broader landscape information can be an informative approach. In chapter 6, for example, I use previous knowledge of the biodiversity value of degraded forest and remnant forest patches within the oil palm landscape as a proxy for potential ecosystem services or dis-services. Although there is debate over the validity of using proxies for ecosystem functions and services (see references in Stephens *et al.* 2015), if the scale, region and outcomes are specifically considered, and recommendations are given with caution, generalising specific biodiversity knowledge at a landscape scale can allow applied questions to be answered and landscape planning to be better informed (see chapters 5 and 6).

Functional diversity research is frequently used to address conservation related issues, and is often strongly linked to ecosystem processes and services. Without testing these elements simultaneously functional diversity metrics alone have little weigh when addressing the specific conservation of ecosystem services. Throughout this thesis, however I believe the investigation of functional diversity is shown to be a powerful tool to; focus the need, give support to and to promote the protection of logged forests by highlighting the wider biodiversity value of selectively logged forests (see chapters 2 and 3). This ‘value’ is especially important within HCV assessments and in turn meeting RSPO or FSC criteria, as well as government guidelines for forest protection status. Selectively logged forests have varied appreciation and value between countries and states. In Sabah, Malaysia, where this thesis research is based, ~95,000 ha of Class II commercial forest reserve has *de facto* protection from further logging which is vital for conservation in this biodiversity hotspot (Reynolds et al. 2011), and with time there is hope this may be increased to Class I protection (the highest available land protection status). Often, however there is little protection from further degradation or conversion, in Indonesia the 2010 moratorium on new plantations excluded logged forests, this missed a significant opportunity to highlight the government’s commitment to reducing forest emissions (Sloan et al. 2012). Furthermore, increasing the awareness and value of selectively logged forests is critical to avoid further deforestation, for example in Indonesia between 2000 and 2010 25% of ‘natural timber concessions’ were reclassified to ‘industrial plantation concessions’ allowing the legalisation of deforestation (Gaveau et al. 2013). Gathering evidence for the protection of logged forest is thus vital for the conservation of Southeast Asian lowland rainforest ecosystem and the species there in. With little overall forest cover left in the region after decades of conversion to agriculture (principally oil palm and rubber plantations), areas of selectively logged forest are pivotal to the future conservation of the region when combined with the remaining primary forest (see Gaveau et al. 2013 and references there in).

Land-use planning for Conservation

The spatial extent and prioritisation of protected areas is an important element of conservation, however as the demand for land increases conservation discussions focus increasingly on how best to manage and design landscapes within and around anthropogenic developments (i.e. concessions, mines, infrastructure and agricultural environments) to benefit biodiversity and ecosystem services (Hansen & DeFries 2007; Smith *et al.* 2010; Lambin & Meyfroidt 2011; Gilroy *et al.* 2014; Reed *et al.* 2016). The use of integrated mapping of data can bring together a wealth of knowledge towards global, regional and local conservation aims, using techniques such as land-use zonation for target-based planning. Recent studies have evaluated environmental value and agricultural potential to create a strategy for road construction (Laurance *et al.* 2014), and mapped potential protected area expansion to meet Aichi targets (Di Marco *et al.* 2016).

I explored two key aspects for understanding how to manage biodiversity within selective logging concessions and oil palm plantations; the impact of logging roads to evaluate the long term implications on biodiversity (chapter 5) and the value of remnant forest patches within oil palm plantations for yield output (chapter 6). Declines in dung beetle community and functional metrics, and shifts in community composition were found to penetrate 100m into the logged forest away from logging roads, more than 20 years after logging ceased (chapter 5). These results are likely to indicate a similar response of mammals and more widely other taxonomic groups, and are comparable to studies of birds in the Amazon (Laurance, Stouffer & Laurance 2004). Under a best case scenario, which this study concession represents, due to very limited assess (chapter 5), a significant area of logged forest is impacted (871km^2) highlighting the expansive impacts of roads, and something which will increase with road density. Land-use planning for selective logging practices must acknowledge the long term and spatially extensive impacts through better designed concessions.

Low impact extraction methods help to reduce soil damage and collateral damage, and carbon, timber yields and biodiversity all benefit from such techniques, yet more attention is needed to increase the sustainability of forest management (Putz *et al.* 2008). Initial planning of road systems should emphasise minimising the size and extent of roads as well as skid trails, which would maintain connectivity and reduce overall habitat degradation, secondary damage and edge effects (Pinard & Cropper 2000; Wilcove *et al.* 2013; Bicknell, Struebig & Davies 2015). Additionally, I think developing criteria based around a minimum volume of timber which can be extracted per km of road would prevent long stretches of road being developed (and in turn the primary and secondary damage that follows) for a handful of trees. Furthermore, concession planning must consider future logging rotations to effectively close logging roads to allow regeneration and prevent encroachment, yet allow re-assess in key areas for subsequent timber harvests to prevent new roads from being constructed (Bicknell *et al.* 2015; Kleinschroth, Healey & Gourlet-Fleury 2016).

Incorporating spatial analyses and mapping of tree species distributions, growth rates, sampling establishment and topography, along with projected timber values would allow for multiple logging rotations to be mapped for the most efficient extraction, yet coupled with a road system designed for minimal ecological impact. Indeed new concessions are embracing technology to accurately measure and record trees in initial inventories, which allows more precise cutting, and the removal of target species and volumes during extraction. Incorporating such ideas into certification or government requirements (i.e. restrictions and guidelines around road construction and closures) could be a future development to increase the uptake of sustainability in logging practices and increase the conservation of forests, as the long term management of logging concessions is rarely the most economically valuable use of land (Fisher *et al.* 2011), and added incentives are likely to promote better management practices. How road network design can be practically enforced and integrated into logging practices, government guidelines or certification schemes is an important question to address. Variations in; political and financial stability, openness to change, willingness to adopt environmentally focused policies and levels of corruption mean a universal approach will require adaptation at the country and regional level to ensure conservation policies can be successfully applied. Furthermore, understanding how wide logging roads should be or how they can be planned more efficiency to maximise yield but minimise habitat damage are important questions to ensure sustainable timber practices.

Within agricultural systems there is a careful balance needed between in-situ and ex-situ preservation of natural habitat (Koh, Levang & Ghazoul 2009; Phalan *et al.* 2011; Fischer *et al.* 2014). An array of remnant habitat often remains within monocultures, such as isolated trees, fragments or riparian strips, however the conservation and biodiversity value of these varies depending on context and scale. Encouraging biodiversity and natural habitat within an agricultural environment can have clear benefits, for example through maintaining riparian strips to protect quality of water supplies, providing habitat for pollinators to enhance yield, or acting as a stepping stone for biodiversity (Duelli & Obrist 2003; Klein, Steffan-Dewenter & Tscharntke 2003; Broadmeadow & Nisbet 2004; Hawes *et al.* 2008; Herrera & Garcia 2009). However, putting too much effort into conserving remnant (particularly small) habitat patches may compromise the ability to conserve a much large area of habitat outside of the agricultural environment, which is frequently shown to be better for conservation (Edwards *et al.* 2010). Indeed, chapter 6 provides no evidence of any gain in oil palm fruit yield from proximity to forest within plantations, therefore providing further support for the conservation of large tracks of contiguous forest. Furthermore, in selectively logged forest, I show that edge effects from logging roads persist long after logging has ceased (chapter 5), therefore irrespective of the amount of timber that is removed the construction of a logging road will entail a large impact on biodiversity, thus supporting the conservation of a large road-free area of forest under a land-sparing approach (Edwards *et al.* 2014). Palm oil remains one of the biggest global crops, and there is strong evidence that oil palm plantations support minimal biodiversity (chapter 2 & 3), future research therefore needs to focus on ensuring habitat protection (e.g. rainforest or Imperata grassland) for example through no deforestation policies, and in turn how the uptake of certification can be increased.

Moving forwards – a balance of scales for integrated management

As land availability decreases and human population demands grow the conflict for land and resources increases, and thus a trade-off between economic development, food security, intrinsic biodiversity and ecosystem services must be met. These interacting aims occur at global, regional and local scales and are influenced by various factors also occurring at different scales. The scale at which land-use change and its associated effects are observed, monitored, and managed influences greatly our understanding of biodiversity and the approach taken to conserving ecosystems (chapter 4; Kremen 2005; DeFries *et al.* 2010; du Toit 2010; Sayer *et al.* 2013). Modelling the landscape as an open system, with local-scale land-uses tied to the global-scale flow of trade has been suggested as a means of accepting and utilising globalisation (Lambin & Meyfroidt 2011). For example, the promotion and increased adoption of new and sustainable agricultural practices through certification schemes could provide local scale benefits to biodiversity and landscape configuration (i.e. reducing fragmentation, increasing connectivity) by a global scale initiative that aims to target the global production of key commodities. However, increasing incentives to adopt such schemes, such as higher commodity prices or increased pressure from multi-national companies are likely to be necessary for certification schemes to have their full effect (Lambin & Meyfroidt 2011; Putz *et al.* 2012; Edwards & Laurance 2012).

More broadly, utilising sources of data from different scales for integrated spatially managed approaches for land-use conservation can help meet the balance between forest and agriculture (Lambin & Meyfroidt 2011). Remote sensing and GIS techniques can provide a low cost, large scale effective means for land-use conservation through monitoring, planning, and research (Chambers *et al.* 2007;

Bustamante *et al.* 2016). Moving forwards I believe the most important next step for conservation in Sabah, and in turn across Southeast Asia, is to assess the spatial arrangement, connectivity and value of the remaining forests within this highly disturbed region. There are few remaining areas of undisturbed forest in the region, and increasingly degraded (often selectively logged) forests, which are frequently shown to be highly valuable (Berry et al. 2010; Edwards et al. 2011, chapters 2,3, 5), are also diminishing (Gaveau et al. 2016). I therefore think it is pivotal for us to map and prioritise conservation efforts in a region of highly fragmented forest refugium to allow limited conservation funds and resources to be managed where there is most likely to be a positive outcome for conservation and local people. By documenting areas; in need of greater protection; with potential for restoration (which could aid connectivity); and those best suited for conversion and development, conservation bodies and governments alike can prioritise the use of precious land. There is a wealth of spatial data and analyses to allow us to map changes over time and project future changes relative to multiple factors (i.e. population growth, economic demand for crops, climate change) for forest cover, biodiversity and to a degree ecological functions and processes (Peres, Barlow & Laurance 2006; Chambers *et al.* 2007; Asner *et al.* 2009; Bustamante *et al.* 2016). I think it is critical to concentrate such efforts into understanding how large tracks of forest, whether it be primary or selectively logged, can be protected and managed (in the case of land under a logging concession license), and in turn which areas could be restored. I note that restoration is a difficult process, especially in the region as there is no seed bank but by specifically mapping key areas which will connect and enlarge existing tracks of forest, conservation resources are less likely to be wasted. Governments should also be encouraged to prevent conversion of forest (including logged forest) to plantations, specifically logging concessions should be encouraged to be classified under the

IUCN protected area category VI as a *natural timber concession* and therefore protect them from reclassification and thus deforestation (Gaveau et al. 2013). Furthermore, I think it is critical to encourage plantation managers to restore riparian strips, maintain existing forest fragments (i.e. prevent poaching and timber extraction), and improve pesticide use to prevent water pollution. However, I think there is a careful balance needed as conservation efforts and resources can easily be wasted in in-situ conservation within plantations, which have frequently been shown to be poorly diverse (chapters 2,3; Foster et al. 2011), and those species which remain are often of little conservation concern. Whereas logging concessions provide a unique opportunity to maintain and boost biodiversity, vast areas, especially in Sabah, are now not viable for harvesting for a significant period of time and as a long as these areas are protected they provide an ideal habitat for the majority of species. In other parts of Southeast Asia and indeed globally, where logging is in its infancy it is critical that concessions can be managed with minimal secondary damage. Roads are a critical and obvious point of habitat destruction, and I believe an aspect which enforcement can be applied to maximise timber extraction but also benefiting biodiversity. Plantations and logging concessions provide a huge amount of the economic wealth of the countries in this region and conservation therefore must work with them to create conservation successes.

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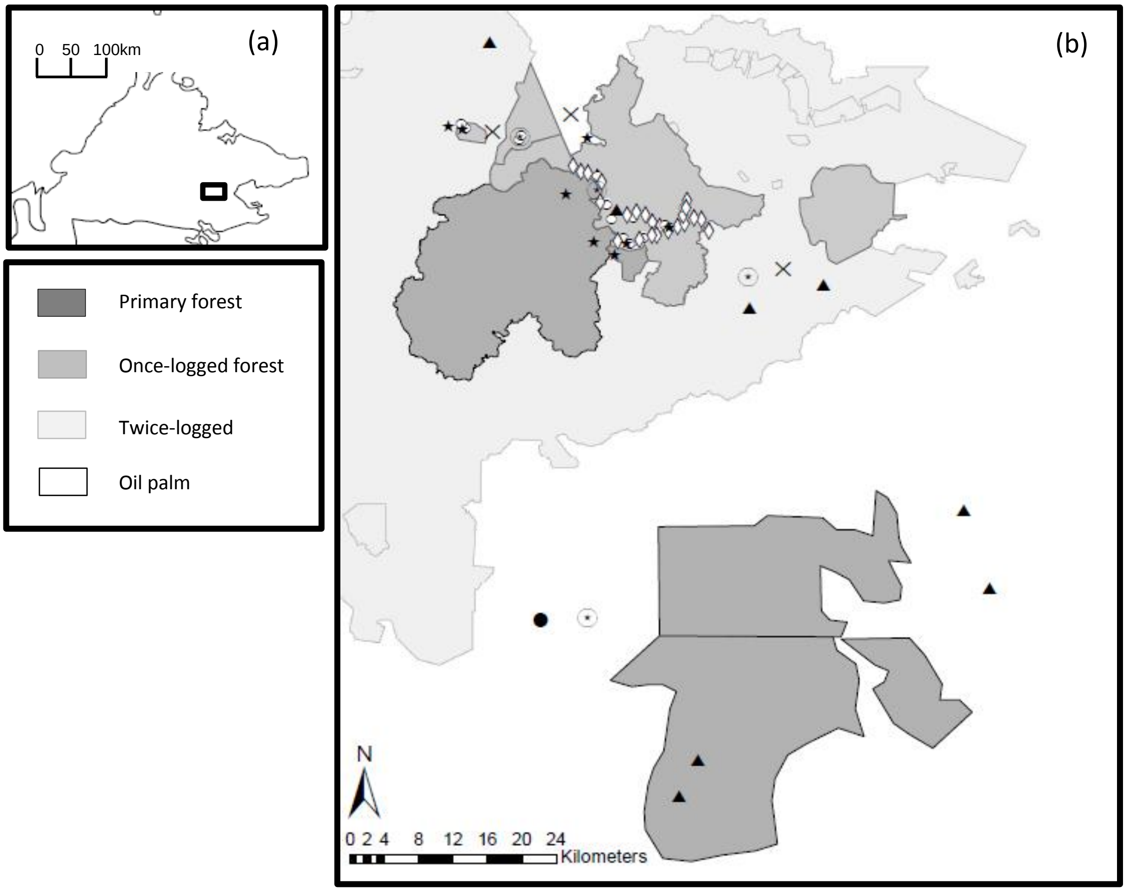
Appendices

Appendix 1



Appendix 1: (a) A map of Sabah, Malaysian Borneo. The box outlines the study area. (b) A map of the study area. The dark grey solid area represents primary rainforest, mid-grey solid area represents once-logged forest, light-grey solid area represents twice-logged forest, and the adjacent white area represents oil palm plantations. The symbols on the map identify the sampling sites across the chapters in this thesis; solid stars represent sites where dung beetles, birds and ants were sampled for chapter 4, plus sites for chapters 2 & 3; solid stars encased in an open circle represents where dung beetles, birds and ants were sampled for chapter 4 and were also used in chapter 3; a cross represents where dung beetles and birds were sampled for chapter 4, as well as chapter 3; solid circles were where dung beetles were sampled only for chapters 3 & 4; solid triangles are where birds were sampled only for chapters 2 & 4; white diamonds represent road edge plots where dung beetles were sampled for chapter 5; white circles represent control plots where dung beetles were sampled for chapter 5.

Appendix 2

Bird species recorded in the study area with their associated number (#) codes used in the RLQ plot in chapter 2 (Figure 2.4).

Common species name	Scientific species name	# Code
Arctic Warbler	*Phylloscopus borealis*	1
Ashy Tailorbird	*Orthotomus ruficeps*	2
Asian Black Hornbill	*Anthracoceros malayanus*	3
Asian Brown Flycatcher	*Muscicapa dauurica*	4
Asian Fairy-Bluebird	*Irena puella*	5
Asian Glossy Starling	*Aplonis panayensis*	6
Asian Paradise-Flycatcher	*Terpsiphone paradisi*	7
Banded Bay Cuckoo	*Cacomantis sonneratii*	8
Banded Broadbill	*Eurylaimus javanicus*	9
Banded Kingfisher	*Lacedo pulchella*	10
(Bornean) Banded Pitta	*Pitta guajana (schwaneri)*	11
Banded Woodpecker	*Picus mineaceus*	12
Bar-winged Flycatcher-Shrike	*Hemipus picatus*	13
Black Eagle	*Ictinaetus malayensis*	14
Black Magpie	*Platysmurus leucopterus*	15
Black-and-red Broadbill	*Cymbirhynchus macrorhynchos*	16
Black-and-yellow Broadbill	*Eurylaimus ochromalus*	17
Black-backed Kingfisher	*Ceyx erithaca*	18
Black-capped Babbler	*Pellorneum capistratum*	19
Black-headed Bulbul	*Pycnonotus atriceps*	20
Black-headed Munia	*Lonchura malacca*	21
Black-headed Pitta	*Pitta ussheri*	22
Black-naped Monarch	*Hypothymis azurea*	23
Black-throated Babbler	*Stachyris nigricollis*	24
Black-throated Wren-Babbler	*Napothera atrigularis*	25
Black-winged Flycatcher-Shrike	*Hemipus hirundinaceus*	26
Blue-banded Pitta	*Pitta arcuata*	27
Blue-crowned Hanging-Parrot	*Loriculus galgulus*	28
Blue-eared Barbet	*Megalaima australis*	29
Blue-headed Pitta	*Pitta baudii*	30
Blue-rumped Parrot	*Psittinus cyanurus*	31
Blue-throated Bee-eater	*Merops viridis*	32
Bold-striped Tit-Babbler	*Macronous bornensis*	33
Bornean Blue-Flycatcher	*Cyornis superbus*	34
Bornean Bristlehead	*Pityriasis gymnocephala*	35
Bornean Ground-Cuckoo	*Carpococcyx radiatus*	36
Bornean Ground-Babbler	*Ptilocichla leucogrammica*	37
Brahminy Kite	*Haliastur indus*	38
Brown Barbet	*Calorhamphus fuliginosus*	39
Brown Fulvetta	*Alcippe brunneicauda*	40
Buff-necked Woodpecker	*Meiglyptes tukki*	41
Buff-rumped Woodpecker	*Meiglyptes tristis*	42
Buff-vented Bulbul	*Iole olivacea*	43
Bushy-crested Hornbill	*Anorrhinus galeritus*	44
Cattle Egret	*Bubulcus ibis*	45
Changeable Hawk-Eagle	*Spizaetus cirrhatus*	46
Chequer-throated Woodpecker	*Picus mentalis*	47
Chestnut-backed Scimitar-Babbler	*Pomatorhinus montanus*	48

Appendix 2: *(continued)*

Common species name	Scientific species name	# Code
Chestnut-breasted Malkoha	*Phaenicophaeus curvirostris*	49
Chestnut-capped Thrush	*Zoothera interpres*	50
Chestnut-naped Forktail	*Enicurus ruficapillus*	51
Chestnut-necklaced Partridge	*Arborophila charltonii*	52
Chestnut-rumped Babbler	*Stachyris maculata*	53
Chestnut-winged Babbler	*Stachyris erythroptera*	54
Cinnamon-rumped Trogon	*Harpactes orrhophaeus*	55
Collared Kingfisher	*Todiramphus chloris*	56
Cream-vented Bulbul	*Pycnonotus simplex*	57
Crested Fireback	*Lophura ignita*	58
Crested Goshawk	*Accipiter trivirgatus*	59
Crested Jay	*Platylophus galericulatus*	60
Crested Partridge	*Rollulus rouloul*	61
Crested Serpent-Eagle	*Spilornis cheela*	62
Crimson Sunbird	*Aethopyga siparaja*	63
Crimson-winged Woodpecker	*Picus puniceus*	64
Dark-necked Tailorbird	*Orthotomus atrogularis*	65
Dark-sided Flycatcher	*Muscicapa sibirica*	66
Dark-throated Oriole	*Oriolus xanthonotus*	67
Diard's Trogon	*Harpactes diardii*	68
Dollarbird	*Eurystomus orientalis*	69
Drongo Cuckoo	*Surniculus lugubris*	70
Dusky Broadbill	*Corydon sumatranus*	71
Dusky Munia	*Lonchura fuscans*	72
Emerald Dove	*Chalcophaps indica*	73
Ferruginous Babbler	*Trichastoma bicolor*	74
Fiery Minivet	*Pericrocotus igneus*	75
Finsch's Bulbul	*Alophoixus finschii*	76
Fluffy-backed Tit-Babbler	*Macronous ptilosus*	77
Giant Pitta	*Pitta caerulea*	78
Gold-whiskered Barbet	*Megalaima chrysopogon*	79
Great Argus	*Argusianus argus*	80
Great Slaty Woodpecker	*Mulleripicus pulverulentus*	81
Greater Coucal	*Centropus sinensis*	82
Greater Green Leafbird	*Chloropsis sonnerati*	83
Greater Racket-tailed Drongo	*Dicrurus paradiseus*	84
Green Broadbill	*Calyptomena viridis*	85
Green Imperial-Pigeon	*Ducula aenea*	86
Green Iora	*Aegithina viridissima*	87
Grey-and-buff Woodpecker	*Hemicircus concretus*	88
Grey-bellied Bulbul	*Pycnonotus cyaniventris*	89
Grey(Streaky)-breasted Spiderhunter	*Arachnothera affinis*	90
Grey-cheeked Bulbul	*Alophoixus bres*	91
Grey-chested Jungle-Flycatcher	*Rhinomyias umbratilis*	92
Grey-headed Babbler	*Stachyris poliocephala*	93
Grey-headed Canary-Flycatcher	*Culicicapa ceylonensis*	94
Grey-rumped Treeswift	*Hemiprocne longipennis*	95
Hairy-backed Bulbul	*Tricholestes criniger*	96

Appendix 2: *(continued)*

Common species name	Scientific species name	# Code
Helmeted Hornbill	*Rhinoplax vigil*	97
Hill Myna	*Gracula religiosa*	98
Hooded Pitta	*Pitta sordida*	99
Horsfield's Babbler	*Malacocincla sepiaria*	100
Indian Cuckoo	*Cuculus micropterus*	101
Jerdon's Baza	*Aviceda jerdoni*	102
Large Green-Pigeon	*Treron capellei*	103
Large Woodshrike	*Tephrodornis gularis*	104
Large-billed Blue-Flycatcher	*Cyornis caerulatus*	105
Lesser Cuckoo-Shrike	*Coracina fimbriata*	106
Lesser Fish-Eagle	*Ichthyophaga humilis*	107
Lesser Green Leafbird	*Chloropsis cyanopogon*	108
Little Bronze-Cuckoo	*Chrysococcyx minutillus*	109
Little Egret	*Egretta garzetta*	110
Little Green-Pigeon	*Treron olax*	111
Little Spiderhunter	*Arachnothera longirostra*	112
Long-billed Spiderhunter	*Arachnothera robusta*	113
Long-tailed Parakeet	*Psittacula longicauda*	114
Magpie Robin	*Copsychus saularis*	115
Malaysian Blue-Flycatcher	*Cyornis turcosus*	116
Mangrove Blue-Flycatcher	*Cyornis rufigaster*	117
Maroon Woodpecker	*Blythipicus rubiginosus*	118
Maroon-breasted Philentoma	*Philentoma velata*	119
Moustached Babbler	*Malacopteron magnirostre*	120
Moustached Hawk-Cuckoo	*Cuculus vagans*	121
Olive-backed Sunbird	*Cinnyris jugularis*	122
Olive-backed Woodpecker	*Dinopium rafflesii*	123
Olive-winged Bulbul	*Pycnonotus plumosus*	124
Orange-backed Woodpecker	*Reinwardtipicus validus*	125
Orange-bellied Flowerpecker	*Dicaeum trigonostigma*	126
Orange-breasted Trogon	*Harpactes oreskios*	127
Oriental Honey-Buzzard	*Pernis ptilorhyncus*	128
Oriental Pied Hornbill	*Anthracoceros albirostris*	129
Pale Blue-Flycatcher	*Cyornis unicolor*	130
Pied Fantail	*Rhipidura javanica*	131
Plain Sunbird	*Anthreptes simplex*	132
Plain(Brown)-throated Sunbird	*Anthreptes malacensis*	133
Plaintive Cuckoo	*Cacomantis merulinus*	134
Puff-backed Bulbul	*Pycnonotus eutilotus*	135
Purple-naped Sunbird	*Hypogramma hypogrammicum*	136
Purple-throated Sunbird	*Nectarinia sperata*	137
Raffles's Malkoha	*Phaenicophaeus chlorophaeus*	138
Red-bearded Bee-eater	*Nyctyornis amictus*	139
Red-eyed Bulbul	*Pycnonotus brunneus*	140
Red-naped Trogon	*Harpactes kasumba*	141
Red-throated Barbet	*Megalaima mystacophanos*	142
Red-throated Sunbird	*Anthreptes rhodolaema*	143
Rhinocerous Hornbill	*Buceros rhinoceros*	144

Appendix 2: *(continued)*

Common species name	Scientific species name	# Code
Ruby-cheeked Sunbird	*Chalcoparia singalensis*	145
Rufous Piculet	*Sasia abnormis*	146
Rufous Woodpecker	*Celeus brachyurus*	147
Rufous-bellied Eagle	*Hieraaetus kienerii*	148
Rufous-chested Flycatcher	*Ficedula dumetoria*	149
Rufous-crowned Babbler	*Malacopteron magnum*	150
Rufous-fronted Babbler	*Stachyris rufifrons*	151
Rufous-tailed Shama	*Trichixos pyrropygus*	152
Rufous-tailed Tailorbird	*Orthotomus sericeus*	153
Rufous-winged Philentoma	*Philentoma pyrhoptera*	154
Scaly-crowned Babbler	*Malacopteron cinereum*	155
Scarlet Minivet	*Pericrocotus flammeus*	156
Scarlet-rumped Trogon	*Harpactes duvaucelii*	157
Short-tailed Babbler	*Malacocincla malaccensis*	158
Short-toed Coucal	*Centropus rectunguis*	159
Slender-billed Crow	*Corvus enca*	160
Sooty-capped Babbler	*Malacopteron affine*	161
Spectacled Bulbul	*Pycnonotus erythropthalmos*	162
Spotted Dove	*Streptopelia chinensis*	163
Spotted Fantail	*Rhipidura perlata*	164
Streaked Bulbul	*Ixos malaccensis*	165
Striped Wren-Babbler	*Kenopia striata*	166
Thick-billed Green-Pigeon	*Treron curvirostra*	167
Thick-billed Spiderhunter	*Arachnothera crassirostris*	168
Velvet-fronted Nuthatch	*Sitta frontalis*	169
Verditer	*Eumyias thalassinus*	170
Violet Cuckoo	*Chrysococcyx xanthorhynchus*	171
Wallace's Hawk-Eagle	*Spizaetus nanus*	172
Whiskered Treeswift	*Hemiprocne comata*	173
White-bellied Munia	*Lonchura leucogastra*	174
White-bellied Woodpecker	*Dryocopus javensis*	175
White-bellied Yuhina	*Yuhina zantholeuca*	176
White-breasted Waterhen	*Amaurornis phoenicurus*	177
White-chested Babbler	*Trichastoma rostratum*	178
White-crowned Forktail	*Enicurus leschenaulti*	179
White-crowned Hornbill	*Aceros comatus*	180
White-rumped(-crowned) Shama	*Copsychus malabaricus (stricklandii)*	181
Wreathed Hornbill	*Aceros undulatus*	182
Yellow-bellied Bulbul	*Alophoixus phaeocephalus*	183
Yellow-bellied Prinia	*Prinia flaviventris*	184
Yellow-breasted Flowerpecker	*Prionochilus maculatus*	185
Yellow-crowned Barbet	*Megalaima henricii*	186
Yellow-rumped Flowerpecker	*Prionochilus xanthopygius*	187
Yellow-vented Bulbul	*Pycnonotus goiavier*	188

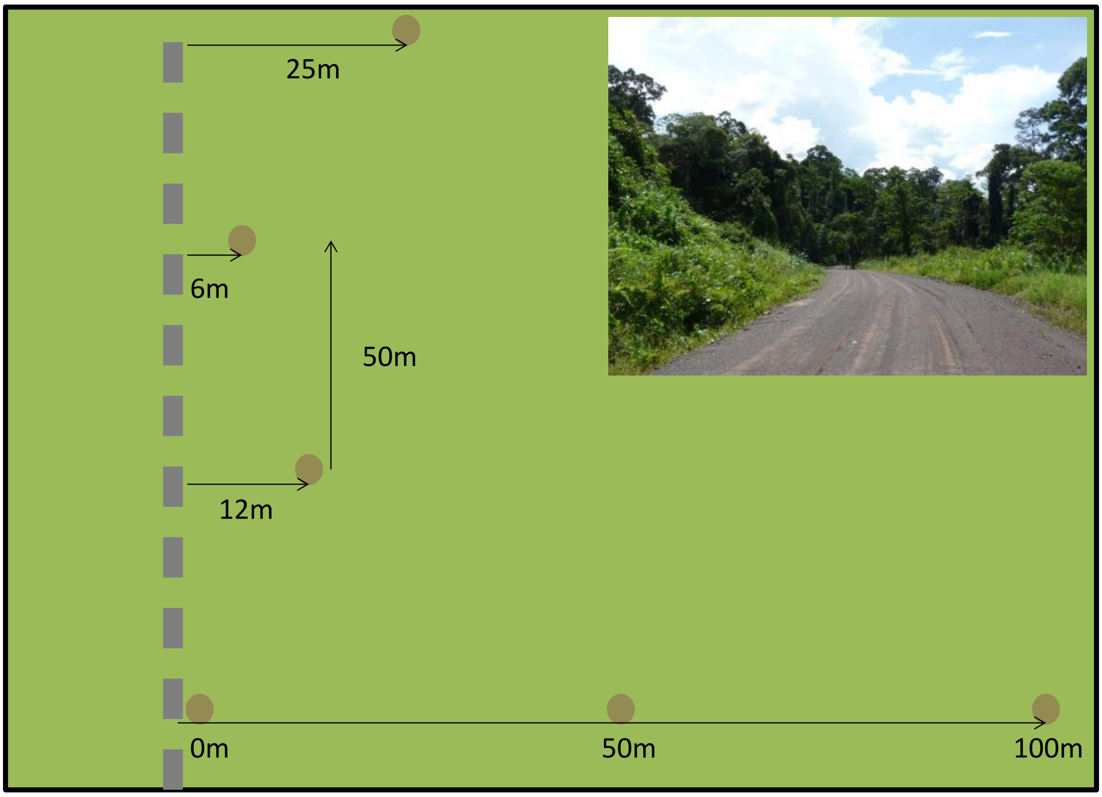
Appendix 3

Appendix 3: Functional dissimilarity measured as the overlap of dung beetle species within functional space referred to in chapter 3. Species are plotted within four-dimensional functional trait space. **(a)** Axes 1 and 2: primary and twice-logged forest (light grey), once-logged forest (mid-grey), and oil palm (dark grey), and **(b)** Axes 3 and 4: primary, once-logged, and twice-logged forest (light grey); oil palm (dark grey).

Appendix 4

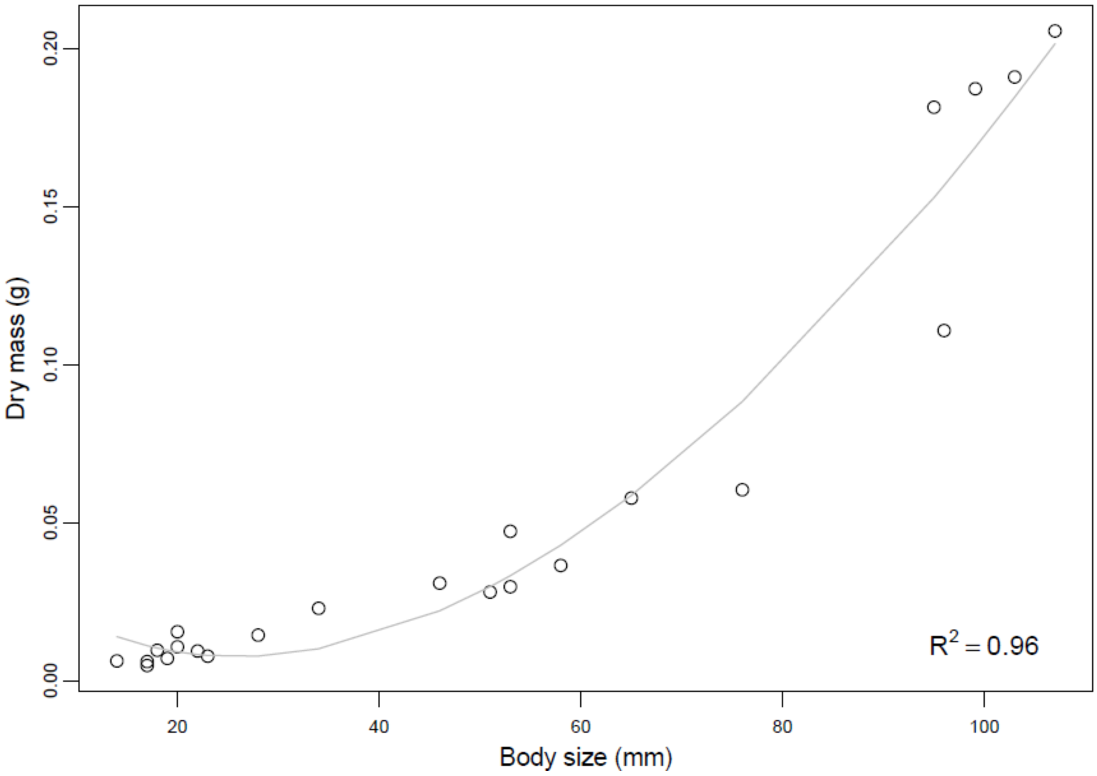
I used a power test to highlight combinations of species abundances (for a particular number of sites) where it will not be possible to detect any interaction between them. I ran simulations to look at power to detect segregation and aggregation between pairs of species for a specific numbers of sites, and across all possible combinations of different abundances of species for that number of sites. This approach generates species pairs which are either entirely aggregated or segregated, these pairs are tested using a null model that assess species overlap. If the output p-value is greater than 0.05 then these pairs should be excluded from further analyses due to low power of detection. This code was developed by Tom M. Fayle (2016).

Appendix 5



Appendix 5: The design of road edge plots to measure edge effects, as part of chapter 5. Traps (brown circles) were placed at distances of; 0m, 6m, 12m, 25m, 50m and 100m from the road edge (grey dashed line), and at least 50m apart from each other. Inset picture shows a section of a logging road in the Yayasan Sabah logging concession, Sabah, Malaysian Borneo.

Appendix 6



Appendix 6: The relationship between body size (mm) and dry mass (g) based on 23 dung beetle species (181 individuals) from Sabah, Malaysian Borneo, used to extrapolate dry mass for the remaining species, used in chapter 5.

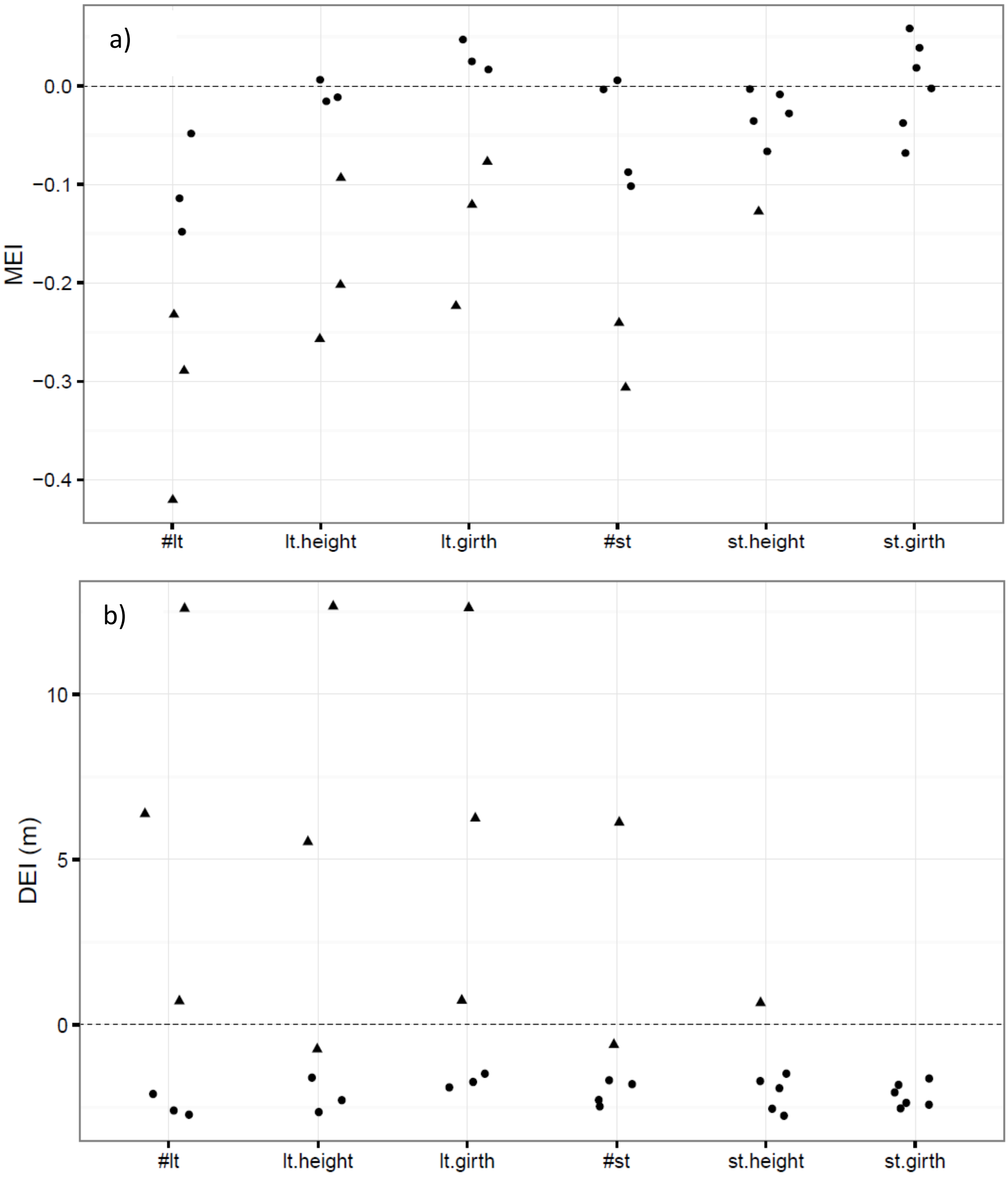
Appendix 7: Summary of piecewise regression outputs for the impact of distance away from the road edge and vegetation structure and soil characteristics. * indicates where linear models were shown (via AIC selection) to be the better model than a piecewise regression.

	t value	p value	breakpoint (m)	SE breakpoint (m)
Soil characteristics				
Soil mositure (%)*	1.64	0.1	na	na
Soil bulk density (g/cm3)*	-0.59	0.56	na	na
Soil temperature (°C)	-0.22	0.05	na	na
Leaf litter depth (mm)	-2.01	0.05	na	na
Vegetation structure				
Ground cover (%)	-1.43	0.15	na	na
Canopy cover	1.6	0.11	na	na
Number of small trees	2.78	0.006	32.5	10.4
Small tree girth (cm)	1.84	0.07	na	na
Small tree height (m)*	1.41	0.16	na	na
Number of large trees	2.82	0.005	27.4	8.6
Large tree girth (cm)	2.86	0.005	19.7	6
Large tree height (m)	4	< 0.001	18.4	3.9
Large vine density*	0.56	0.56	na	na
Small vine density*	0.21	0.84	na	na
Sucessional vegetation density	-4.28	< 0.001	34.3	8

Appendix 8: Mean (SD) micro-habitat variables in each distance category from the road edge and interior logged forest.

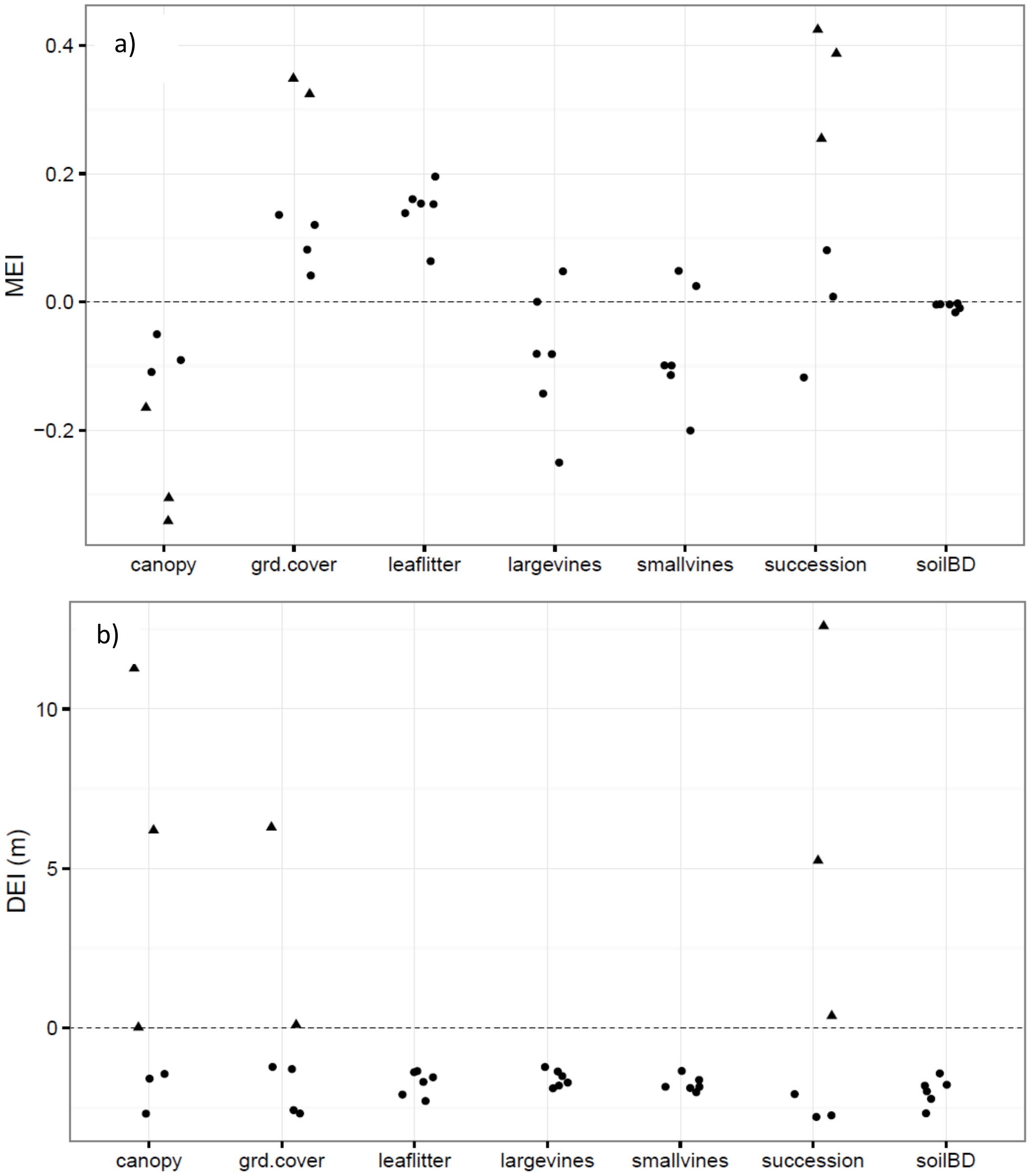
	Distance from the road edge (m)						
Micro-habitat variable	0	6	12	25	50	100	Interior
Soil characteristics							
Soil mositure (%)	34.4 (8.4)	38.0 (7.5)	41.8 (9.7)	40.4 (7.2)	42.2 (7.4)	41.6 (10.2)	42.3 (9.3)
Soil bulk density (g/cm3)	0.3 (0.04)	0.3 (0.03)	0.3 (0.03)	0.3 (0.02)	0.3 (0.02)	0.3 (0.03)	0.3 (0.04)
Soil temperature (°C)	25.2 (0.7)	25.1 (0.8)	25.0 (0.7)	24.9 (0.5)	24.8 (0.6)	24.7 (0.7)	24.8 (0.3)
Leaf litter depth (mm)	3.1 (2.0)	2.6 (1.4)	3.2 (1.3)	3.4 (1.0)	3.0 (1.1)	3.1 (1.2)	2.3 (1.0)
Vegetation structure							
Ground cover (%)	62.9 (30.5)	59.6 (26.5)	35.8 (26.2)	38.8 (26.3)	40 (32.2)	33.0 (24.6)	30.4 (21.5)
Canopy cover	38.3 (30.7)	35.4 (33.4)	51.7 (33.8)	60.2 (31.8)	65.2 (30.2)	57.9 (34.5)	72.1 (28.4)
Number of small trees	22.3 (16.2)	19.4 (12.3)	29.8 (17.6)	30.6 (12.5)	36.3 (17.6)	36.9 (17.2)	36.5 (11.5)
Small tree girth (cm)	18.0 (6.8)	19.2 (5.3)	20.6 (4.6)	22.4 (4.2)	23.3 (4.6)	21.5 (5.6)	20.7 (4.8)
Small tree height (m)	5.1 (1.9)	6.6 (1.8)	6.5 (3.8)	5.8 (1.9)	6.3 (1.7)	6.2 (1.4)	6.6 (1.7)
Number of large trees	11.2 (7.9)	8.3 (5.9)	12.7 (9.3)	16.2 (10.9)	18.5 (10.5)	15.1 (7.8)	20.3 (8.9)
Large tree girth (cm)	77.1 (36.3)	95.4 (57.9)	104.2 (35.8)	127.8 (40.6)	133.6 (43.1)	125.7 (38.9)	121.6 (28.4)
Large tree height (m)	10.7 (5.2)	12.0 (5.8)	15.0 (4.5)	17.6 (3.8)	18.3 (3.9)	17.5 (4.6)	18.0 (4.2)
Large vine density	0.5 (0.7)	0.9 (1.0)	0.6 (0.8)	0.8 (0.9)	0.7 (0.9)	0.7 (0.8)	0.8 (0.8)
Small vine density	1.3 (1.1)	1.7 (1.2)	1.8 (1.2)	1.3 (1.0)	1.1 (0.8)	1.3 (0.8)	1.6 (0.8)
Sucessional vegetation density	5.4 (2.6)	5.9 (2.6)	4 (2.8)	2.8 (2.4)	1.9 (1.7)	2.4 (2.5)	2.4 (1.6)

Appendix 9



Appendix 9: The variation in the magnitude (a) and the extent (b) of edge influence for tree characteristics. Triangles represent significant edge influence, while circles represent non-significance. The magnitude of the edge influence (MEI) is bounded by 1 and -1, a positive value indicates a value at the edge>interior, a negative value indicates a value at the edge<interior, and a value of zero equals no difference between edge and interior forest. The distance of edge influence (DEI) is measured in metres away from the road edge. X-axis labels refer to (unless clearly stated); *#lt*-number of large trees, *lt.height*-large tree height, *lt.girth*=large tree girth, *#st*-number of small trees, *st.height*-small tree height, and *st.girth*=small tree girth.

Appendix 10



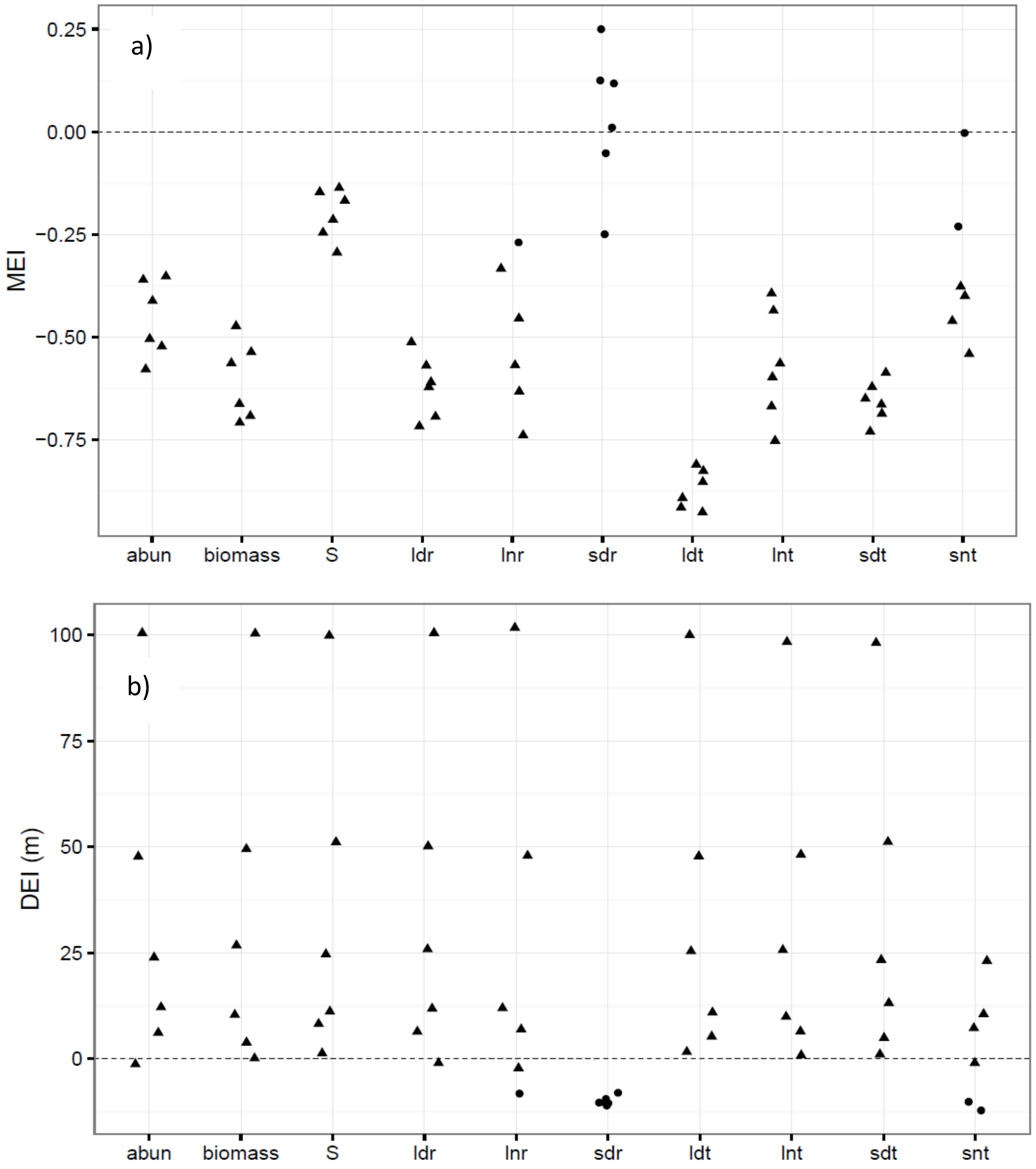
Appendix 10: The variation in the magnitude (a) and the extent (b) of edge influence for vegetation structure and soil characteristics. Triangles represent significant edge influence, while circles represent non-significance. The magnitude of the edge influence (MEI) is bounded by 1 and -1, a positive value indicates a value at the edge>interior, a negative value indicates a value at the edge<interior, and a value of zero equals no difference between edge and interior forest. The distance of edge influence (DEI) is measured in metres away from the road edge. X-axis labels refer to (unless clearly stated); *canopy*-canopy cover, *grd.cover*-ground cover, *succession*=successional vegetation, and *soilBD*-soil bulk density.

Appendix 11: The variation in the magnitude of the edge influence (MEI) for dung beetle community and functional metrics in road edge plots compared to interior logged forest. Distance is measured in metres away from the road edge. The MEI is bounded by 1 and -1, a positive value indicates a value at the edge>interior, a negative value indicates a value at the edge<interior, and a value of zero equals no difference between edge and interior forest. The p-values determine the distance of edge influence (DEI), P <0.05 indicates a significant difference at a given distance from the interior community. Significant results are highlighted in **bold**. Abbreviations refer to; *ldr*-large diurnal roller, *lnr*-large nocturnal roller, *sdr*-small diurnal roller, *ldt*-large diurnal tunneller, *lnt*-large nocturnal tunneller, *sdt*-small diurnal tunneller, *snt*-small nocturnal tunneller, and 'int' = interior.

Variable	Distance	Mean	error	MEI	p(edge<=int)
Abundance	0	34	47.4	-0.58	**0.0001**
	6	40	58.2	-0.52	**0.0001**
	12	42	34.3	-0.50	**0.0001**
	25	53	51.8	-0.41	**0.0005**
	50	61	54.0	-0.35	**0.0019**
	100	60	72.7	-0.36	**0.0019**
Species richness	0	9	4.9	-0.29	**0.0001**
	6	10	5.2	-0.25	**0.0001**
	12	10	4.8	-0.21	**0.0003**
	25	12	6.0	-0.14	**0.0081**
	50	12	3.7	-0.15	**0.0035**
	100	11	5.5	-0.17	**0.0021**
Biomass	0	2	3.5	-0.71	**0.0001**
	6	3	3.7	-0.69	**0.0001**
	12	3	3.5	-0.66	**0.0001**
	25	4	3.8	-0.56	**0.0002**
	50	4	4.1	-0.54	**0.0001**
	100	5	5.8	-0.47	**0.0002**
LDR	0	4	7.6	-0.62	**0.0002**
	6	3	6.1	-0.72	**0.0001**
	12	3	4.6	-0.69	**0.0001**
	25	5	5.8	-0.57	**0.0004**
	50	4	5.8	-0.61	**0.0001**
	100	6	11.2	-0.51	**0.0006**
LNR	0	0	0.4	-0.74	**0.0004**
	6	0	0.6	-0.63	**0.0014**
	12	0	0.8	-0.57	**0.0027**
	25	1	1.5	-0.27	0.0792
	50	1	1.0	-0.33	**0.0371**
	100	1	1.2	-0.45	**0.0133**

Variable	Distance	Mean	error	MEI	p(edge<=int)
SDR	0	12	17.0	-0.25	0.1281
	6	18	27.0	-0.05	0.4502
	12	21	25.0	0.01	0.5521
	25	26	31.3	0.12	0.7383
	50	34	39.6	0.25	0.921
	100	26	35.4	0.13	0.7456
LDT	0	1	3.0	-0.81	**0.0001**
	6	1	1.6	-0.92	**0.0001**
	12	1	0.9	-0.93	**0.0001**
	25	1	2.2	-0.85	**0.0001**
	50	1	1.6	-0.89	**0.0001**
	100	1	2.6	-0.83	**0.0001**
LNT	0	2	2.2	-0.75	**0.0001**
	6	2	4.2	-0.67	**0.0001**
	12	3	3.7	-0.60	**0.0001**
	25	3	3.5	-0.56	**0.0001**
	50	4	4.9	-0.44	**0.0004**
	100	5	4.9	-0.39	**0.0013**
SDT	0	12	19.8	-0.65	**0.0001**
	6	9	8.7	-0.73	**0.0001**
	12	12	8.9	-0.66	**0.0001**
	25	15	16.5	-0.59	**0.0002**
	50	11	6.7	-0.69	**0.0001**
	100	13	13.4	-0.62	**0.0001**
SNT	0	3	3.6	-0.46	**0.007**
	6	2	2.5	-0.54	**0.0012**
	12	3	3.6	-0.38	**0.0216**
	25	3	3.5	-0.40	**0.0166**
	50	7	8.9	0.00	0.5156
	100	4	6.4	-0.23	0.1207

Appendix 12



Appendix 12: The variation in the magnitude (a) and the extent (b) of edge influence for dung beetle community and functional metrics. Triangles represent significant edge influence, while circles represent non-significance. The magnitude of the edge influence (MEI) is bounded by 1 and -1, a positive value indicates a value at the edge>interior, a negative value indicates a value at the edge<interior, and a value of zero equals no difference between edge and interior forest. The distance of edge influence (DEI) is measured in metres away from the road edge. X-axis labels refer to (unless clearly stated); *abun*-abundance, *S*-species richness, *ldr*-large diurnal roller, *lnr*-large nocturnal roller, *sdr*-small diurnal roller, *ldt*-large diurnal tunneller, *lnt*-large nocturnal tunneller, *sdt*-small diurnal tunneller, and *snt*-small nocturnal tunneller.

Appendix 13: GLMM model outputs investigating the relationship between community metrics and the abundance of functional groups with key micro-habitat variables. Abbreviations refer to SNR – small nocturnal roller, LDR – large diurnal roller, LNR – large nocturnal roller, SDT – small diurnal tunneller, SNT – small nocturnal tunneller, LDT – large diurnal tunneller, LNT – large nocturnal tuneller. Variables with a significance at P>0.05 are highlighted in **bold**.

Response	*Estimate*	*Std.Error*	*z-value*	*Pr(>|z|)*
Abundance				
Intercept				
SuccessionalVeg	-0.137	0.082	-1.677	0.094
GroundCover	0.015	0.071	0.218	0.828
CanopyCover	-0.004	0.080	-0.046	0.964
Number of large trees	-0.095	0.089	-1.067	0.286
Number of small tress	0.035	0.090	0.388	0.698
Large tree height	0.101	0.108	0.931	0.352
Small tree height	0.037	0.068	0.546	0.585
Large tree girth	0.062	0.093	0.667	0.505
Species richness				
Intercept	2.315	0.057	40.750	<2e-16
SuccessionalVeg	-0.083	0.044	-1.890	0.059
GroundCover	0.036	0.039	0.930	0.354
CanopyCover	0.018	0.043	0.410	0.681
Number of large trees	-0.025	0.046	-0.540	0.592
Number of small tress	0.009	0.048	0.190	0.846
Large tree height	0.046	0.054	0.860	0.389
Small tree height	0.067	0.033	2.020	**0.043**
Large tree girth	0.011	0.046	0.240	0.807
Biomass				
Intercept	0.793	0.184	4.319	0.000
SuccessionalVeg	-0.146	0.089	-1.633	0.102
GroundCover	0.212	0.077	2.751	**0.006**
CanopyCover	0.030	0.088	0.341	0.733
Number of large trees	-0.007	0.090	-0.074	0.941
Number of small tress	0.239	0.100	2.386	**0.017**
Large tree height	0.062	0.098	0.637	0.524
Small tree height	0.020	0.073	0.275	0.783
Large tree girth	0.221	0.086	2.563	**0.010**

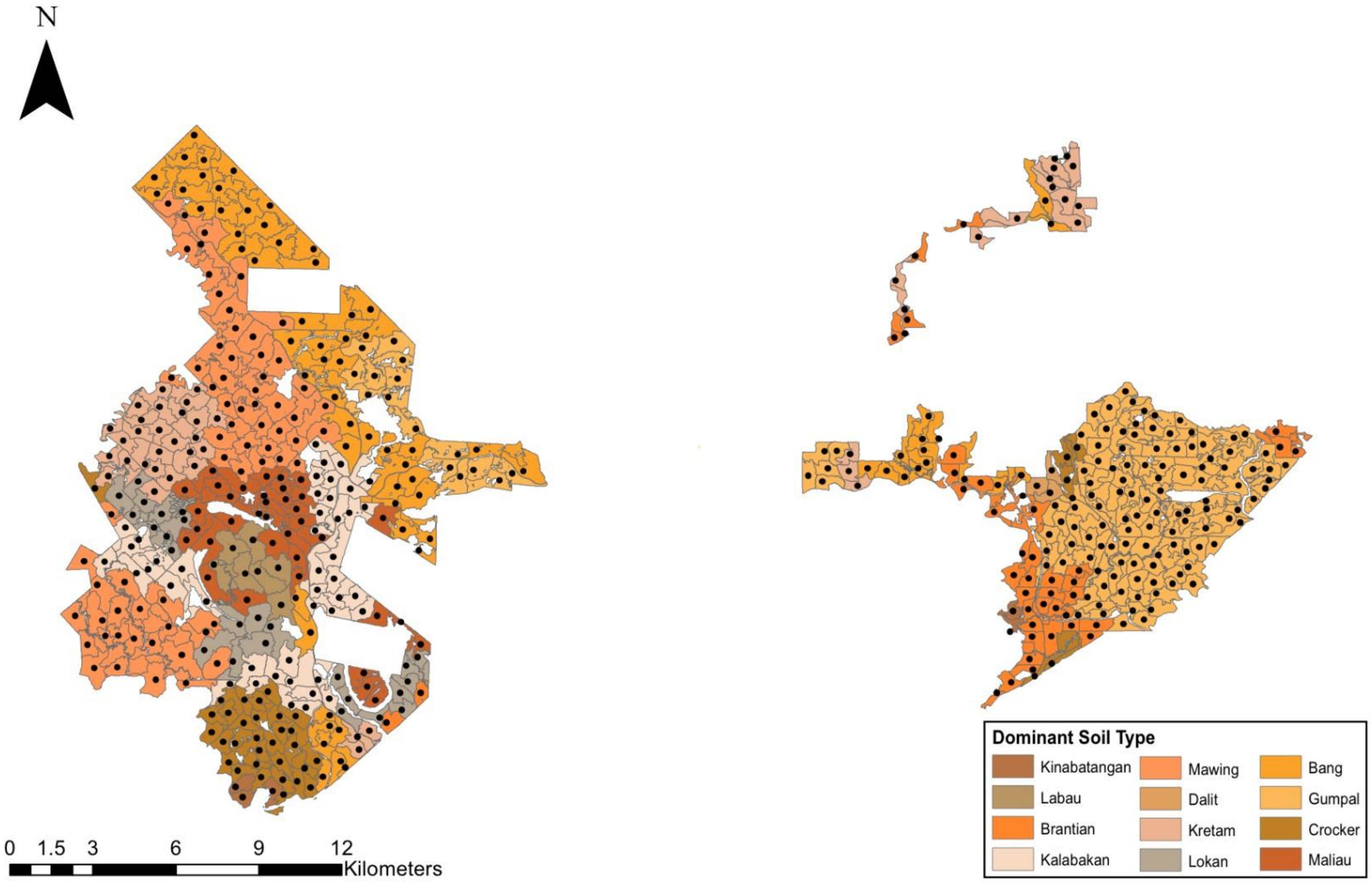
Response	*Estimate*	*Std.Error*	*z-value*	*Pr(>|z|)*
SDR				
Intercept	2.467	0.192	12.878	<2e-16
SuccessionalVeg	-0.078	0.110	-0.711	0.477
GroundCover	-0.096	0.096	-0.992	0.321
CanopyCover	-0.040	0.106	-0.378	0.705
Number of large trees	-0.114	0.122	-0.931	0.352
Number of small tress	-0.011	0.116	-0.097	0.923
Large tree height	0.143	0.149	0.961	0.337
Small tree height	0.049	0.096	0.509	0.611
Large tree girth	0.112	0.126	0.889	0.374
LDR				
Intercept	0.736	0.219	3.360	0.001
SuccessionalVeg	-0.054	0.149	-0.361	0.718
GroundCover	0.187	0.128	1.455	0.146
CanopyCover	0.007	0.146	0.051	0.959
Number of large trees	0.064	0.159	0.399	0.690
Number of small tress	0.138	0.159	0.867	0.386
Large tree height	0.120	0.204	0.590	0.555
Small tree height	-0.150	0.135	-1.114	0.265
Large tree girth	0.141	0.178	0.797	0.426
LNR				
Intercept	-1.021	0.254	-4.023	0.000
SuccessionalVeg	-0.121	0.178	-0.683	0.494
GroundCover	0.324	0.170	1.902	0.057
CanopyCover	0.045	0.184	0.245	0.806
Number of large trees	0.322	0.165	1.957	0.050
Number of small tress	0.070	0.198	0.355	0.723
Large tree height	0.348	0.229	1.519	0.129
Small tree height	-0.006	0.111	-0.055	0.957
Large tree girth	-0.051	0.194	-0.265	0.791

Response	*Estimate*	*Std.Error*	*z-value*	*Pr(>|z|)*
SDT				
Intercept	2.302	0.098	23.371	<2e-16
SuccessionalVeg	-0.125	0.087	-1.439	0.150
GroundCover	0.142	0.080	1.772	0.076
CanopyCover	0.050	0.090	0.558	0.577
Number of large trees	-0.148	0.094	-1.570	0.116
Number of small tress	0.045	0.095	0.476	0.634
Large tree height	0.047	0.116	0.402	0.688
Small tree height	0.057	0.069	0.828	0.408
Large tree girth	-0.049	0.100	-0.492	0.623
SNT				
Intercept	0.782	0.196	3.986	0.000
SuccessionalVeg	-0.378	0.118	-3.204	**0.001**
GroundCover	0.061	0.100	0.607	0.544
CanopyCover	0.032	0.114	0.282	0.778
Number of large trees	-0.014	0.124	-0.110	0.912
Number of small tress	0.055	0.128	0.432	0.666
Large tree height	0.117	0.140	0.836	0.403
Small tree height	0.143	0.099	1.443	0.149
Large tree girth	0.039	0.126	0.308	0.758
LDT				
Intercept	-0.806	0.289	-2.787	0.005
SuccessionalVeg	0.354	0.202	1.757	0.079
GroundCover	0.480	0.176	2.737	**0.006**
CanopyCover	0.061	0.216	0.281	0.779
Number of large trees	0.090	0.217	0.414	0.679
Number of small tress	-0.006	0.234	-0.027	0.978
Large tree height	0.735	0.263	2.792	**0.005**
Small tree height	-0.155	0.181	-0.857	0.391
Large tree girth	-0.325	0.234	-1.390	0.165
LNT				
Intercept	0.638	0.186	3.423	0.001
SuccessionalVeg	-0.355	0.121	-2.925	**0.003**
GroundCover	0.254	0.106	2.398	**0.016**
CanopyCover	0.055	0.114	0.483	0.629
Number of large trees	-0.040	0.117	-0.342	0.732
Number of small tress	0.375	0.130	2.884	**0.004**
Large tree height	-0.067	0.129	-0.517	0.605
Small tree height	0.202	0.085	2.380	**0.017**
Large tree girth	0.355	0.111	3.185	**0.001**

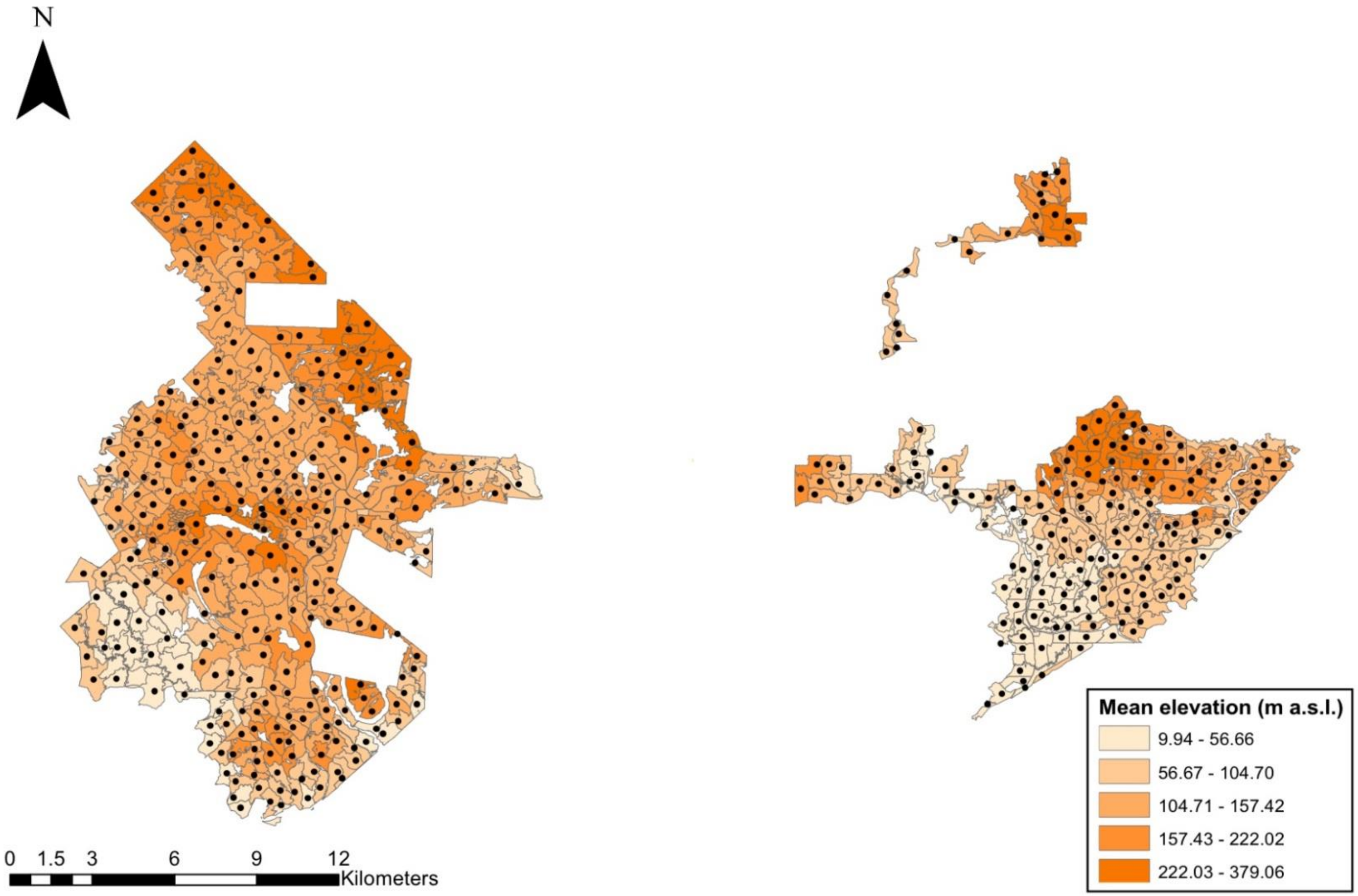
Appendix 14: The description of soil types across the study area, used in chapter 6, in Sabah, Malaysian Borneo. The Soil association refers to the soil name from The Soils of Sabah map (Director of National Mapping 1974), Parent material describes the underlying geology, and the Main soil units and Sub soil units refer to the individual characteristics of the soil. Asterisks refer to those soils grouped for analyses.

Soil association	Parent material	Main soil untis	Sub soil units
Kinabatangan*	Alluvium	Acrisol	Gleyic
		Luvisol	Gleyic
		Gleysol	Dystric, Eutric and Humic
Labau*	Alluvium	Acrisol	Orthic
		Cambisol	Dystric and Gleyic
		Fluvisol	Dystric and Eutric
Brantian*	Alluvium	Acrisol	Ferric, Gleyic, and Orthic
		Podzol	Gleyic
Kalabakan	Mudstone and Sandstone	Acrisol	Ferric and Orthic
		Luvisol	Chromic, Ferric, and Orthic
Mawing	Mudstone and Sandstone	Acrisol	Orthic
		Cambisol	Dystric
Dalit	Mudstone, Sandstone, Alluvium	Acrisol	Ferric, Gleyic, and Orthic
Kretam	Mudstone, Sandstone, and Miscellaneous rocks	Acrisol	Orthic and Ferric
		Luvisol	Ferric, Chromic and Orthic
Lokan	Mudstone, Sandstone, Alluvium	Acrisol	Orthic
		Cambisol	Dystric
Bang	Mudstone, Sandstone, and Miscellaneous rocks	Acrisol	Orthic
		Cambisol	Dystric
Gumpai	Mudstone, Sandstone, and Miscellaneous rocks	Acrisol	Orthic
		Luvisol	Orthic
		Cambisol	Dystric and Eutric
		Lithosol	
Crocker	Mudstone and Sandstone	Acrisol	Orthic
		Cambisol	Chromic and Dystric
		Lithosol	
Maliau	Mudstone and Sandstone	Acrisol	Orthic
		Cambisol	Dystric
		Gleysol	Humic
		Podzol	Gleyic
		Lithosol	

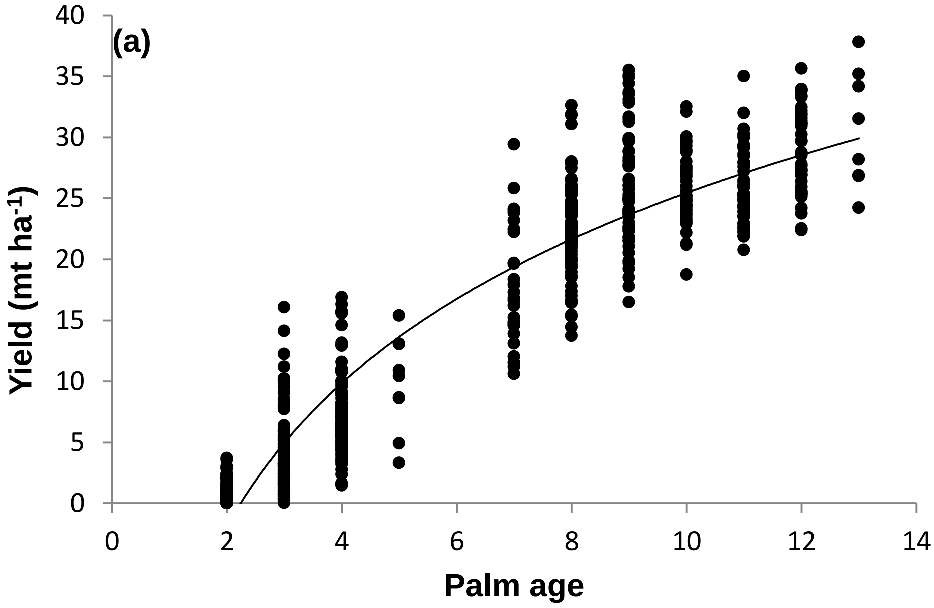
Appendix 15: The distribution of the dominant soil type per oil palm coupe across the study area in Sabah, Malaysian Borneo, used in chapter 6**.** Soil types are classified from The Soils of Sabah Map (Director of National Mapping 1974) and refer to the dominant soil type by area.

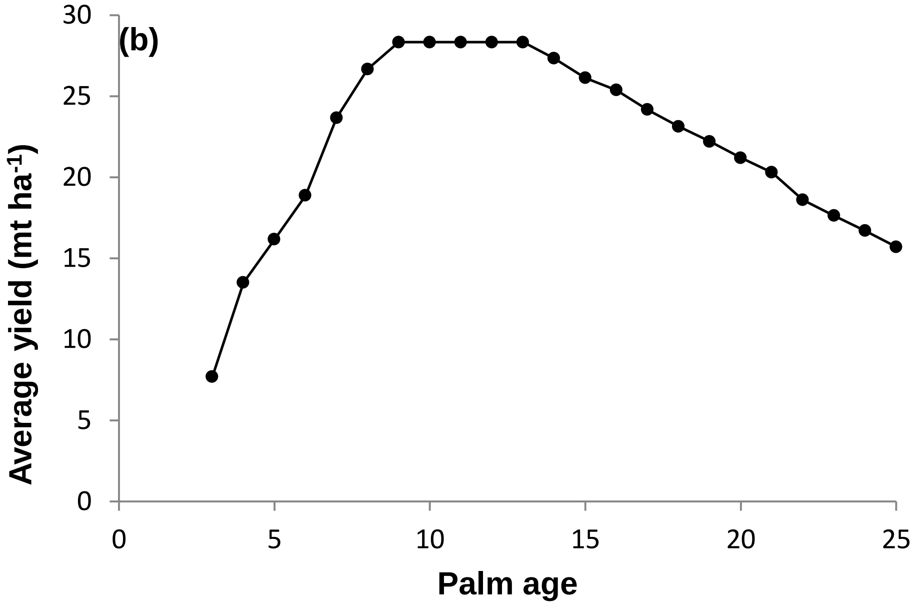


Appendix 16: The distribution of the mean elevation (m a.s.l.), per oil palm coupe, across the study area in Sabah, Malaysian Borneo, used in chapter 6.



Appendix 17





Appendix 17: Oil palm yield-by-age curves used to calculate the deviation from the mean oil palm yield values, used in chapter 6. Data was generated from (a) Sabah Softwood plantation for oil palm coupes with available data for 2008 and 2009, and (b) the average yield curve as produced by Butler *et al.* (2009). Oil palm yield is measured as the fresh fruit bunch weight per hectare (mt ha^{-1}).